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GLOBAL CLIMATE CHANGE AND FOREST PRODUCTIVITY

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Abstract

Will terrestrial ecosystems continue to be a potential sink for atmospheric CO_2 mitigating the effects of global climate change? The biological, climatological and political implications of this question are enormous. Here we address this question in the light of the findings of various studies on the long term effects of elevated CO_2 on productivity of plants in general and forests in particular.

Native forests are dominated by plants with C_3 type of photosynthesis. Because C_3 photosynthesis is CO_2-limited at the existing atmospheric CO_2 concentration, elevated CO_2 increases photosynthetic rates in these plants at any given light intensity. Increased photosynthesis at very low light intensities has relevance to forest undergrowths and shaded leaves of large trees in the forest where photosynthesis is usually light-limited. Several studies show that the initial stimulation in photosynthesis may decrease with time depending upon the nutrition level and sink capacity of the plants, but the photosynthetic rates will not go below the rates observed at the current levels of CO_2. Increased canopy photosynthesis and decreased respiration and transpiration rates led to increased biomass at the cost of reduced amounts of water in plants and ecosystems that were exposed to elevated CO_2. Plants grown at elevated CO_2 had higher efficiency of water, light and nutrient utilization and altered tissue composition, particularly increased carbohydrate and decreased protein contents. This can alter the CN ratio and thus the quality of litter affecting its decomposition in a future world rich in CO_2. Long-term regulation of these biological processes in response to elevated CO_2 will have a direct impact on the carbon and water balance of ecosystems.

Keywords: Elevated CO_2, forest productivity, photosynthesis, respiration, transpiration.

Introduction

The ever-increasing industrial activity and urbanization lead to tremendous emission of green house gases into the atmosphere mostly due to the burning of fossil fuels. This, along with the large-scale deforestation due to population pressure is causing progressive rise in the concentration in CO_2 in the atmosphere (Ca). Between 1750 and 1850, CO_2 increased at the rate of 0.05 to 0.1 ppm yr^{-1}, but between 1850 and 1950, this was as high as 0.5 ppm yr^{-1} (Neftal *et al.*, 1985). During the past 50 years the rate of increase in CO_2 was around 0.83 ppm yr^{-1} and at present it is 1.8 ppm yr^{-1} (John and Lloyd, 1992). There is an environmental cost for every developmental activity and rising CO_2 and global climate change are the cost that the human kind is paying to sustain its present way of living.

Photosynthesis, respiration and transpiration are the primary biological processes by which plants respond directly to the increasing CO_2. Of late, there has been a lot of interest on the effect of increasing CO_2 on the productivity of natural and managed ecosystems. Understanding the long-term acclamatory responses of the above plant functions is critical to any predictions on the productivity of ecosystems in a future world rich in CO_2. Often this understanding is missing in several climate change models (Schimel, 1990). For instance, it is generally assumed in several models that stimulation in photosynthesis at elevated CO_2 is a short-term response and other limiting factors become operational restricting the continued stimulation at elevated CO_2 (Bazzaz, 1990) which is not so in most cases (Drake *et al.*, 1997).

Why do plants respond to rising CO_2 concentration?

1. The primary carboxylase enzyme in C_3 plants, ribulose–1, 5-bisphosphate carboxylase/oxygenase (Rubisco) – the most abundant protein on the planet – has the dual function of carboxylase (leading to photosynthetic CO_2 assimilation) and oxygenase (leading to photorespiratory release of CO_2) at the same time. This enzyme is CO_2 limited at the present CO_2 concentration. A doubling of CO_2 from the present level can inhibit oxygenase activity by 50 per cent and thus inhibit photorespiration and increases photosynthesis (Sharkey *et al.*, 1989). This explains the immediate and marked response of C_3 plants to elevated CO_2 (Long, 1991). While most studies show that photosynthesis will increase and continue to stay at the increased rate, there are also reports that long-term growth at an elevated CO_2 can sometimes reduce the photosynthetic rates.
2. Stomata are very sensitive to CO_2 in the ambient air. Increasing CO_2 closes stomata and thus decreases transpiration. Doubling of CO_2 concentration decreased transpiration by 10 to 40 per cent in different species (Kimble and Idso, 1983; Allen, 1990; Wong and Dunin, 1987; Jones *et al.*, 1985). Changes in stomatal density have also been reported in plants grown at elevated CO_2 (Gunderson and Wullschleger, 1994; Beerling and Chaloner, 1993). The reduced stomatal conductance does not limit photosynthesis due to the large CO_2 concentration gradient existing between the leaf intercellular spaces and the ambient air at elevated CO_2. A reduction in the leaf transpiration rate will make the leaf temperature go up slightly. This will have other effects on the leaf metabolism that is sensitive to temperature.
3. Elevated CO_2 has a direct inhibitory effect on the Cytochrome c oxidase pathway, but not on the cyanide resistant alternative pathway of the mitochondrial respiration (Gonzalez-Meller *et al.*, 1996). In spite of an increase in the concentration of sugars, a considerable reduction in the respiration rates was seen in the mature tissues of plants grown at elevated CO_2 (Amthor, 1991; Bunce, 1990). But in several studies, the increased photosynthetic rates seen in the young leaf stimulated respiration at elevated CO_2 (Havelka *et al.*, 1984; Porter *et al.*, 1988).

The relevant question here is how far will these effects reflect at the ecosystem level? What will be the nature and extent of their acclimation to increased CO_2 in the long-term? These are issues that have a direct relationship to ecosystem productivity in a future CO_2 enriched world.

From single leaf to ecosystem level processes

Although the extent of elevated CO_2-induced stimulation in leaf photosynthesis can decline with time, the rates are still more than the present normal CO_2 (Jacob *et al.*, 1994; Stitt, 1991; Long and Drake, 1992). Down regulation in leaf photosynthesis with time was related to the acclimatory response of the biochemical apparatus of photosynthesis. Reduced concentration of Rubisco (Jacob *et al.*, 1994; Stitt, 1991), altered nitrogen allocation to various components and tissues (Woodrow, 1994) and increased concentrations of sugars (Nie *et al.*, 1995; Long and Drake, 1992) are the major reasons for photosynthetic acclimation.

While the nitrogen dynamics of the plants may be related to the nitrogen nutrition, accumulation of carbohydrates may reflect reduced sink capacity. In this context, it is interesting to note that several annual crop plants grown in small pots with restricted root growth had greater down regulation in photosynthesis than many perennial plant species exposed to elevated CO_2 in their native habitat (Thomas and Strain, 1991; Cure and Acock., 1986; Long and Drake, 1992; Arp, 1991; Arp and Drake, 1991; Gunderson *et al.*, 1993). The sink demand for more photosynthates may help to maintain a steady high rate of photosynthesis at elevated CO_2 by preventing the accumulation of sugars in the leaves. For large forest tree species, the timber can act as a potential sink for photosynthates.

Several studies conducted in the natural environment show how the effects of elevated CO_2 on photosynthesis and respiration observed at the single leaf level were translated to whole plant and ecosystem levels. Net ecosystem carbon uptake was considerably increased in native species grown at elevated CO_2 in the field for several years which led to increased dry matter production per unit land area (Long and Drake, 1992). Continuous growth at elevated CO_2 in the field for several years maintained a high canopy photosynthetic rate and low respiratory rate and showed high primary production of both shoot and root systems resulting in the accumulation of carbon in the soil (Drake, 1992). Native ecosystems of a

Table 1. Effect of continuous growth at elevated CO_2 on tissue composition, photosynthesis and respiration

	CO_2 Concentration		% change
	350 ppm	700 ppm	
Soluble sugars (g m^{-2})	16.5 (1.88)	25.2 (3.75)	+53
Starch (g m^{-2})	55.3 (5.45)	83.4 (5.77)	+51
Soluble proteins (g m^{-2})	1.94 (0.24)	1.19 (0.10)	-39
N content (%)	1.15 (0.17)	0.79 (0.09)	-31
Photosynthesis (mmol m^{-2} leaf area s^{-1})	14.3 (2.3)	24.4 (4.5)	+71
Ecosystem photosynthesis (mmol m^{-2} land area s^{-1})	24.6 (3.6)	42.7 (5.2)	+75
Ecosystem Respiration (mmol m^{-2} land area s^{-1})	6.1 (1.4)	3.3 (1.2)	-50

grassland (Field *et al.*, 1995) and priarie (Ham *et al.*, 1995) and a wheat crop (Pinter *et al.*, 1996) showed increased biomass production at elevated CO_2. Except in the arctic tundra, long-term exposure to elevated CO_2 increased canopy photosynthesis in all the field level experiments with native and agricultural ecosystems (Drake *et al.*, 1997). Thus terrestrial ecosystems may continue to be a sink for increasing atmospheric CO_2.

A brief summary of some of the important findings from the longest running field experiment on the effects of elevated CO_2 on native ecosystem is given in Tables 1 and 2. These results show how the leaf level responses to elevated CO_2 were translated to ecosystem level processes.

Table 2. Long-term effects of continuous exposure to elevated CO_2 in a wetland ecosystem dominated by *Scirpus olneyi*, a C_3 sedge

Single leaf level	% change compared to normal ambient CO_2
Photosynthesis	+20 to 100
Carbohydrates	+25 to 50
Soluble Proteins	- 40 to 52
Rubisco	- 30 to 55
Tissue N content	- 18
Nitrogen Use Efficiency	+60 to 80
Respiration Ecosystem level	- 30
Photosynthesis	+40
Respiration	- 45
Evapotranspiration	- 20
Water Use Efficiency	+79
Shoots & Leaves	+12 to 15
Roots	+40
Insects & Fungi	- 30
Decomposition	- 22
Soil invertebrates	+25 to 100
Soil C	+5

Scirpus olneyi, a C_3 sedge growing in a wetland marsh ecosystem was exposed to elevated CO_2 in its natural habitat using open top chambers (Jacob *et al.*, 1994) for several years. Each value is a mean of more then 10-15 replications. SE is shown in parenthesis.

Growth at elevated CO_2 increased leaf area per plant (Devakumar, 1994) and extensive branching in many species (Rogers *et al.*, 1984) and more tillering in grasses (Sionit *et al.*, 1981). Several species showed an increase in the specific leaf weight presumably due to increase in the starch content at elevated CO_2 (Huber *et al.*, 1984). Root growth was found stimulated at elevated CO_2 (Del castillo *et al.*, 1989; Devakumar and Jacob, 1997; Baker *et al.*, 1990; Dey *et al.*, 1996). Elevated CO_2 can also influence the reproductive biology of plants (Marc and Gifford, 1984) which can be an indirect effect of CO_2 concentration through altering the development process (Lawlor and Mitchel, 1990).

Will warmer regions of the world respond better to elevated CO_2?

At elevated temperatures, Rubisco will tend to be more of an oxygenase than carboxylase due to better solubility of O_2 in water and increased specificity of Rubisco for O_2 compared to CO_2. By making more CO_2 available to the enzyme, elevated CO_2 prevents the increased oxygenase activity (Long and Drake, 1992). Thus stimulation in photosynthesis induced by elevated CO_2 is more at warmer than at cooler temperatures (Table 3).

Scirpus and scrub oak were exposed to elevated CO_2 (700 ppm) in their natural environment day and night throughout the growing season. The other three species were grown at normal ambient CO_2 and exposed to elevated CO_2 while making the measurements. Each value is a mean of 10-15 replications. SE is shown in parenthesis.

Table 3. Extent of elevated CO_2 stimulated leaf photosynthetic rates at 30°C and 10°C

Species	Measurement Temperature 10°C			Measurement Temperature 30°C		
	CO_2= 350ppm	CO_2= 700ppm	% increase	CO_2= 350ppm	CO_2= 700ppm	% increase
Scirpus	5.5 (1.1)	6.9 (1.8)	25	14.3 (2.1)	24.5 (2.9)	71
Scrub oak	2.5 (0.8)	3.4 (1.1)	36	8.6 (1.7)	14.5 (2.1)	69
Hevea	3.4 (1.2)	4.1 (0.9)	21	11.5 (2.9)	18.7 (3.7)	63
Sunflower	13.7 (2.2)	16.7 (3.9)	22	23.5 (3.2)	35.8 (4.1)	52
Wheat	14.4 (2.9)	18.1 (3.4)	26	21.5 (2.8)	32.4 (3.7)	51

Ecosystem photosynthesis also showed greater stimulation at elevated CO_2 and warmer temperatures (Long, 1991; McMurtrie and Wang, 1993). When CO_2 was increased from 360 to 550 ppm, canopy photosynthesis in wheat was stimulated by 40 per cent in summer and only 10 per cent in spring (Pinter *et al.*, 1996). There was little stimulation in canopy photosynthesis at elevated CO_2 in the arctic tundra (Oechel *et al.*, 1994). Thus the warmer tropics and subtropics may be a better sink for CO_2 and gain more biomass than the temperate regions as CO_2 goes up due to the favorable effect of high temperature on photosynthesis. But a minor offset can be expected because of the stimulation in dark respiration rates at warmer temperatures.

Water, light and nitrogen use efficiency

Because of increased photosynthetic and decreased transpiration rates, instantaneous water use efficiency was markedly improved in plants grown at elevated CO_2. Several studies show increased water use efficiency at elevated CO_2 (Ziska *et al.*, 1991). The trend was similar in both C_3 and C_4 species (Morison, 1985). Studies in the wetland (Arp, 1991), prairie (Ham *et al.*, 1995) and grassland (Field *et al.*, 1995) ecosystems have shown that reduced transpiration rates of the leaves led to decreased water consumption at the ecosystem levels. Elevated CO_2 led to more than 75 per cent increase in field level water use efficiency in wheat (Pinter *et al.*, 1996). This can increase the soil moisture status and thus delay the onset of soil moisture deficit.

Elevated CO_2 increases light-limited photosynthesis by increasing the apparent quantum yield for photosynthesis and thus decreases the light compensation point if respiration is not increased (Long and Drake, 1992). Thus the photosynthetic light use efficiency is substantially increased at elevated CO_2 (Pinter *et al.*, 1996). This will benefit the forest undergrowths and other lower canopy leaves in the forests in which photosynthesis is always limited by low light. It is expected that elevated CO_2 may increase the rate of growth of tree seedlings (Devakumar *et al.*, 1996; Kubiske and Pregitzer, 1996). One of the practical applications of this is to expose nursery seedlings to elevated CO_2 for better initial growth (Table 4) which will reduce the nursery period and also help to get robust seedlings which can establish better under the unmanaged conditions of the filed.

Continuous growth at elevated CO_2 often reduces the tissue nitrogen level considerably both due to reduction in the absolute levels of several proteins, particularly Rubisco and due to the increased carbohydrate contents. In spite of less tissue nitrogen, the plants have high photosynthesis and biomass production and hence their nitrogen use efficiency is high. This is because when there is more CO_2 available for photosynthesis, the plants only require far less amounts of Rubisco to perform photosynthesis (Sharkey, 1985; Long, 1991). Changes in Rubisco contents can alter the tissue nitrogen level significantly because this enzyme is present in very large quantities in photo-synthesizing organs (Jacob *et al.*, 1995).

These plants were exposed to elevated CO_2 using an indigenous method (Devakumar *et al.*, 1996) for 90 days from their germination. There was species difference in the extent of dry matter production by the seedlings at elevated CO_2.

Litter decomposition and nutrient turnover

Studies have shown that increased supply of nitrogen increases photosynthesis and that photosynthetic acclimation is more when nitrogen is limiting (Bowes, 1993; Curtis, 1996). Therefore an important factor that can impair the photosynthetic productivity of native forest ecosystems can be the limited amounts of available nitrogen in the soils. When the litter decomposition is poor due to various reasons including soil biology, litter composition or weather

Table 4. Increased dry matter production in nursery seedlings when exposed to elevated CO_2

Species	% increase in dry matter per seedling
Annona squamosa	36
Zizyphus jujuba	125
Tamarindus indica	12
Acacia auriculiformis	14
Dalbergia sissoo	193
Spathodia campanulata	88
Derris indica	135
Feronia elephantum	17
Artocarpus integrifolia	155
Swietenia microphylla	101
Eucalyptus citriodora	51
Tectona grandis	460
Dalbergia latifolia	36
Hevea brasiliensis	25

conditions - all of which are expected to change in a future world - more and more nitrogen will get locked up in the organic matter making nitrogen unavailable to the plants.

Changes in the biochemical composition of the tissue (Jacob *et al.*, 1995) affect the forage quality and palatability of the litter (Thompson and Drake, 1994). Plants grown at elevated CO_2 tended to have a high C/N ratio which reduced the nutrient value of the litter (Drake *et al.*, 1997). This has been attributed as the reason for the reduced insect and fungus infestation in the plants grown at elevated CO_2 (Thomson and Drake, 1994). When there is no choice of food, the larvae may increase the quantity of consumption to make up for the poor quality of the feed. Growth at elevated CO_2 increased phenolics and tannins in *Eucalyptus* and the beetles that were fed with this had poor growth and high mortality (Lawler *et al.*, 1997).

Differential response of species to elevated CO_2 can create competition among various species in a natural vegetation (Bazzaz and Carlson, 1984). This may lead to changes in the composition of the vegetation (Leadley and Stocklin, 1996). It is possible that such changes can affect the composition and structure of herbivorous pests and microbes which are vital links in the nutrient cycle in native ecosystems. An increase in the soil microbial biomass has been reported at elevated CO_2 by Schenk *et al.* (1995). While a lot of information is available on the effects of elevated CO_2 on primary productivity, little is known about its effect on litter decomposition and nutrient cycling which can put a ceiling on the maximum response of forest ecosystems to rising concentration of CO_2 in the atmosphere.

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