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EFFECTS OF INCREASING LEVELS OF CO_2 AND O_2 DERIVED COMPOUNDS ON BIOGEOCHEMICAL CYCLES AND SHAPING OF THE BIOSPHERE

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SUMMARY

Plants reduce CO_2 to molecular species of increasing energy content. These compounds are then moved by heterotrophic organisms through decreasing energy levels as the organic matter is returned to inorganic form by successive oxidations. Thus, CO_2 and O_2 are the major substrates of biospheric reactions.

Oxygen is toxic for anaerobic and, in excess, for aerobic organisms. Its toxicity is overcome by aerobic organisms by using it as an electron terminal acceptor in respiration and by developing biochemical defenses. It still determines phenomena such as anaerobiosis, the depth limit of higher aquatic plants, or bioluminiscence, and perhaps others like the diurnal vertical migration of zooplankton.

Low photosynthetic efficiency in light use, shape and color of vegetation may result from the peculiar availability of light and CO_2. Therefore, slight changes in these factors would produce life shapes deeply alien to the world we now perceive.

Atmospheric CO_2 levels have increased by about 70 μmol mol^{-1} over the past 240 years, as has been shown by ice core studies and Mauna Loa data. Parallel to this increase, some plant changes have already been found: an overall decrease from 121% to the present-day 100% level in stomatal density, and from 144 % to present-day 100% leaf nitrogen content of 14 herbarium specimens of trees, shrubs and herbs collected over the last 240 years in Catalonia, a Mediterreanean area. Similar declines have also been reported in experimental studies on leaves of plants grown in enriched CO_2 environments. Consequently the C/N ratio has increased in leaves which together with the decrease in the specific leaf area (SLA) may have consequences for herbivores, decomposers and ecosystems.

Increases in oxygen-derived compounds, mainly ozone, have potentially large biospheric effects. Nowadays, they seem to play an important role in forest decline and some decreased crop productions, as has been shown in laboratory experiments. Increased photosynthetic rates are expected with increasing CO_2 levels in the decades to come, but regional ozone increase is expected to decrease plant production. Responses of ecological systems are however complex and difficult to predict.

Finally, a possible change in photosynthetic efficiency, plant shape and color is speculated to be expected because of increasing CO_2 levels, and the role of anthropospheric activities in the balance between reduction and oxidation in the biosphere is emphasized.

KEY WORDS: Carbon dioxide, oxygen, biogeochemical cycles, biosphere.

SOLAR RADIATION AND BIOGEOCHEMICAL CYCLES

Life is riding on the dissipation of solar radiation to the outer space, a dissipation that generates a gradient between reduced and oxidised substances. Photosynthesis takes advantage of solar radiation to generate molecules of more negative redox potential from which animals and bacteria then take the energy, transforming them into molecules of progressively more positive redox potential. The cycle of matter closes when these molecules are again used by plants thanks to the open energy flux from sun to space.

On a global scale, life charges the biospheric battery and afterwards, the differences of potential are not abruptly wasted in only one jump. Instead, there are a lot of little jumps among different components that have been multiplying and becoming more complex during evolution, generating viruses, bacteria, algae, trees, animals, and finally, beings as complex as humans. The reason for this complication of organisms, their communities and of their products must be sought in the action of selection forces that have been retarding the flux of solar energy in a non-uniform manner. In this way we can understand the existence of structures as complex as plants and animals in a biosphere that could otherwise be constituted only by procariota, thanks to their enormous metabolic versatility and capacity of adaptation to the use of available energy. The organization of living matter has been successful in increasing the persistence of complex structures, able to present stronger relations, domination of space and time and capacity of regulation. On one hand - in the surrounding space - more entropy has been generated, but on the other hand - the biosphere - more memory, information and organization have been stored.

With carbon, oxygen and hydrogen, three other elements - nitrogen, sulfur and phosphorus (with a chemical position quite different from the other two) - are of particular interest in the study of our planet's biosphere. They have been selected because of their unique atomic qualities. Through the active intervention of the biosphere, each of these elements follows a closed cycle, passing through molecular species of increasing energy content as the elements are incorporated into living tissue, and then moving through decreasing energy levels as the organic matter is returned to inorganic form. CO_2 reduction and organic matter oxidation are the major components of this global process. It is expected then that CO_2 and O_2 greatly influence the characteristics of the biosphere: CO_2 because of its scarcity and O_2 because of its toxicity for anaerobes and, in excess or through its derived compounds, for aerobes.

The approximation I am going to use here is to a certain extent taken from the field of economics, in order to provide insights into the selective pressures on characteristics such as leaf reflectivity, effective leaf size, stomatal conductance, size of photosynthetic enzyme pools, plant shape and color, nitrogen fixation, etc. This is a cost-benefit approach that has been criticized on a number of grounds (GOULD & LEWONTIN, 1979; HARPER, 1982). Principal among these criticisms are the non-falsability of the assumption of adaptation, the *post hoc* nature and untestability of optimality models, failure to consider nonselective factors shaping evolution, particularly the nature of available genetic variation and developmental constraints, the inappropriateness of an atomistic approach, and teleological and Panglossian assumptions. Analyses of different authors reviewed by GIVNISH (1986) have effectively rebutted many of these criticisms.

THE ROLE OF CO_2 AND LIGHT. PLANT PRODUCTION, PHOTOSYNTHETIC EFFICIENCY, SHAPE AND COLOR

From studying IBP (International Biological Program) data collected between 1964 and 1974, it can be seen that primary production in terrestrial environments follows a gradient from Poles to Equator that is not found in oceans. This fact shows that radiation, temperature, water and nutrients are the determinant factors of production in terrestrial ecosystems, and nutrients and radiation (and predators) are the determinants in oceanic ecosystems (BEGON *et al*., 1986). Globally, however, a final limiting factor can be considered: the low CO_2 concentration in the Earth's atmosphere, specially compared with a primitive atmosphere.

Radiation, although used inefficiently, can be limiting during the day in the interior of the canopy, in C4 plants, under the shade of higher leaves, under the shade of the chloroplasts of the same leaf, in deep water, etc. Plants adapt to systematic changes in light environment (diurnal and seasonal) for example with senescence, falling or movement of leaves, or with special metabolic pathways and anatomies for shade and sun conditions. At the canopy level, they optimize LAI, leaf angle inclination, and density distribution.

Linked to radiation, temperature is another key factor. Apart from its effect on respiration, it determines transpiration, and therefore water availability.

Water is another of the most important limiting factors of primary production, as a carrier of necessary elements. It is also responsible for many of the anatomical and metabolic characteristics of plants.

Primary production also depends on a well-formed soil and its mineral nutrients, especially nitrates of mainly biological origin.

These previous considerations are well accepted by the scientific community, but besides those, many of the most familiar characteristics of plants - low photosynthetic efficiency, shape, disposition of branches and leaves and color - may also be consequences in the last instance of the present low levels of CO_2 in the Earth's atmosphere.

In optimal laboratory conditions, the highest light use efficiency that has been found is 20% under low light and 8% under intense light. In the field it is usually around 1%. These low field values can be explained by the loss of photons falling on soil and moribund materials, or consumed in water evaporation. But even under optimal laboratory conditions, efficiencies as low as 8% are obtained under intense light conditions. The explanation of this low efficiency seems to be the existing high amounts of photosynthetic pigments present in plants, with which they can take advantage of low light, the most usual condition plants must face: mornings, dawns, dusks, shady environments, shade from other plants, leaves or chloroplasts. Therefore, the excess of photons under intense light cannot find a sufficiently high number of production active centers. The pigment composition of the photosynthetic antennae is the result of an old decision. Photosystem I was originated under reducing conditions, with different proton suppliers. Later the capacity to split water was acquired by adding a Photosystem II. The high number of chlorophyll molecules per antenna (200 to 900) makes each reaction center act as a bottleneck, and thus a limit is set to the production of the biosphere. In ecology this important limitation is rarely considered (FALKOWSKY, 1983; MARGALEF, in press). Only some mutants of *Chlorella*, higher plants and the heterocysts of cyanobacteria - specialist cells in the avoidance of oxygen problems in their nitrogen fixation - show lower pigment ratios. They may represent the promise of a substantial increase in efficiency of primary producers.

But a more general explanation of the low efficiency comes from considering the very low concentration of CO_2 on present-day Earth. When photosynthesis appeared, it had to adapt to the availabilities of that time. Among them it should be pointed out that CO_2 was surely much more abundant than now, radiation was lower and the temperature was higher (WALKER, 1986). Photorespiration could be an added mechanism to get rid of oxygen, when there was much more CO_2 available. In relatively recent geological ages, atmospheric CO_2 concentration has been largely decreasing until this last century, in which man's activities are increasing it again. Now, with much less CO_2 availability, under high temperatures, photorespiration has been mainly reduced in C4 and CAM plants, mostly in tropical and dry environments. In temperate environments, lower temperatures and higher water availability make possible the persistence of C3 plants with high levels of photorespiration.

Plants have tended to take profit of CO_2 for the maximum time possible and as light is low most of time, they are adapted to do their best at these most frequent low light conditions. In fact, when the CO_2 supply increases, the photosynthesis rate rises too. More support for this theory comes from the existence of the mentioned metabolic and anatomical structures (C4 and CAM) specialized in the activation of CO_2 absorption under drought and heat conditions when the other important element, water, is more difficult to obtain. These mechanisms may also constitute an adaptation to increasing O_2 concentration. Aquatic plants have also acquired equivalent capacities by using bicarbonate as well as CO_2 as a source of carbon (PEÑUELAS, 1985; BOSTON *et al.*, 1989).

The fact that photosynthesis is not continuous but has a 24 hour oscillation has probably been important in building internal stores of usable CO_2, as an adaptation to anticipate change. CAM plants are to a certain extent like migratory animals that go in search of spring. CAM metabolism prepares them in the dark to use the rising sun immediately.

The shape of plants can also be understood as a result of the low efficiency of photosynthesis under high light and the low availability of CO_2 (COLINVAUX, 1986). Leaves and branches have arrangements in trees, as well as in herbs, that seem to be directed to diffuse the light in such a way that the maximum photosynthetic tissue receives light and CO_2 in optimal conditions. In light environments trees have small divided leaves, arranged in depth in a multilayer design, while those of shady environments tend to have bigger leaves arranged in a monolayer design to take advantage of all the low light already in the first interception. The same happens in herbs where erect leaves receive light in an inclined plane increasing the photosynthetic area that absorbs CO_2 under optimal radiation.

There are also two energetic tradeoffs that underlie many photosynthetic adaptations related to carbon source availability. The first arises from the inevitable association of carbon gain with water loss. CO_2 and water vapor diffuse in and out of the same pathway with parallel increases of photosynthesis and transpiration. The second results from the conflict between leaf photosynthetic capacity and the energetic costs of constructing and maintaining tissue capable of high photosynthetic rates (nitrogen, phosphorus, and so on; GIVNISH, 1984, GULMON & CHU, 1981). Together these tradeoffs link photosynthesis to the costs of transpiration and needed nutrients.

Plants also appear to have decreased leaf absorptance or increased leaf angle as a means of reducing water loss, thus to extend their period of activity into prolonged drought periods and as a means of reducing photon flux at irradiances higher than those necessary to saturate the photosynthesis process (EHLERINGER & WERK, 1986). For instance, the PAR incident on the vertical surfaces of unshaded cacti or on both sides of the leaves of unshaded agaves for various latitudes and seasons averages only about 20 mol m^{-2} d^{-1} on clear days (NOBEL, 1986).

The variation in orientation of the leaves of agaves, and many other plants from almost erect near the central stem to almost horizontal near the ground, helps to ensure a relatively even distribution of PAR throughout the canopy, which in turn tends to lead to a higher net productivity. Furthermore, these plants also have hairs to help.

At the other extreme, when light is low and limiting, velvety leaf surfaces, red undersurfaces, and blue iridiscence appear to enhance the absorption of light by leaves slightly and have thus been selected in many taxonomically unrelated groups ecologically restricted to extreme shade in tropical rain forests (LEE, 1986).

In the aquatic environment, although the most limiting factor does not seem to be CO_2 (PEÑUELAS, 1985) but light, the existence of C4 like, sediment CO_2 users, CAM and HCO_3^- users plants shows that CO_2 is also an importing limiting factor. In that medium, and relative to light availability, pigments that make some algae brown (Phaeophyceae) and red (Rhodophyceae) absorb wavelengths that terrestrial plants reflect. Green aquatic plants solve the problem by adopting a dense array of pigments (among them, also carotenoids that absorb partially in the green window).

The photosynthetic use of visible wavelengths in vegetation is the result of molecular compromise between sensitivity to destruction by energetic UV radiation, and the response of chemical bonds to low energy IR radiation. But, in fact, a possible partial explanation of green color in plants, with the luxury of not using that most abundant radiation, resides in the low availability of the other limiting factor of photosyntesis, CO_2, which means that light is in excess most of the time.

If shape and color of vegetation are then accepted to result from the peculiar availability of light and CO_2, then the consequent abundance of animals is also another result. Small changes in these factors would be expected to produce a selection of life shapes deeply alien to the world we now perceive (COLINVAUX, 1986).

THE ROLE OF OXYGEN AND ITS DERIVED COMPOUNDS. RESPIRATION AND BIOCHEMICAL DEFENSES

Oxygen was a kind of poison for primitive organisms. The first aerobes had to present or develop defenses and even more than this, to take advantage of it as a better respiratory electron terminal acceptor via cytochrome oxidase or via other alternative oxidases not sensitive to cyanide, sulfide or other reduced components of primitive Earth, when it first became an oxidated planet. Nowadays both respiratory paths remain in plants (LAMBERS, 1985; PEÑUELAS *et al.*, 1988). Several functions for the alternative oxidase have been proposed (AZCÓN-BIETO & PEÑUELAS, 1987) but a general physiological function is not accepted, and the ecological implications of having non-phosphorylating electron transport pathways are not well understood. The alternative oxidase of plant mitochondria could be an evolutionary relic derived from ancestral respiratory oxidases of primitive aerobes; these oxidases could have evolved as "safety valves" in the presence of compounds that occasionally inhibit cytochrome oxidase or the equivalent, or they might even be previous to it. In all cases, keeping electrons flowing within membranes while high energy conserving pathways are blocked increases the "flexibility" of electron transport (AZCÓN-BIETO & PEÑUELAS, 1989). Currently, there are still relevant environments where poisons of cytochrome c oxidase are present. This is the case of anoxic waters and sediments rich in sulfide. Aquatic plants that root under such conditions present an active alternative oxidase (PEÑUELAS *et al.*, 1988). However, the presence of poisons of cytochrome c oxidase in the environment is surely lower than in the early Earth, and alternative oxidase in plants could have developed secondary functions, such as thermogenesis in Aracea (DIAMOND, 1989) and others (LAMBERS, 1985), taking advantage of the flexibility of electron transport.

As far as respiration is concerned, another interesting biological phenomenon could have evolved: bioluminiscence, which provides a way for oxygen detoxification, through reactions that give off a great deal of energy in the form of light. It is difficult to find an alternative hypothesis to explain the origin of light-producing organisms although new uses have appeared in the course of the evolution (MARGALEF, in press).

Oxygen at concentrations higher than normal is still a poison for aerobic organisms as was already recognised by BERT (1878). In plants, WARBURG (1920) found that 100% O_2 inhibits the photosynthetic rate of *Chlorella* by 73%. Oxygen is a substrate of the enzyme Rubisco giving photorespiration waste, and besides it is toxic due to mechanisms that are still being discussed (SULLIVAN *et al*., 1983). Because of spin restrictions, molecular oxygen preferentially undergoes univalent reductions, the products of which are the reactive superoxide radical, hydrogen peroxide, or the hydroxyl radical, an extremely aggressive compound with a high redox potential (1.8V) (ELSTNER, 1982). These are some of the most reactive substances in biological systems; they are linked to membrane lipid peroxidations, nucleic acid oxidation, hyaluronate depolymerization, and enzyme inactivation (CADET & TEOULE, 1978). The targets of active oxygen species are then membranes, pigments, enzymes and nucleic acids (CERUTTI, 1985). They also seem to be basic factors in organism senescence.

In order to eliminate active oxygen species, aerobic organisms have developed cellular defenses: enzymes like superoxidismutase, peroxidases and catalases and small molecules such as glutathion, ascorbic acid, hydroquinones, alpha-tocopherol, carotenoids, and unsaturated fatty acids. These defenses may be overriden by oxygen levels higher than atmospheric ones.

The oxygen biotoxicity determines biospheric characteristics in several ways, sometimes as clear as in the distinction between aerobic and anaerobic worlds, sometimes in a less expected way as, for example, in the mechanisms by which hydrostatic pressure acts on vascular plants in fresh water. Their inhibited growth below depths of 10-12 m is mainly related to the increase of oxygen partial pressure in their aerial spaces caused by the linear increase of hydrostatic pressure with depth (PEÑUELAS, 1987). The oxygen toxic effect, the carboxylation resistance and the CO_2 compensation concentration increase linearly with O_2 partial pressure.

Another unexpected example of its action which is still to be confirmed, is the diurnal migration of zooplankton up to the surface during night to eat phytoplankton and down to deep waters during the day, plausibly in order to avoid oxygen-derived active compounds formed as a consequence of chlorophyll receiving photons that cannot be processed photosynthetically (PEÑUELAS *et al*., in press a).

Thus, changes in concentration of oxygen or its derived compounds, as well as those of CO_2, would make it very difficult for the shape of the biosphere to remain as it is now on Earth.

And, in fact, nowadays, concentrations of CO_2 and oxygen-derived compounds such as ozone are clearly increasing in the Earth's atmosphere.

ACTUAL CHANGES IN CO_2, OZONE AND OTHER ATMOSPHERIC GASES CONCENTRATION

CO_2 has changed in the course of the Earth's history but the present increase is fundamentally different from past changes because now there is an increase at rates and levels for which we have no historical or natural analogue back to the last two interglacial events (FRIEDLI *et al.*, 1986).

There is also increasing evidence that the abundance of an oxygen derived compound, tropospheric ozone, is increasing over large regions, and that the phenomenon of urban smog is no longer confined to cities and developed countries (PRINZ *et al.*, 1984). Nowadays it is also marked in Third World tropical countries because of frequent burning of savanna gramineae (GRAEDEL & CRUTZEN, 1989).

This has clear implications for productivity in impacted areas and may be expected to affect biogeochemical cycling significantly over extensive regions. The chemistry of tropospheric ozone assumes additional importance in that the abundance of the OH radical may be expected to change in response to exchanges in lower atmospheric ozone. The OH radical is the ultimate cleansing agent for a wide range of gases emitted to the atmosphere. It regulates oxidation of nitrogen and sulfur compounds, carbon monoxide, and hydrocarbons and is responsible for the removal of a wide variety of industrial halocarbons.

Together with the increase in concentration of these gases, the expected derived climatic changes are also relevant to terrestrial biogeochemistry, altering the balance between carbon fixation and release because photosynthesis responds differently to temperature than to respiration, and water availability strongly influences carbon storage and release. The atmospheric pollution changing the supply of carbon, nitrogen, phosphorus or sulfur can also change the storage and release of all these elements.

Some effects of all these present changes, especially of carbon dioxide and ozone increases, have already been noticed in vegetation.

PRESENT CHANGES IN VEGETATION BECAUSE OF CO_2 INCREASE, AND BIOSPHERIC CONSEQUENCES

Estimates of historical concentrations of atmospheric CO_2 suggest that plants have existed and evolved for at least 10 million years at CO_2 mole fractions in the range of 250 to 290 μmol mol^{-1} (GAMMON *et al.*, 1985). Thus, important physiological and anatomical changes are to be expected nowadays, at 348 μmol mol^{-1} CO_2. A decrease in stomatal density in herbarium specimens of tree leaves collected over the last 200 years (WOODWARD, 1987), and an increase in the growth rate of bristlecone pines (LaMARCHE *et al.*, 1984) have already been reported and have been related to the increase from 278 to 348 μmol mol^{-1} CO_2 in the last 240 years. Now, WOODWARD & BAZZAZ (1988) have also found in controlled experiments at different CO_2 levels that stomatal density and stomatal index increase markedly as the CO_2 mole fraction is reduced below 340 μmol mol^{-1}.

Both stomatal parameters have also been found to increase with altitude (KORNER *et al.*, 1979) and in simulated altitude conditions (WOODWARD & BAZZAZ, 1988), under lower CO_2 partial pressure conditions. So this is what we would expect to find in plants grown in previous centuries under lower CO_2 mole fractions.

Higher plant growth is also expected with increasing CO_2 so it would also impose an increased demand upon nutrients. Thus N, S or P could be among the first limiting factors (LEMON, 1983 and the references cited therein). The increased carbon gain associated with higher atmospheric CO_2 levels should increase the amount of carbon relative to other essential elements in plant tissue because it is questionable whether additional optimum amounts of other mineral nutrients will be obtained by all plants unless there is increased symbiotic nitrogen fixation (NORBY & SIGAL, 1989).

To check plausible changes in stomatal density, specific leaf area of plants and nitrogen and sulfur leaf content in natural environments along with the rising atmospheric CO_2 levels, all these parameters have been measured in the leaves of 14 species of trees, shrubs and herbs (*Pinus uncinata*, *P. pinea, Betula pendula, Juniperus communis, Ceratonia siliqua, Buxus sempervirens, Pistacia lentiscus, Helleborus foetidus, Rhododendron ferrugineum, Amaranthus caudatus, Papaver alpinum, Cynodon dactylon* and *Gentiana alpina*) collected over the last 240 years both from wet and dry habitats of mountains and plains in Catalonia and stored as dried herbarium specimens (PEÑUELAS & MATAMALA, 1990). Present vegetation was also studied for changes in response to the present day higher levels of CO_2 relative to the last centuries.

Although some of the herbarium specimens may well have been growing in widely varying conditions before collection, surely explaining part of the important intraspecific variability that was found, and although the relative changes along the years were not the same in all the studied species (PEÑUELAS & MATAMALA, 1990), the stomatal density and the specific leaf area were found to decrease in most species with a significant mean overall - all species together - reduction. The linear regression lines for overall relative changes of leaves showed a 121-100% reduction in the stomatal density, a 184-100% reduction in the specific leaf areas, and a reduction from 144 % to the present 100% in the N leaf content. Consequently, the C/N ratio has increased overall. The main changes took place under the first slower increases in concentration of CO_2. During the last years the change has been smaller. Sulfur content presented its highest values mostly in 1940s samples, when increased quantities of sulfur rich carbon were burnt.

The ice record data show that the CO_2 in the atmosphere has increased by about 70 µmol mol^{-1} or 25 % (FRIEDLI *et al.*, 1986). This could well be one of the main reasons for these changes in stomatal density, SLA and C/N ratios of leaves.

The higher stomatal density can be understood because the lower CO_2 levels of the pre-industrial era made the uptake of CO_2 more expensive in terms of water loss than at present. The photosynthetic rate of plants from the last centuries may have been lower, indicating the likelihood of lower water use eficiencies than the present (WOODWARD, 1987).

The increase in CO_2 levels and the consequent decrease in leaf nitrogen concentration found in plants nowadays (PEÑUELAS & MATAMALA, 1990) have also been found experimentally to produce a decrease in SLA (LARIGAUDERIE *et al.*, 1988), as was found in those herbarium specimens. Although it might well be an artifact of studied material with more decomposition in elder specimens, it has been found that the growing leaf, which preferentially uses its own photosynthate (DICKSON & SHIVES, 1982), is a very efficient system for the use of extra assimilates from CO_2 enrichment (GAUDILLÈRE & MOUSSEAU, 1989). The higher rate of photosynthesis under present-day higher CO_2 levels would have increased the amount of carbohydrate available for plant growth. In some experiments, a decrease in SLA even nearly proportional to the increases in photosynthetic rate have also been found under artificially increased CO_2 levels (ACOCK *et al.*, 1982). The decrease in SLA could also be an indirect result of increased levels of CO_2 through higher temperatures and higher vapor pressure deficits.

Decreases in N leaf content have also been found experimentally. In effect, cotton (WONG, 1979) and soybean seedlings (WILLIAMS *et al.*, 1986) have been found to present much lower percent N values associated with starch accumulation under increased CO_2. Data relating N availability to plant growth and carbohydrate content indicate that under N-limiting conditions stored carbohydrates accumulate (WILLIAMS *et al.*, 1986). Several other authors have also reported decreases in leaf nitrogen concentration under CO_2 enrichment during vegetative growth (LARIGAUDERIE *et al.*, 1988 and references therein) in spite of increases in root/shoot ratio and in both, favorable and low level N availability (LARIGAUDERIE *et al.*, 1988). Because raising the CO_2 decreases the nitrogen requirements for maintaining a given level of leaf photosynthesis (PEARCY & BJORKMAN, 1983), the C:N ratio can increase. However, the reasons for this N decline are not yet clear. Several mechanisms such as the increase in starch and structural compound content or reduced N uptake as a result of stomatal closure at high CO_2 (MADSEN, 1975) have been proposed. An N availability limitation or N redistribution in higher leaf areas could also be added. The well demonstrated N deficiencies in many unfertilised plant communities show that nutrient uptake often cannot be increased in response to plant demand.

If these results were confirmed, as atmospheric CO_2 rises the areas of moderately infertile soils could become strongly nutrient-limited, and areas where moderate nutrient deficiencies occur would expand. The increase in CO_2 interacting with N, S and P would make many terrestrial communities progressively more oligotrophic and could also lead to nutrient deficiencies and acidification of susceptible soils and freshwater (SKIBA & CRESSER, 1988). And in agricultural lands, it would almost certainly be necessary to add more N fertilizer to crops or to develop new nitrogen fixing technologies in order to take advantage of the increased CO_2 (BAKER & LAMBERT, 1979). However, it is also true that nowadays there is already an excess of nitrogen compounds in man-ruled ecosystems. N and S content in precipitation has also increased, although not uniformly, and the natural plant nitrogen fixation is increased under higher CO_2 supplies (NORBY & SIGAL, 1989).

Changes in carbon supply can then simultaneously affect the costs of transpiration, nutrient uptake, mechanical support, and/or herbivory. Similarly, shifts in leaf nitrogen content would affect photosynthetic capacity, cost of nutrient absorption, and exposure to herbivory (MOONEY & GULMON, 1982).

At the biospheric level, such effects of increased CO_2 might then be important. The decrease in SLA together with the increase of C/N ratios (PEÑUELAS & MATAMALA, 1990) and possible increase in starch or structural and phenolic compounds (WULFF & STRAIN, 1982) could have substantial effects on feeding efficiency of herbivory (LINCOLN *et al.*, 1986; FAJER *et al.*, 1989). Polyphenols may reduce grazing because of toxicity or reduced digestibility. Increased C/N ratio and increased structural and phenolic compound production could also have important effects on decomposers and consequently profound effects on nutrient cycling and plant growth (OECHEL & STRAIN, 1985). It would also produce the accumulation of hard structures that make it easy for the plant to obtain new nitrogen and phosphorus resources. However, recent results (LARIGAUDERIE *et al.*, 1988) have shown that finally, at the end of the vegetative growth, leaf nitrogen contents do not differ as a consequence of higher CO_2 levels, so litter quality would probably be the same with respect to C/N ratio.

Together with previous studies (WOODWARD, 1987; LaMARCHE *et al.*, 1984; PEÑUELAS & MATAMALA, 1990) the results presented here emphasize that the overall rise in CO_2 is already having important effects on the biosphere. It can thus be added to the other important impacts of man on the biosphere.

PRESENT EFFECTS OF TROPOSPHERIC OZONE INCREASE ON VEGETATION

Ozone is considered to be the main air pollutant in the USA and its importance is increasing as much in Europe and even in tropical countries. It could have a persistent and long-lasting effect on plants. Besides the well known high concentrations in summer, monitoring of ozone has also shown potential phytotoxic concentrations under certain circumstances in autumn and even in winter (FRICKE, 1983; PRINZ *et al.*, 1984).

The widespread decline of conifers, hardwoods and field crops in Europe and USA is believed to be caused by a combination of stresses. The decline shows a clear gradient of increasing severity with higher elevation (JOHNSON & SICCAMA, 1983; PRINZ *et al.*, 1982; BLANK, 1985). This is consistent with a natural increase in environmental stress, altitudinal gradients in ozone concentration (McLAUGHLIN, 1985) and deposition rates of acidic cloud moisture (FRIEDLAND *et al.*, 1984). Ozone formation and distribution in the atmosphere correlate with this spatial and temporal development of forest decline (PRINZ *et al.*, 1982; ARNDT *et al.*, 1982). The levels may be high enough to cause acute injury to sensitive plant species (ROBERTS, 1984; SKARBY & SELLDEN, 1984; PEÑUELAS *et al.*, in press b).

Some decrease in the productivity of certain crops, especially summer ones, can also be understood as a consequence of elevated summer ozone concentrations. This may well be the case in crop fields of ozone rich areas such as the Ebro Delta or Maresme (Catalonia).

Research concerned with the effects of ozone on Norway spruce and Sitka spruce, of special interest to an understanding of European forest decline, including Pyrenean spruces, has been carried out in our laboratory and at Lancaster University Field Station (PEÑUELAS *et al.*, in press b). Three-year-old saplings of the spruces *Picea abies* (L.) Karst and *P. sitchensis* (Bong.) Carr. were exposed in solar domes to 70 ppb O_3 - a fairly usual concentration in summer - for all the summer, seven hours a day, under approximately natural conditions, and in cabinets at the same ozone concentrations under 14 h 250 µE m^{-2} s^{-1} at 20 ^{o}C day/ 15 ^{o}C night. No visible injury nor different growth rates were found in ozone fumigated trees. However, old needles presented a slight increase in the fluorescence stress index and an increased cyanide resistant respiration, and both young and old needles of fumigated trees presented more negative water potentials, higher dry weight/fresh weight ratios, lower chlorophyll concentrations, lower nitrogen and sulfur percentages, higher C/N and C/S ratios, surprisingly lower needle electrolyte leakage, and lower respiration rates.

Apparently, older leaves were more damaged by ozone, and this is consistent with symptoms of forest decline affecting high-altitude forests in acid soils, as is the case in the high Pyrenees mountains. Crown thinning and premature shedding of older needles are observed in damaged forests at high altitude (PRINZ *et al.*, 1982). The restriction of damage to previous year's needles may be due to the inability of older tissues to repair damaged membranes (LEVITT, 1980) or to the lower ability of older tissues to detoxify pollutants.

The changes in water potential, fresh weight loss, fresh weight / dry weight ratio and cuticle width strongly suggest that the leaves of spruces exposed to ozone are less efficient in their use of water. Ozone decreases photosynthetic pigment concentration, so it may be suggested that it contributes to chlorosis shown by declining forest trees and crop plants like watermelon in the Ebro Delta. A clear decrease was also found in the carbon, nitrogen and sulfur content of fumigated trees. In many investigations, decreases in total protein content due to exposure to pollution have also been reported (ROWLAND *et al.*, 1988). Such changes could either be the result of a decrease in the rate of protein synthesis and/or an increase in the rate of protein degradation. The question remains as to whether these changes indicate damage to the balanced metabolism or a plant response to mitigate any potential damage.

Currently it is believed that ozone causes deterioration of cell membranes and cuticular waxes, and other cellular membranes, such as the envelopes of the mitochondria or chloroplasts, which are similarly damaged but to a lesser extent as the effect of ozone and its toxic radicals are progressively diluted and absorbed from the outside inwards. This partially explains the disturbance of ultrastructure within both these organelles and inhibition of both photosynthesis and respiration caused by high doses of ozone (WELLBURN, 1988) that were found incipient under normal doses (higher values of fluorescence stress indexes - indicative of wasted light energy - and lower oxygen uptake) especially in old needles. These disturbed functions within spruces are also supported by the observed losses of chlorophyll in ozone fumigated spruces.

Little is known of interactions among environmental stresses involving ozone. Several authors have suggested that the decline, although involving air pollution, may be triggered by frost or drought or other stresses (REHFUESS, 1986). The circumstancial evidence in support of this view is compelling because of the temporal and spatial correlations with elevation, temperature inversions, low temperature minimum frequencies, drought years, frost episodes (reviewed in DAVISON *et al.*, 1987) but there is little experimental evidence. Spruces exposed to ozone in summer might show indirect effects many weeks later, for example reduced frost resistance (BROWN *et al.*, 1987).

In our laboratories, three-year-old saplings of the Sitka spruce *Picea sitchensis* were exposed in solar domes to 70 ppb O_3 for all the summer, seven hours a day, and afterwards they were hardened for 10 days at 20 ^oC, 10 hours light / 4 ^oC, 14 hours darkness and for further 10 days at 18 ^oC, 9 hours light / 2 ^oC, 15 hours darkness. Finally they were submitted to night temperatures of -2 ^oC after an accidental 32 ^oC maximum day temperature which lasted a few minutes. Both ozone fumigated and control trees were visibly damaged, but the damage was clearly greater in fumigated trees. They presented lower chlorophyll concentration, higher respiration, and lower N and S percentages, but no difference in electrolite leakage nor in dry weight / fresh weight ratio. These results indicated that present ozone levels may affect spruces, predisposing them to posterior stresses like drought, winter desiccation, freezing injury or parasites. Interaction among these factors may be an important element contributing to the decline of sub-alpine stands of spruces throughout Europe. New studies should be carried out in the direction of interaction between environmental stresses.

FORESEEABLE FUTURE CHANGES BECAUSE OF INCREASING LEVELS OF CO_2, OZONE AND OTHER GASES. FROM PLANTS TO ECOSYSTEMS

New gradual increases in CO_2 concentration are expected during the next decades. Current global circulation models differ in their projections of global mean temperature and precipitation with increasing CO_2. However, even with precise climate scenarios for the next century, accurate biological predictions still cannot be made because of the poor knowledge about the response of ecosystems to increasing CO_2.

There are powerful techniques to predict responses such as modelling (PASTOR &

POST, 1988) and historical reconstruction (DAVIS & ZABINSKI, in press, PEÑUELAS & MATAMALA, 1990), but they need to be supplemented by experimentation. Besides other ecological and climatic consequences, these increases are supposed to raise photosynthesis and plant growth in the case of a good supply of other limiting factors. Thus, changes in anatomical and physiological characteristics of vegetation (LEMON, 1983) like those cited up to now with consequent reduced water loss and changes in plant phenology (CARLSON & BAZZAZ, 1980) are also expected. In fact, most studies carried out with agricultural crops and species from natural communities indicate that productivity and yield increase with elevated CO_2 levels (STRAIN & CURE, 1985). There are also differences in response to elevated CO_2 among species and among genotypes within species, but the differences have not been fully investigated (BAZZAZ *et al.*, 1985, PEÑUELAS & MATAMALA, 1990).

What is currently known is that at the leaf level, net assimilation rates are increased instantaneously and, to a lesser degree, over time, that photosynthesis and respiration may be reduced or increased after prolonged exposure to elevated CO_2 (ACOCK & ALLEN, 1985; DRAKE *et al.*, 1988; OECHEL & STRAIN, 1985); that the effect of CO_2 enhancing photosynthesis increases with temperature, and is greater for C3 plants (PEARCY & BJORKMAN, 1983); that the conductance is decreased and water use efficiency increased, preferentially in C3 plants (PEARCY & BJORKMAN, 1983); that whole plant water use may, however, increase because of the increase in leaf area (ACOCK & ALLEN, 1985); that water stressed plants may have enhanced productivities (IDSO, 1988); that root-shoot ratio response, although variable, often increases (CURE, 1985; OECHEL & STRAIN, 1985); that leaf area increases although proportionally less than leaf specific weight (ACOCK & ALLEN, 1985); that C/N ratios of tissues increase (STRAIN & BAZZAZ, 1983); that nutrient deficiencies reduce CO_2 enhancement effects (CONROY *et al.*, 1988), even though nutrient use efficiencies increase; that the herbivore feeding rate on tissues may increase (LINCOLN *et al.*, 1986), competitive relations are altered in most instances (CURTIS *et al.*, 1989), and that phenological development may be accelerated, although there are examples of delayed senescence (OECHEL & STRAIN, 1985).

High CO_2 concentrations may change the pattern of carbon allocation to plant parts, but the available data are inadequate for describing general patterns (BAZZAZ *et al.*, 1985, 1987). There may also be shifts in the kinds of chemical defenses in plant tissues and changes in rates of plant tissue consumption by herbivores (LINCOLN *et al.*, 1986) if nitrogen leaf content decrease is confirmed (PEÑUELAS & MATAMALA, 1990). Decomposition rates and nutrient cycling may change in response to altered plant C/N and lignin/N ratios, and starch content, leading to negative feedback via decomposition restricting the positive effects of CO_2 enhancenment (MELILLO *et al.*, 1982).

The response to enhanced CO_2 concentrations at the ecosystem level has been the subject of only a few experiments (TISSUE & OECHEL, 1987; DAVIES, 1988) and is largely unknown.

Hardly anything is known either about the ecosystem response to long-term exposure (DRAKE *et al.*, 1988). Elevated CO_2 should have modest effects on light-limited systems because the light requirement of photosynthesis is only moderately sensitive to CO_2 (EHLERINGER & BJORKMAN, 1977). Elevated CO_2 should decrease the nutrient investment required for photosynthesis (though probably not the nutrient investment required for growth). Effects on water-limited systems should be quite dramatic, because increased CO_2 decreases the stomatal conductance - and hence water loss - required to sustain a given rate of photosynthesis. These few studies of whole communities, however, do not always show enhanced productivity. A community of short-stature annuals showed no response (WILLIAMS *et al.*, 1988) and short term measurements of some deciduous trees showed only a small enhancement in growth (WILLIAMS *et al.*, 1986). Whole ecosystems respond significantly, but in different ways - nutrient limited low temperature systems, such as the tundra, show little response (HILBERT *et al.*, 1987), whereas nutrient rich marsh systems show a large response (DRAKE *et al.*, 1988; CURTIS *et al.*, 1989). Experimental studies in which whole plant communities have been subjected to elevated CO_2 also show that competitive hierarchies change. The resulting community structure is influenced by other environmental factors such as moisture, light, nutrients and/or temperature (BAZZAZ *et al.*, 1985). It is important to note that the response at the community level may not be directly predictable from the response of individual species to elevated CO_2 or to other environmental factors because of changes in species composition and interactions with heterotrophic organisms.

Responses of ecological systems are complex because of the inherent intricacies of ecological systems and their interactions with the physical system, and because these processes depend on the influence of history and scale. Besides, they encompass a great temporal variability. Time-lags in the ecological response to global change result not only from differences in longevity or life cycles among organisms, but also from non-linear processes. For example, low availability of nitrogen, the most frequently limiting nutrient in terrestrial ecosystems (PASTOR *et al.*, 1984), may prevent ecosystems from changing in response to changing climate until after temperature thresholds are exceeded by dominant species. As previously dominant species are replaced by others, consequent changes in carbon and nitrogen cycles can happen rapidly, amplifying ecosystem response (PASTOR & POST, 1988). In general, rapid response within a year can be produced in biotic factors such as microbial communities, plankton density, reproductive success of plants and animals, transpiration, photosynthesis and respiration rates, pathogen outbreaks, animal behavior, and densities of annual plants and short-lived animals. A lag of several years or decades can be found in other processes, such as plant community structure. Moreover, changes in the genetic structure of populations depend on generation time. Whether redundancy within an ecosystem can delay responses of the system to environmental changes requires investigation, as this may be an important and perhaps unexpected influence of biodiversity on ecosystem processes (DAVIS, 1988). It is then a fundamental question in the context of global change whether changes in species composition and diversity will significantly affect ecosystem function.

The increase in CO_2 is also expected to change climate, as is well known. The enormous significance of the rate of temperature change can be appreciated when spatial displacement is considered. There would be lags of decades in the adjustment of ecological systems to rapidly changing climate.

Critical foci for experimental ecosystem studies on the effects of these changes are wet tundra, boreal forests, temperate forests receiving anthropogenic nitrogen and sulfur deposition, tropical forests and semiarid ecosystems. Rivers offer an excellent integration of biogeochemical processes operating in specific watersheds. Oceans must also be studied because they are by far the largest active reservoir of carbon. In order to obtain global data, remote sensing of vegetation and land form characteristics will be necessary (TUCKER *et al.*, 1986; PEÑUELAS *et al.*, in press c; GAMON *et al.*, in press).

Three research approaches should be used to increase our ability to predict biotic responses to global change and feedback to the global system: (1) laboratory and field experiments at the organism level, and compilation of existing data on population and community patterns; (2) experiments on intact ecosystems, using large-scale manipulations and taking advantage of natural experiments; and (3) ecosystem models assembled coupling population-community models with process -functional models for simulation of the response of ecosystems to large, rapid changes in environmental factors.

Present models assume that individuals are identical, but as more complex models are built, besides scaling up from single plants to landscape and incorporating spatial dimension, patterns of genetic variation will also have to be incorporated.

Our knowledge of past responses of natural systems to changed CO_2 concentrations is also limited. Data from previous centuries reviewed before are still scarce. The fossil record should also be inspected for changes at the end of the last glacial period that may be related to changing CO_2 concentration in the atmosphere.

The other anthropogenic changes in the concentration of other tropospheric gases like oxygen derived compounds also have potentially large, landscape-level effects on ecological systems, primarily through effects on ecosystem components, especially those with slow turnover rates such as soil organic matter and long lived organisms such as trees and fish. Synergistic effects of various oxygen derived pollutants (O_3, NO_x, SO_2.) are well known from simple laboratory experiments (MANSFIELD *et al.*, 1987; WELLBURN, 1988) and these effects will certainly be found in the study of ecosystems (MATHY, 1988).

Changes in stratospheric constituents, especially depletion of ozone concentration, would also importantly affect ecosystems as the intensity of ultraviolet radiation reaching the terrestrial and marine portion of the biosphere increases. Previous investigations in arctic and alpine regions indicate that the changes in ultraviolet irradiance would cause changes both in productivity and in the distribution of specific vegetation types (DAVIS, 1988). Intensified ultraviolet radiation would increase mutation rates, but it is not clear what effect this would have on population structure and viability (GRIBBIN, 1988). The subject of the ozone hole and the penetration of UV radiation has also to be considered in the context of the magnetosphere.

SOME SPECULATIONS ON FUTURE SHAPE AND COLOR OF LANDSCAPE IN AN ANTHROPOSPHERIC EARTH

Let me now speculate about what might happen in the long term as a consequence of the mentioned future changes in CO_2 and O_2 derived compounds. They might result in the development of new landscapes, new ecosystem types or new biomes.

If CO_2 determines the efficiency, shape and color of vegetation, changes in these characteristics might be expected because of higher availability of CO_2. For example, leaves may be bigger, not as much divided as nowadays, and tending more to the monolayer design because they are already going to produce more with the first light interception by disposing of more CO_2 substrate. More efficiency can be expected in the field because under higher light intensity, higher production will be obtained. Nowadays, when light is low and limiting, as previously mentioned, red undersurfaces and blue iridiscence appear to slightly enhance absorption of leaves restricted to extreme shade in tropical rain forests (LEE, 1986). Similarly, under future increased CO_2 availability a higher use of light might be necessary; under such conditions one could expect that luxurious plant green color might evolve to blues and reds: in order to take advantage of the higher availability of CO_2, plants might need to use the maximum possible radiation, and therefore the green wavelength range. In this way, they would not be able to reflect it; they would not be green. However, it must not be forgotten that life continues by preserving "information" and "structure", an activity in which it seems more "interested" than in growing "like mad".

All these atmospheric changes are consequences of man's activities, mainly burning fossil fuels. With his activity, man has also begun to alter the trend towards reduction that life was following until the beginning of the industrial era by accumulating reduced organic material and releasing oxygen to the atmosphere. Now, man is burning that fossil organic material and returning carbon to the atmosphere at such a rate that no natural reservoir can absorb all of it and therefore there is a hindrance to this trend of reduction. This anthropospheric action may impede the biosphere evolution towards a stronger redox gradient that could lead to an oxidated planet, with an explosive atmosphere, richer in oxygen, and with upper layers of the hydrosphere converted into a hydrogen peroxide soup (MARGALEF, in press). Mankind, with its combustion - and therefore oxidation of fossil fuels, now so criticized because of the generation of CO_2 increase in the atmosphere and the subsequent greenhouse effect - may in fact be avoiding this fatal oxidated destiny. Perhaps Gaia (LOVELOCK, 1979) has found in the anthroposphere (PEÑUELAS, 1988b) another of life's self-regulation mechanisms. Who knows?

It is because of anthropogenic causes of global change that possible continuation and/or even a surpassing of LOVELOCK's (1979) Gaia theory can be established. If the current trends of human behavior do not change abruptly - which seems improbable- soon it will not be possible to consider all the Earth acting as a kind of superorganism that regulates the physical, chemical, biological and geological conditions of the planet, in order to maintain itself homeostatically, as the Gaia theory postulates. The organization resulting from evolution and actuation of Gaia has given rise to mankind and its realizations, creating a special environment, a new planet layer, the anthroposphere (PEÑUELAS, 1988b, in press), that is now taking the main role in the regulation and organization of our planet.

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REFERENCES

ACOCK, B. & ALLEN, H. 1985. Crop responses to elevated carbon dioxide concentrations. In: *Direct effects of increasing carbon dioxide on vegetation.* (B.R. Strain & J.D. Cure, eds): 53-97. US Department of Energy ER-0238, Washington, DC

ACOCK B., BAKER, D.N., REDDY, V.R., McKINION, J.M., WHISLER, F.D., CASTILLO, D., & HODGES, H.F. 1982. Soybean responses to CO_2 In: *Response of Vegetation to Carbon Dioxide.* Dept. of Energy and Dept. Agriculture USA

ARNDT, U., SEUFERT, G. & NOBEL, W. 1982. Die Beteiligung von Ozon an der Komplexkrankheit der Tanne (*Abies alba* Mill) eine prufenswerte Hypothese. *Staub Reinhalt Luft*, 42: 243-247.

AZCÓN-BIETO, J. & PEÑUELAS, J. 1987. Cyanide resistant respiration in photosynthetic organs of freshwater aquatic plants. *Plant Physiology,* 84:

701-707.

BAKER, D.N. & LAMBERT, J.R. 1979. Report of the AAAS-DOE *Workshop on Environmental and Societal Consequences of a Possible CO_2-Induced Climate Change*. Annapolis, MD

BARNES, J.D. & DAVISON, A.W. 1986. Assessment of pollution-induced injury by chlorophyll fluorescence analysis. Direct effect of dry and wet deposition on forest ecosystems in particular canopy interactions. *Proc. COST- CE C Workshop.* Roskille. Goteborg, 1986

BARNES, J.D. & WILSON, J.M. 1984. Assessment of the frost sensitivity of *Trifolium* species by chlorophyll fluorescence analysis. *Ann. Appl. Biol.*, 105: 107-116

BAZZAZ, F.A., GARBUTT, K. & WILLIAMS, W.E. 1985. Effect of increased atmospheric carbon dioxide concentration on plant communities. In: *Direct Effects of increasing carbon dioxide on vegetation.* (B.R. Strain & J.D. Cure, eds.): 166-170. National Technical Information Service. Springfield Va.

BAZZAZ, F.A., CHIARELLO, N., COLEY, P.D. & PITELKA, L. 1987. The allocation of resources to reproduction and defense. *Bioscience*, 37: 58-67.

BEGON, M., HARPER, J.L. & TOWNSEND, C.R. 1986. *Ecology. Individuals, Populations and communities.* Blackwell. Oxford.

BERI, R.M. & LEMON, H.W. 1969. Chemical examination of the wax from needles of black spruce (*Picea marina*) and balsam fir (*Abies balsamea*). *Can. J. Bioch.*, 48: 67-69.

BERT, P. 1878. *La pression barométrique.* Masson. Paris (Reprinted 1979), CNRS, Paris.

BLANCK, L.W. 1985. A new type of forest decline in Germany. *Nature*, 314: 311-314.

BOSTON, H.L., ADAMS, M.S. & MADSEN, J.D. 1989. Photosynthetic strategies and productivity in aquatic ecosystems. *Aquatic Botany*, 34: 27-57.

BROWN, K.A., ROBERTS, T.M. & BLANK, L.W. 1987. Interactions between ozone and cold sensitivity in Norway Spruce: a factor contributing to the forest decline in central Europe? *New Phytologist*, 105: 149-155.

CADET, J. & TEOULE, R. 1978. Comparative study of oxidation of nucleic acid components by hydroxyl radicals, singlet oxygen and superoxide anion radicals. *Photochem. Photobiol.*, 28: 661-667.

CARLSON, R.W. & BAZZAZ, F.A. 1980. The effects of CO_2 concentrations on growth, photosynthesis, transpiration, and water use efficiency of plants. In: *Environmental and Climatic Impact of Coal Utilization* (J.J. Singh & A. Deepak, eds.): 609-623. Academic Press. New York.

CERUTTI, P.A. 1985. Prooxidant states and tumor promotion. *Science*, 227: 375-381.

CITERNE, A., BANVOY, J. & DIZENGREMEL, P. 1988. Pollution atmosphérique et métabolisme respiratoire de l'epicéa. In: *Air pollution and ecosystems* (P. Mathy, ed.): 678-683. Reidel. Dordrecht.

COLINVAUX, P. 1986. *Ecology.* John Wiley. New York

CONROY, J.P., KUPPERS, M., KUPPERS, B., VIRGONA, J. & BARLOW, E.W.R. 1988. The influence of CO_2 enrichment, phosphorus deficiency and water stress on the growth, conductance and water use of *Pinus radiata* D. Don. *Plant Cell & Environment,* 11: 91-98.

COYNE, P.I. & BINGHAM, G.E. 1982. Variation in photosynthesis and stomatal conductance in and O_3-stressed ponderosa pine stand. *For. Sci.*, 28:. 257-273

CROSSLEY, A. & FOWLER, D. 1986. The weathering of scots pine epicuticular wax in polluted and clean air. *New Phytologist*, 103: 207-218.

CURE J.D. 1985. Carbon dioxide doubling responses: a crop survey. In: *Direct effects of increasing carbon dioxide on vegetation.* (Strain, B.R. & Cure, J.D., eds): 99-116. US Department of Energy ER-0238, Washington DC.

CURTIS, P.S., DRAKE, B.G. & WHIGHAM, D.F. 1989. Nitrogen and carbon dynamics in C3 and C4 estuarine marsh plants grown under elevated CO_2 in situ. *Oecologia*, 78: 297-301.

DAVIS, M.B. 1988. Ecological systems and dynamics. In: *Towards an understanding of global change:* 69-106. National Academy Press. Washington D.C.

DAVIS, M.B. & ZABINSKI, C. in press. Changes in geographical range resulting from greenhouse warming effects on biodiversity in forests. In: *Consequences of the greenhouse effect for biological diversity.*

DAVISON, A.W. & BARNES, J.D. 1986. Effects of winter stress on pollutant responses. How are the effects of air pollutants on agricultural crops influenced by the interaction with other limiting factors? *Proc. COST-CE C Workshop*: 16-32. Roskilde.

DAVISON, A.W., BARNES, J.D. & RENNER, C.J. 1987. Interactions between air pollutants and cold stress. *Proc. 2nd Int. Symp. Air Pollutant and plant Metabolism*: 307-328.

DIAMOND, J.M. 1989. Hot sex in Aracea. *Nature*, 339: 258-259.

DICKSON, R.E., SHIVES, J.B.Jr. 1982 $^{14}CO_2$ fixation, translocation and carbon metabolism in rapid expanding leaves of *Populus deltoides. Ann. Bot.*, 50: 37-47.

DOMINY, P.J. & HEATH, R.L. 1985. Inhibition of the K^+ stimulated ATPase of the plasmalemma of pintobean leaves by ozone. *Plant Physiol.*, 77: 43.

DRAKE, B.G., LEADLEY, P.W., ARP, W., CURTIS, P. & WHIGHAM, D. 1988. The effect of elevated atmospheric CO_2 on C3 and C4 vegetation on Chesapeake Bay. In: *Proceedings of Symposium on the Physiological Ecology of Aquatic Plants.* Aarhus. Denmark.

EHLERINGER, J.R. & BJORKMAN, O. 1977. Quantum yields for CO_2 uptake in C3 and C4 plants: dependence on temperature, CO_2 and O_2 uptake. *Plant Physiology*, 59: 86-90.

EHLERINGER, J.R. & WERK, K.S. 1986. Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level. In: *On the economy of plant form and function* (T. J. Givnish. ed.): 57-82. Cambridge University Press. Cambridge.

ELSTNER, E.F. 1982. Oxygen activation and oxygen toxicity. *Ann. Rev. Plant Physiology,* 33: 73-96.

FAJER, E.D., BOWERS, M.D. & BAZZAZ, F.A. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science,* 243: 1198-1200.

FALKOWSKI, P.G. 1983. Light-shade adaptation and vertical mixing of marine phytoplankton: A comparative field study. *J. Mar. Res.*, 41: 215-237.

FRICKE, W. 1983. Grossräumige Verteilung und Transport von Ozon und Varlaufern. VDI. Berichte 500 Säure, Niederschlage. Ursachen und Wirkungen VDI-Verlag.

FRIEDLAND, A.J., GREGORY, R.A., KARENLAMPI, L. & JOHNSON, A.H. 1984. Winter damage to foliage as a factor in red spruce decline. *Can. J. For. Res.*, 14: 963-965.

FRIEDLI, H., LOTSCHER, H., OESCHGER, H., SIEGENTHALER, U. & STAUFFER, B. 1986. Ice core record of the $^{13}C/^{12}C$ ratio of atmospheric CO_2 in the past two centuries. *Nature*, 324: 237-238.

GAMMON, R.H., SUNDQUIST, E.T. & FRASER, P.J. 1985. History of carbon dioxide in the atmosphere. In: *Atmospheric carbon dioxide and the overall carbon cycle* (J.R. Trabalka, ed.): 26-62. U.S. Department of Energy. Washington D C.

GAMON, J., PEÑUELAS, J., FIELD, C. & BJORKMAN, O. in press. Spectral shifts in vegetation reflectance under water and nutrient stress. *Plant, Cell and Environment.*

GAUDILLÈRE, J.P. & MOUSSEAU, M. 1989. Short term effect of CO_2 enrichment on leaf development and gas exchange of young poplars (*Populus euramericana* cv I 214). *Oecologia Plantarum* , 10(1): 95.

GIVNISH, T.J. 1984. Leaf and canopy adaptations in tropical forests. In: *Physiological Ecology of Plants of the Wet Tropics* (E. Medina, H.A. Mooney & C. Vásquez-Yáñez, eds.): 51-84. Junk. The Hague.

GIVNISH, T.J. (ed.). 1986. *On the economy of plant form and function.* Cambridge University Press. Cambridge.

GOULD, S.J. & LEWONTIN, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond.*, Ser. B, 205: 581-598.

GRAEDEL, T.E. & CRUTZEN P.J. 1989. Una atmósfera cambiante. *Investigación y Ciencia*, 158: 22-31.

GRIBBIN, J. 1988. *The hole in the sky.* Corgi. London.

GULMON, S.L. & CHU, C.C. 1981. The effect of light and nitrogen on photosynthesis, leaf characteristics, and dry matter allocation in the chaparral shrub *Diplacus aurantiacus. Oecologia*, 49: 207-212.

HARPER, J.L. 1982. After description. In: *The plant community as a working mechanism.* (E. I. Newman, ed.): 11-25. Blackwell. Oxford.

HEATH, R.L. 1975. Ozone. In: *Response of plant to air pollution.* (J.B. Mudd, & T.T. Kozlowski, eds.): 23-28. Academic Press. New York.

HEATH, R.L. 1980. Initial events in injury to plants by air pollutants. *Ann. Rev. Physiol,* 31: 395-401.

HILBERT, D.W., PRUDHOMME, T.I. & OECHEL, W.C. 1987. Response of tussock tundra to elevated carbon dioxide regimes: analysis of ecosystem CO_2 flux through nonlinear modelling. *Oecologia,* 72: 466-472.

IDSO, S.B. 1988. Three phases of plant response to atmospheric CO_2 enrichment. *Plant Physiology*, 87: 5-7.

INSKEEP, W.P. & BLOOM P.R. 1985. Extinction coefficients of chlorophyll a and b in NN-dimethylformamide and 80% acetone. *Plant Physiol.*, 77(2): 483-492.

JOHNSON A.H. & SICCAMA, T.G. 1983. Acid deposition and forest decline. *Environmental Sci. Tech.*, 17: A244-A304.

KORNER, C., SCHEEL, J.A. & BAUER, H. 1979. Maximum leaf diffusive conductance in vascular plants. *Photosynthetica*, 13: 45-82

LaMARCHE, V.C.Jr, GRAYBILL, D.A., FRITTS, H.C. & ROSE, M.R. 1984. Increasing atmospheric carbon dioxide: Tree-ring evidence for growth enhancement in natural vegetation. *Science*, 225: 1019-1021.

LAMBERS, H. 1985. Respiration in intact plants and tissues: its regulation and dependence on environmental factors, metabolism and invaded organisms. In: *Encyclopedia of Plant Physiology*, 18 (R. Douce & D.A. Day, eds): 418-473. Springer. Heidelberg

LAMBERS, H., DAY, D.A. & AZCÓN-BIETO, J. 1983. Cyanide-resistant respiration in roots and leaves. Measurements with intact tissues and isolated mitochondria. *Physiol. Plant.*, 58: 148-154.

LARIGAUDERIE, A., HILBERT, D.A. & OECHEL, W. 1988. Effect of CO_2 enrichment and nitrogen availability on resource acquisition and resource allocation in a grass, *Bromus mollis. Oecologia*, 77: 544-549.

LAVOREL, J. & ETIENNE, A.L. 1977. In vivo chlorophyll fluorescence. In: *Primary processes of photosynthesis; topics in photosynthesis* (J. Barber, ed.): 203-268. Elsevier. Amsterdam.

LEACH, J.E., WOODHEAD, T. & DAY, W. 1982. Bias in pressure chamber measurements of leaf water potential. *Agric. Meteorol.*, 27: 257-263.

LEE, D.W. 1986. Unusual strategies of light absorption in rain-forest herbs. In: *On the economy of plant form and function* (T. J. Givnish, ed.): 105-132. Cambridge University Press. Cambridge.

LEE, T.T. 1967. Inhibition of oxidative phosphorylation and respiration by ozone in tobacco mitochondria. *Plant Physiol.*, 69: 1444.

LEE T.T. 1968. Effect of ozone on swelling on tobacco mitochondria. *Plant. Physiol.*, 43: 133.

LEMON, E.D. (ed.). 1983. *CO_2 and plants. The response of plants to rising levels of atmospheric carbon dioxide.* AAAS Selected Symposium 84. Westview Press. Boulder, Colorado

LEVITT, J. 1980. *Responses of plants to environmental stresses. I: Chilling. Freezing and high temperature stress.* (T.T. Kozlowski, ed.). Academic Press. New York & London.

LINCOLN, D.E., COUVET, D. & SIONIT, N. 1986. Response of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. *Oecologia*, 69: 556-560.

LOVELOCK, J.E. 1979. *Gaia, a new look at life on*

Earth. Oxford University Press. Oxford.

LUCAS, P.W., COTTAM, D.A. & MANSFIELD, T.A. 1987. A large-scale fumigation system for investigating interactions between air pollution and cold stress on plants. *Environmental pollution*, 43: 15-28.

LUCAS, P.W., COTTAM, D.A., SHEPPARD, L.J. & FRANCIS, B.J. 1988. Growth responses and delayed winter hardening in Sitka spruce following summer exposure to ozone. *New Phytologist*, 108: 495-504.

MADSEN, E. 1975. Effect of CO_2 enrichment on growth, development, fruit production, and fruit quality of tomato from a physiological viewpoint. *Phytotronics*, III: 318-330.

MANSFIELD, T.A., WHITMORE, M.E., PANDE, P.C. & FREER-SMITH, P.H. 1987. Responses of herbaceous and woody plants to the dry deposition of SO_2 and NO_2. In: *Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems* (T.C. Hutchinson & K. Meema, eds.): 131-144. Springer. New York.

MARGALEF, R. 1974. *Ecología.* Omega. Barcelona.

MARGALEF, R. 1980. *La biosfera entre la termodinámica y el juego.* Omega. Barcelona.

MARGALEF, R. in press. *A view of the biosphere.* Chicago University Press.

MATHY, P. (ed.). 1988. *Air pollution and ecosystems.* D. Reidel. New York.

MCDOWALL, F.D.H. 1965. Stages of ozone damage to respiration of tobacco leaves. *Can. J. Bot.*, 43: 419

McLAUGHLIN, S.B. 1985. Effects of air pollution on forests. A critical review. *J. Air Poll. Control Assoc.*, 35: 512-521.

MELILLO, J.M., ABER, J.D. & MURATORE, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, 63: 621-626.

MOONEY H.A. in press. Biological response to climate change: the scope of the problem and an agenda for research. *Oikos.*

MOONEY, H.A. & GULMON, S.L. 1982. Constraints on leaf structure in relation to herbivory. *BioScience*, 32: 198-206.

NOBEL, P.S. 1986. Form and orientation in relation to PAR interception by cacti and agaves. In: *On the economy of plant form and function* (T.J. Givnish, ed.): 83-104. Cambridge University Press. Cambridge.

NORBY, R. J. & SEGAL, L.L. 1989. Nitrogen fixation in the lichen *Lobaria pulmonaria* in elevated atmospheric carbon dioxide. *Oecologia*, 79: 566-568.

OECHEL, W. C. & STRAIN, B.R. 1985. Native species responses to increased carbon dioxide concentration. In: *Direct Effects of increasing carbon dioxide on vegetation* (G.R. Strain & J.D. Cure, eds.): 117-154. US Department of Energy. DOE/ER-0238.

PASTOR, J., ABER, J.D., McCLAUGHERTY, A. & MELILLO, J.M. 1984. Above ground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology*, 65: 256-268.

PASTOR, J. & POST, W.M. 1988. Responses of northern forests to CO_2-induced climate change. *Nature*, 334: 55-58.

PEARCY, R.W. & BJORKMAN, O. 1983. Physiological effects. In: *CO_2 and plants: the response of plants to rising levels of atmospheric carbon dioxide.* (E.R. Lemon, ed.): 65-106 Westview Press. Boulder, Co.

PEARCY, R.W., BJORKMAN, A., CALDWELL, M.M., KEELEY, J.E., MONSON, R.K. & STRAIN, B.R. 1987. Carbon Gain by Plants in Natural Environments. *Bioscience*, 37(1): 21-29.

PEÑUELAS, J. 1985. Bicarbonate as an inorganic carbon source for *Fontinalis antipyretica* and *Fissidens grandifrons. J. Exp. Bot.*, 36 (164): 441-448.

PEÑUELAS, J. 1987. High oxygen tension inhibits vascular aquatic plant growth in deep waters. *Photosynthetica,* 21(4): 494-502.

PEÑUELAS, J. 1988a. Effects of hydrostatic pressure and irradiance on two submerged aquatic plants. An experimental study. *Pol. Arch. Hydrobiol.*, 35(1): 23-32.

PEÑUELAS, J. 1988b. *De la biosfera a la antroposfera.* Barcanova. Barcelona.

PEÑUELAS, J. in press. Anthroposphere regulation of biosphere. *Environmental Conservation.*

PEÑUELAS, J., MURILLO, J. & AZCÓN-BIETO, J. 1988. Actual and potential dark respiration rates and different electron transport pathways in freshwater aquatic plants. , *Aquatic Botany*, 30: 353-362.

PEÑUELAS, J., RIERA, T. & ZABALA, M. in press a. Mysids go back every night to cave to avoid light induced radicals formation. *Marine Biology.*

PEÑUELAS, J., AZCÓN-BIETO, J. & LUCAS, P. in press b. Effects of ozone normal summer concentration on Norway and Sitka spruces. *J. Environ. Exp. Bot.*

PEÑUELAS, J., GAMON, J. & FIELD, C. in pressc. Leaf reflectance related to remote sensing and biochemical and structural characteristics of sunflower crops. *Oecologia.*

PEÑUELAS, J. & MATAMALA, R. 1990. Changes in N and S leaf content, stomatal density and specific leaf area of 14 plant species along the last three centuries of CO_2 increase. *J. Exp. Bot..* 41: 1119-1124

PRINZ, B., KRAUSE, G.H.M. & STRATMAN, H. 1982. *Waldschaden in der Bundesrepublik Deutschland.* LIS-Berichte, 28: 1-154. Landesanstalt für des Landes NRW, Essen, FRG.

PRINZ, B., JUNK, K.D. & KRAUS, G.H.M. 1984. Forest effects in West Germany. *Symposium on air pollution and the productivity of the forest.* Publ. Izaac Walton League of America.

REHFUESS, K.E. 1986. *Perceptions on frost diseases in Central Europe.* Foundation for Science and Technology, Royal Society of London, 15 January 1985.

ROBERTS, T. M. 1984. Effects of air pollutants on agriculture and forestry. *Atmospheric environment*, 18: 629-652.

ROWLAND, A.J., BORLAND, A.M. & LEA, P.J. 1988. Changes in aminoacids, amines and proteins in response to air pollutants. In: *Air Pollution and Plant Metabolism.* (S. Schulte-hosted, N.M.

Darrall, L.W. Blank & A.R. Wellburn, eds.): 189-215. Elsevier. London.

SCHONHERR, J. 1976. Water permeability of isolated cuticular membranes: the effect of cuticular waxes on diffusion of water. *Planta*, 131: 159-164.

SCHREIBER, U., VIDAVER, V., RUNECKLES, V. C. & ROSEN, P. 1978. Chlorophyll fluorescence assay for ozone injury in intact plants. *Pl.ant Physiol.*, 61: 80-84.

SKARBY, L. & SELLDEN, G. 1984. The effects of ozone on crops and forest. *Ambio,* 13: 68-72.

SKIBA, U. & CRESSER, M. 1988. The ecological significance of increasing atmospheric carbon dioxide. *Endeavour*, 12(3): 143-147

STRAIN, B.R. & BAZZAZ, F.A. 1983. Terrestrial plant communities. In: *CO_2 and plants. The response of plants to rising levels of atmospheric carbon dioxide.* (E.R. Lemon, ed.): 177-201. Westview Press. Boulder, Co.

STRAIN, B.R. & CURE, J.D. 1985. *Direct effects of increasing carbon dioxide on vegetation.* Duke University Press. Durham, N.C.

SULLIVAN, S.G., WINTERBOURN, C.C. & STERN, A. 1983. Hypothesis: oxygen, superoxide dismutase and catalase form a metabolic pathway that protects against oxidative damage in the red cell. In: *Oxygen Radicals and their Scavenger Systems.* (I. G. Cohen & R.A. Greenwald, eds.): 364-367. Elsevier. Amsterdam.

SWANSON, E.S., THOMSON, W.W. & MUDD J.B. 1973. The effect of ozone on leaves cell membranes. *Can. J. Bot.*, 51: 1213.

TISSUE, D. & OECHEL, W. 1987. Responses of *Eriophorum vaginatum* to elevated CO_2 and temperature in the Alaskan tussock tundra. *Ecology*, 68: 401-410.

TRANQUILLINI, W. 1979. *Physiological ecology of the alpine timberline.* Ecological studies 31. Springer. New York.

TUCKER, C.J. & SELLERS, P.J. 1986. Satellite remote sensing of primary production. *Intern. J. Remote Sensing,* 7(11): 1395-1416.

WALKER, J. C. G. 1986. *Earth History.* Jones & Bartlett. Boston.

WARBURG, O. 1920. Über die Geschwindigkeit der photochemischen Kohlensäurezersetzung in lebenden Zellen. II. *Biochem. Z.*, 103: 188-217.

WELLBURN, A. 1988. *Air pollution and acid rain. The biological impact.* Longman. New York.

WILLIAMS, W.E., GARBUTT, K., BAZZAZ, F.A. & VITOUSEK, P.M. 1986. The response of plants to elevated CO_2 IV. Two deciduous-forest tree communities. *Oecologia*, 69: 454-459

WILLIAMS, W. E., GARBUTT, K. & BAZZAZ, F.A. 1988. The response of plants to elevated CO_2. V. Perfomance of an assemblage of serpentine grassland herbs. *Env. Exp. Bot.*, 28: 123-130.

WONG, S.C. 1979. Elevated partial pressure of CO_2 and plant growth. *Oecologia*, 44: 68-74.

WOODWARD, F.I. 1986. Ecophysiological studies on the shrub *Vaccinium myrtillus* L. taken from a wide altitudinal range. *Oecologia*, 70:580-586.

WOODWARD, F.I. 1987. Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. *Nature*, 327: 617-618.

WOODWARD, F.I. & BAZZAZ, F.A. 1988. The responses of stomatal density to CO_2 partial pressure. *J. Exp. Bot.*, 39: 1771-1781.

WULFF, R.A. & STRAIN, B.R. 1982. Effects of CO_2 enrichment on growth and photosynthesis in *Desmodium paniculatum.* Can. J. Bot., 60: 1084-1091.