Atmospheric Carbon Dioxide and Forests [and Discussion]

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Atmospheric carbon dioxide and forests

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Knowledge about the effects of the rise in atmospheric CO_2 concentration on trees and forest is assessed and, the converse, the possible impact of forests on the atmospheric CO_2 concentration is discussed. At the cellular scale, much is known about the role of CO_2 as a substrate in photosynthesis, but only little about its role as an activator and regulator. At the leaf scale, the response of CO_2 assimilation to CO_2 concentration has been described often and is well represented by biochemically based models, but there is inadequate information to parametrize the models of CO_2-acclimated leaves. Growth and partitioning to the roots of seedlings and young trees generally increases in response to a doubling in atmospheric CO_2 concentration. Experimental results are very variable, because of the differing length of the experiments, the artificial conditions and the artefactual constraints. At larger scales, direct measurements of responses to increase in atmospheric CO_2 are impractical but models of canopy processes suggest that significant increases in CO_2 assimilation will result from the rise in atmospheric concentration. Inferences from the increase in amplitude of the seasonal oscillation in the global atmospheric CO_2 concentration at different latitudes suggest that forest is having a significant impact on the global atmospheric concentration, but it seems unlikely that expansion of the forest resource could effectively reduce the increase in atmospheric CO_2.

INTRODUCTION

The present average atmospheric concentration of CO_2 is *ca.* 350 μmol of CO_2 per mole of dry air†, and the concentration is rising at a rate of *ca.* 1.2 μmol mol^{-1} per annum (Conway *et al.* 1988).

This rapid increase in atmospheric CO_2 concentration at present is largely attributable to the burning of fossil fuels. However, the increase became perceptible about 200 years ago (Neftel *et al.* 1985; Raynaud & Barnola 1985; Pearman *et al.* 1986) when population emigration and the associated intensification of agriculture over large areas, particularly in North America, led to the destruction of extensive areas of forest and the cultivation of organically rich soils (see, for example, Delcourt & Harris 1980). The oxidation of wood and soil organic matter led to a slow, but progressive, increase in atmospheric CO_2 concentration up until about the middle of the 19th century. From the ratio of $^{13}C:^{12}C$ in tree rings (Peng *et al.* 1983) and from the composition of gas bubbles trapped in the polar ice (Pearman *et al.* 1986), it has been estimated that the atmospheric CO_2 concentration then was about 270 μmol mol^{-1}. With the onset of the Industrial Revolution, the exploitation of fossil fuels began around 1860 and the atmospheric CO_2 concentration has increased strongly ever since, with the result that in the past 130 years the concentration has risen about 75 μmol mol^{-1}. Up until *ca.* 1900,

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† At an atmospheric pressure of 10^5 Pa, 350 μmol mol^{-1} is equivalent to a partial pressure of 35.0 Pa and a volume fraction of 350×10^{-6} or 350 cm^3 m^{-3}.

the dominant source of the increase was the oxidation of organic matter from soils and forests; over the past 180 years the increase has been approximately 1.6:1 for soil + forests : fossil fuel (Peng *et al.* 1983). The much steeper rise in atmospheric CO_2 concentration today, however, is completely dominated by the burning of fossil fuels, and, to a much lesser extent, the manufacture of cement (Rotty 1983).

Since the introduction of infrared gas analysers in 1957, when the concentration was *ca.* 315 μmol mol^{-1}, detailed seasonal and annual changes in the atmospheric CO_2 concentration have been measured. From 1953 to 1973 the rate of increase of fossil fuel emissions was 4.3% per annum. During and following the oil crisis, this rate diminished sharply and there was a perceptible reduction in the rate of increase of CO_2 in the atmosphere. However, global fossil fuel emissions have now recovered to a rate of increase of around 4% per annum and the atmospheric CO_2 concentration is, again, increasing at an exponential rate. The consumption of fossil fuels is currently yielding *ca.* 5 Gt per year (5×10^{12} kg per year) of carbon to which may possibly be added a maximum of *ca.* 2 Gt per year of carbon for CO_2 from the oxidation of soil and wood. Combustion of fossil fuels may well be yielding 10 Gt per year of carbon by the end of the century and, depending upon the continuing rate of increase of consumption of fossil fuels, an atmospheric CO_2 concentration of 600 μmol mol^{-1} is variously forecast for some time 60–100 years hence. For practical reasons, in many experiments with plants, the high CO_2 treatment is generally taken as double the present concentration (i.e. *ca.* 700 μmol mol^{-1}) and this might conceivably be reached by the end of the next century.

These predictions are uncertain, not only because of uncertainty as to the future consumption of fossil fuels, but also because of uncertainty in the fate of the CO_2 produced and in the size of the fluxes between the oceans and the atmosphere, and the biosphere and the atmosphere. Of the CO_2 released in the burning of fossil fuels over the past 100 years, only about 56% has contributed to the increase in CO_2 concentration in the atmosphere. The whereabouts of the other 44% is uncertain, but it is presumed that it has been taken up in the oceans and will ultimately be deposited in the deep ocean. There are several hypotheses as to the fate of this CO_2 in the oceans (see, for example, Sarmiento *et al.* 1988) but there is no evidence at present that it is accumulating in surface layers that might become saturated. However, as the climate warms, the physical and biological processes in the oceans may change in ways not currently understood, leading to changes in the carbon distribution and in the potential of the oceans to absorb CO_2.

Figure 1 shows one set of current estimates of the annual influxes and effluxes between biosphere and atmosphere and oceans and atmosphere. The fluxes are all relatively large in relation to the influx derived from the burning of fossil fuels, and suggest that the net change in the atmospheric CO_2 concentration should be quite sensitive to comparatively small changes in the fluxes to and from the atmosphere. However, the estimate of the net flux between the biosphere and the atmosphere, here indicated as zero, is particularly uncertain and it is currently a matter of considerable controversy as to whether the biosphere is a source of CO_2 or a sink for CO_2. There is no doubt that land use is changing extensively throughout the world. In some areas climax forests are being cleared; in other areas young, fast-growing plantations are being established. In some areas forests are being killed by pollution; in other areas they may be fertilized by pollutants. Yields of agricultural crops are increasing, but so also are rates of turnover of organic matter. The problem is essentially one of assessing global changes of land use with a sufficient degree of resolution to estimate likely changes in the net annual CO_2 flux between biosphere and atmosphere with adequate accuracy. Several estimates derived from the inclusion of such data in global ecosystem models suggest a net efflux from the biosphere of 2–4 Gt per year of carbon over the past 10 years (see, for example, Woodwell *et al.* 1978; Moore *et al.* 1981; Houghton *et al.* 1983). However, such estimates are not compatible with a more or less constant proportional uptake by the oceans of 44% over the past 30 years or with the recent increase in amplitude of the seasonal oscillation in atmospheric CO_2 (discussed later). The models of changes in the carbon content of the atmosphere or the oceans are also not sufficiently sensitive to resolve whether the biosphere is a net source or sink for CO_2 at present, so other methods must be addressed.

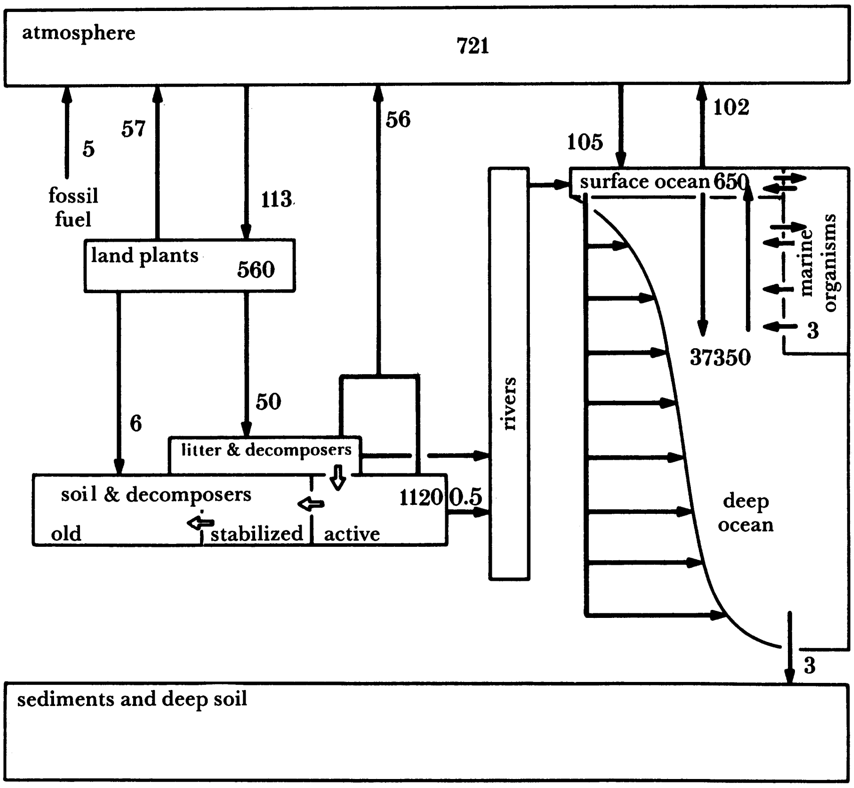


FIGURE 1. A diagram to show current conceptions of the sizes of the carbon reservoirs (in gigatonnes) and of the carbon fluxes (in gigatonnes per year) in the global cycle. From King *et al.* (1987).

The likely consequences for trees and forests of the increase in atmospheric CO_2 concentration fall into two categories, namely the effects of the increase in CO_2 on regional climates and the effects of CO_2 *per se* on productivity and associated biological processes. K. V. Mellanby, writing in *The Times* in January 1983 expressed the opinion that the rise in atmospheric CO_2 concentration was 'probably the most difficult and controversial problem facing mankind'. Only recently has awareness of this problem led to the initiation of one or two small research projects in the U.K. Although in the U.S.A. research projects oriented towards the rise in CO_2 concentration have been in progress since about 1980, the amount of information particularly relevant to trees and forests is small. Effects of the increase in CO_2 on regional climates have yet to be demonstrated definitively and are consequently somewhat speculative, whereas some effects of an increase in CO_2 on processes in trees have been established and may, with caution, be scaled up to provide predictions about likely effects on forests, although these too are rather speculative. This essay is almost entirely concerned with this latter category of effects of the rise in atmospheric CO_2.

CLIMATIC CHANGE

In a review (1982) A. J. Crane wrote 'the increase in atmospheric CO_2 from burning fossil fuels is the one single anthropogenic influence that could produce global, climatic changes observable above the climatic noise within the next 50 years'. The primary prediction is for an increase in average global temperature of 2–3 °C for a doubling in the atmospheric CO_2 concentration. The detection of such an increase is difficult, not least because over the past 50 years the temperature in the temperate region of the Northern Hemisphere has been decreasing at a rate of about 0.15 °C per year as a result of various superimposed climatic cycles (Crane 1982). There is no general agreement that an increase in temperature has so far been detected, although detection of an increase over the past 10 years has recently been claimed (Jones *et al.* 1988), but there is now agreement that such an increase should be clearly noticeable above the climatic noise by the end of the century. Currently global climatic models do indicate such an increase in average temperature, but yield a variety of consequential predictions about the distribution of temperatures, precipitation and evaporation with respect to both latitude and longitude. Some likely consequences of a rise in average temperature of 2–3 °C for trees and forests can be estimated (Cannell *et al.* 1988) but detailed considerations of such a rise seem unwarranted until there is a larger consensus about the likely changes in temperature in the main forested areas of the world and, more particularly, about the likely consequences for the zonal distributions of precipitation and evaporation.

BIOLOGICAL EFFECTS

The questions that should be addressed are of the following kinds.

1. What are the likely effects of the increase in CO_2 concentration on the growth and productivity of stands of commercial tree crops, and will the value of the crop be changed as a result?
2. In planning future forest research, silviculture and management practice, how should the rise in CO_2 concentration be taken into account?
3. At a more ecological level, what are the likely consequences of the rise in CO_2 concentration for the composition and structure of forests and for the wildlife within them?
4. And, conversely, can the rise in atmospheric CO_2 concentration be influenced by manipulating forest or by increasing the area of forest?

There are considerable difficulties in addressing questions of this kind, because of the lack of appropriate information at a stand or forest scale. It is impractical to expose areas of forests experimentally to increases in CO_2 concentration and if it were possible, there might well be ethical objections. The information that is available is confined to experiments in which leaves or small plants have been exposed to elevated CO_2 concentrations for both short and long periods, and to an isolated experiment in which entire trees have been exposed to large CO_2 concentrations for a short period (Wong & Dunin 1987). There are substantial difficulties in scaling up from information at this scale to predict the likely consequences of an increase in CO_2 concentration on forests or even on commercial stands of trees.

In the following paragraphs I review briefly what has been learnt from experiments on chloroplasts, leaves and young trees and, on the basis of that information, make some predictions about the likely consequences for stands. The record of the seasonal changes in atmospheric CO_2 concentration in the Northern Hemisphere does itself provide some information about interactions between atmospheric CO_2 and the temperate and boreal forests, and that will be considered. Finally, the question of manipulating the rise of CO_2 by forests is discussed.

Growth of young trees

Few plants of any kind have been grown from seed that was formed at elevated CO_2 concentrations and none have been grown for several generations at double the present CO_2 concentration. It is likely that no experiments have been done, or responses to CO_2 investigated, on plants that are fully acclimated to a raised CO_2 concentration. At best, plants exposed for weeks or months to elevated CO_2 concentration may be largely acclimated particularly with respect to some organs, but are probably still acclimating slowly as a whole. Natural populations in which many generations of individuals have occurred over the past 100 years are likely to have become genetically adapted to the rise in atmospheric CO_2 concentration through progressive selection, but this is less probable in forests where there may have been only one or two generations during this period.

There is little distinction in the literature between physiological responses that are immediate, responses that have a developmental component and hence depend on the degree of acclimation, and responses that may result from selection of better-adapted genotypes over several generations. However, it is important to keep those distinctions in mind because different processes are likely to be involved.

In several experiments (approximately 30 on conifers and 30 on broadleaves), the effects of a doubling of atmospheric CO_2 concentration on the growth of young trees has been investigated in controlled or partly controlled environments (Eamus & Jarvis 1989). The experiments were generally of short duration for trees, lasting from a few weeks up to $2\frac{1}{2}$ years, and the trees were almost invariably grown in pots, so that the results are somewhat restricted in their applicability to stands of trees or forests. In general, too, rates of growth were rather low (relative growth rates of *ca.* 1% per day) suggesting that the conditions were far from optimum in some respects.

In all cases, the rate of growth of dry matter was increased at the higher CO_2 concentration, the increase being in the range 20–120% with a median of about 40%. In most of the experiments there were increases in the mass of leaves as a result of increases in the number, area or thickness. Masses of both fine and coarse roots were also increased and there was a noticeable increase in partitioning to the roots (i.e. larger root:shoot ratios, especially in plants growing with limited nutrient resources). To a considerable extent, an increase in ambient CO_2 concentration was effective in compensating for lack of light, water or nutrients. In a series of experiments on several species, designed to test the hypothesis that lack of nutrients would prevent a response to a doubling in CO_2 concentration, it was unequivocally shown that this was not the case (see, for example, Norby *et al.* (1986); review in Eamus & Jarvis (1989)). Young trees growing in situations of low nitrogen or phosphorus, or on small volumes of nutrient-poor soils, none the less showed increased growth in response to a doubling in ambient CO_2 concentrations. A scarcity of nutrients does not prevent a growth response to increase in CO_2 concentration. In the longer experiments lasting more than one year, however, the response appeared to have been established in the first few months and there was no evidence of the progressive increase in size difference between the trees in the two treatments that would be expected if a difference in relative growth rate was being maintained. However, this may well have been an artefact resulting from constrained rooting conditions and the lack of an adequate sink for carbohydrates.

The general conclusion from these studies of growth is that increase in CO_2 concentration primarily leads to young trees growing larger more quickly and that the majority of the changes observed are normal, ontogenetic changes associated with growth and development. It is therefore pertinent to consider the processes by which an increase in CO_2 concentration may increase the rate of growth of trees.

Carbon dioxide at the cell and leaf scale

Carbon dioxide is primarily implicated in the growth of plants as the substrate for photosynthesis. None the less, CO_2 both activates and regulates the amount or activity of the enzyme, ribulose bisphosphate carboxylase–oxygenase (Rubisco) and it is not improbable that CO_2 may also regulate some other enzymes that affect plant metabolism and growth. It is not clear at present, for example, whether the larger rates of leaf growth of plants growing at increased CO_2 concentration are solely the result of enhanced CO_2 assimilation and the availability of more substrate for leaf growth or whether there are more direct effects on leaf initiation and development. Carbon dioxide may also both reduce stomatal numbers per unit area of leaf (Woodward 1987) and cause stomatal closure, thereby reducing stomatal conductance to both water vapour and CO_2, by mechanisms that are still speculative but probably result from action on non-photosynthetic processes (Eamus 1986). Whatever the effect, it seems likely that physiological processes in leaves are responding to the CO_2 concentration within the intercellular spaces of the leaves (see, for example, Mott 1988).

The carbon dioxide concentration in the intercellular spaces

The mean intercellular space CO_2 concentration (C_i) is a function of the CO_2 concentration at the leaf surface (C_l), which, in turn, depends upon the degree of coupling between the leaf and the atmosphere above. For well-coupled plants and vegetation, such as trees and forests, the leaf surface concentration of CO_2 does not usually deviate by more than a few micromoles per mole from that in the atmosphere just above the canopy.

The CO_2 within the intercellular spaces lies at some point along a catena between the leaf surface and the carboxylation sites in the chloroplasts, so that C_i depends upon both the stomatal conductance and the rate of CO_2 assimilation. The general relation between C_i and C_l is as follows:

$$C_i = (C_l(1-\eta)+\phi)/(1+\eta). \tag{1}$$

For dry air, the definition of the parameters η and ϕ is given by equation (1*a*) in table 1, as originally proposed 35 years ago for the concentration of CO_2 within the leaf. Although the concentration of carbon dioxide is uniquely defined with respect to dry air, in practice the concentration varies in relation to the amount of water vapour present in the air, as along this catena (Parkinson 1971). Moreover, the flux of CO_2 through the stomata is affected by the flux of water vapour in transpiration (Jarman 1974). These effects on the estimation of C_i are largely taken into account by equation (1*b*): a somewhat more rigorous treatment leads to equation (1*c*).

TABLE 1. DEFINITION OF THE PARAMETERS IN EQUATION (1)

(The subscripts a, w and c indicate dry air, water vapour and carbon dioxide, respectively; i and l indicate the intercellular spaces close to the mesophyll cell walls and the external leaf surface, respectively. g_w is the water vapour conductance of the pathway from mesophyll cell walls to leaf surface. A is the CO_2 assimilation rate (negative) and E is the transpiration rate (positive). D is a binary molecular diffusivity. In equation (1*c*) $\langle x_a \rangle$ is the average molar fraction of dry air through the stomatal pore and is given by $x_{al}+\Delta w/2$; g_w is given by $-\langle x_a \rangle\ E/\Delta w$; where $\Delta w = x_{wl} - x_w^*$. Where, x is the molar fraction and the superscript * indicates saturation at the appropriate temperature.)

Equation	η	ϕ	Reference
1*a*	zero	$(A/g_w)(D_{wa}/D_{ca})$	Penman & Schofield (1951); Gaastra (1959).
1*b*	$(E/2g_w)(D_{wa}/D_{ca})$	$(A/g_w)(D_{wa}/D_{ca})$	von Caemmerer & Farquhar (1981).
1*c*	$(E/2g_w)(D_{wa}/D_{cw})$	$(A/g_w)\langle x_a \rangle \left[\frac{D_{wa}}{D_{ca}} - \frac{D_{wa}}{D_{cw}}\right] + (D_{wa}/D_{cw})$	Leuning (1983).

The derivation of C_i in this way has been widely used but has recently been called into question by observations of 'patchiness' in the distribution of stomatal apertures on abscisic-acid-treated leaves (Terashima *et al.* 1988). Several studies are now in progress to determine whether 'patchiness' in stomatal conductance is a significant feature of normal leaves because 'patchiness' was not observed in much of the classical work done on stomatal physiology with the microscope during the 1930s to 1960s by Stålfelt and others.

Effects on Rubisco

Experiments with herbaceous plants have shown that an increase in CO_2 concentration leads to a reversible deactivation of Rubisco in a matter of minutes: deactivation may reach 30% after ten minutes, and is readily reversible over the same interval (Sage *et al.* 1988).

Exposure to elevated CO_2 concentrations for days or weeks generally leads to a sustained reduction in the activity of Rubisco of similar magnitude. This may result from a reduction in the amount of Rubisco together with some associated reactivation, or from reductions in both the amount and the activation state (Sage *et al.* 1989).

At the leaf scale, this loss of activity of Rubisco in response to long-term exposure to elevated CO_2 concentration is seen as a reduction in slope of the relation between CO_2 assimilation rate (A) and the mean intercellular space CO_2 concentration (C_i), the so-called A/C_i relation (figure 2). This relation shows that assimilation is a function of the CO_2 concentration around the cells within the leaf mesophyll. In accordance with the biochemistry of photosynthesis, this observed relation is considered to be the resultant of two response functions of assimilation to carbon dioxide that intersect at the arrow (von Caemmerer & Farquhar 1981). At concentrations of CO_2 below the arrow, carboxylation is limited by the activity of Rubisco: above the arrow, carboxylation is limited by the rate of turnover of the photosynthetic carbon reduction cycle (i.e. the Calvin cycle) and hence by the potential rate of electron transport, or by the availability of inorganic phosphorus. Thus the rate of carboxylation (V_c) at any CO_2 concentration is the minimum of the Rubisco-limited rate (W_c) and the electron transport limited rate (W_j); i.e.

$$V_c = \min\,[W_c, W_j].$$

The rate of assimilation of CO_2 is the rate of carboxylation of ribulose bisphosphate less the

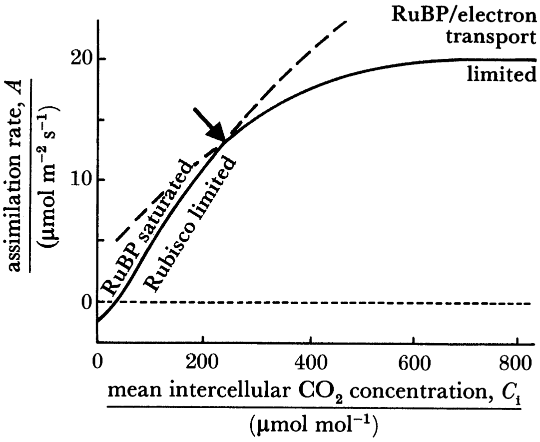


FIGURE 2. The relation between assimilation rate (A) and the mean intercellular space CO_2 concentration (C_i) in needles of *Picea sitchensis* in the following conditions: quantum flux density 1100 μmol m^{-2} s^{-1}, needle temperature 20 °C water vapour saturation deficit 1.0 kPa. The line has been fitted in two sections to 72 data points. The dashed sections are the hypothetical extensions of the two sections of the curve in the model of Farquhar & von Caemmerer (1982).

rates of photorespiration ($V_o/2$) and non-photorespiratory respiration (R_d, the so-called 'day' respiration) i.e.

$$A = V_c - V_o/2 - R_d.$$

Photorespiration proceeds at half the rate of the competitive oxygenation of ribulose bisphosphate (V_o) because one CO_2 molecule is evolved for every two molecules oxygenated. $V_o/2$ is given by $V_c \Gamma_* / C$, where Γ_* is the photorespiratory CO_2 compensation concentration and C is the molar fraction of CO_2 at the site of carboxylation–oxygenation in the chloroplasts. Thus, if C is approximated by C_i, the assimilation rate is

$$A = \min\,[W_c, W_j][1.0 - \Gamma_*/C_i] - R_d. \qquad (2)$$

The parameters Γ_* and R_d can be estimated from A/C_i relations at different quantum flux densities (Brooks & Farquhar 1985).

Expressions for W_c and W_j, and methods of estimation, are discussed by Farquhar & von Caemmerer (1982) and von Caemmerer & Farquhar (1981, 1984). The rate of carboxylation when ribulose-bisphosphate-saturated and Rubisco-limited is

$$W_c = (V_{cm}\,C_i)/(C_i + K_c(1 + O/K_o)), \qquad (3)$$

where K_c and K_o are the Michaelis constants for CO_2 and O_2, respectively; O is the oxygen concentration at the active sites and V_{cm} is the rate of carboxylation at infinite C_i. The term $V_{cm}/[K_c(1 + O/K_o)]$ can be identified with the more familiar mesophyll conductance (g_m). Substituting equation (3) into equation (2) gives the expression for A as a function of C_i, when Rubisco limited. In practice, the parameters in this expression can be found by fitting A to C_i data, particularly if the values of Γ_* and R_d are already known.

The rate of carboxylation when the rate of turnover of the carbon reduction cycle is limited by the rate of potential electron transport (J) is

$$W_j = J/4(1 + 2\Gamma_*/C_i). \qquad (4)$$

The 4 appears because approximately four electrons are required for each carboxylation and oxygenation. J is expressed as a function of the absorbed, effective quantum flux density (Q) per photosystem, i.e.

$$J^2 + (J_m + Q/2)\,J + J_m Q/2 = 0. \tag{5}$$

Substitution of equations (4) and (5) into equation (2) gives the expression for A as a function of C_i and Q, when limited by the potential rate of electron transport. At the arrow, assimilation is co-limited by both sets of processes (i.e. $(V_c - W_c)(V_c - W_j) = 0$) and there is evidence to show that the balance of investment between the two adjusts, (see, for example, von Caemmerer & Farquhar 1984) so that assimilation is in the co-limited region at the prevailing ambient CO_2 concentration.

As shown in figure 3, young trees grown at double the current atmospheric CO_2 concentration show a reduction in slope of the A/C_i curve below the arrow and hence an implied loss in activity of Rubisco. A range of stresses, nitrogen deficiency for example, also cause a reduction in this slope and in Rubisco activity. One may suppose that the amount of Rubisco is reduced in plants growing at high CO_2 concentration, because amounts of carbon commensurate with the availability of other resources, such as nitrogen, can be assimilated by a lesser amount of Rubisco and the nitrogen can therefore be more effectively utilized in proteins other than Rubisco. One consequence is that plants that have become acclimated to high CO_2 concentrations show a reduced rate of assimilation, in comparison with plants kept at the current CO_2 concentration, when returned to the current CO_2 concentration.

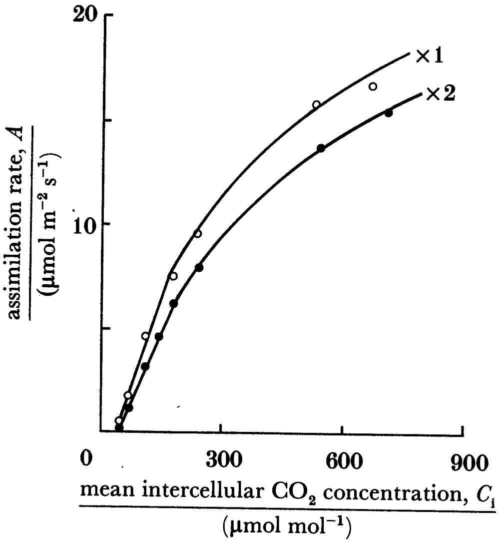


FIGURE 3. The average relation between assimilation rate (A) and the mean intercellular space CO_2 concentration (C_i) for shoots of *Picea sitchensis* developed and grown on plants that were three months in current (×1) ($n = 5$) and double the current (×2) ($n = 5$) atmospheric CO_2 concentration. The slopes of the linear sections of the curves are 0.061 and 0.051 mol m^{-2} s^{-1} for ×1 and ×2 CO_2, respectively. Measurement conditions were: leaf temperature 20 °C, saturation deficit 0.6 kPa and quantum flux density 1200 μmol m^{-2} s^{-1}. Unpublished data of A. J. Brenner, A. P. Sandford and P. G. Jarvis.

Sink strength

A reduction in the relation of the A/C_i slope has been observed, particularly after long-term exposure to plants to high CO_2 concentrations, especially at high quantum flux densities, in several experiments with crop plants and in one or two with tree seedlings (Eamus & Jarvis

1989). In some cases quantum yield has also been reduced and substantial starch accumulation in the chloroplasts demonstrated. It seems likely that these are not acclimation responses to elevated CO_2 but indicate the lack of adequate sinks for assimilate. In rapidly growing or fruiting citrus, where growing active sinks were available, assimilation was maintained at high rates in high ambient CO_2 concentrations and Rubisco did not decline in activity (Koch *et al.* 1986; Downton *et al.* 1987). The maintenance of high rates of assimilation in response to elevated CO_2 concentration appears to require the existence of sustained active sinks for carbon and these did not occur in many of the experiments made on young trees in small pots.

Photorespiration

Carbon dioxide and oxygen compete for the same active sites on Rubisco. When O_2 is the substrate, carbon previously fixed into ribulose bisphosphate is channelled into the photorespiratory carbon oxidation cycle (i.e. the glycolate pathway) with the subsequent release of CO_2 in photorespiration. Photorespiration represents a significant loss of previously fixed carbon. An increase in ambient CO_2 concentration increases the rate of supply of CO_2 to the active sites and shifts the balance towards carboxylation rather than oxygenation, leading to a reduction in photorespiration. This both conserves carbon and leads to enhanced availability of NADPH and ATP, which would otherwise be used in the glycolate pathway, and hence represents an increase in the efficiency of carbon fixation.

A result of the partial suppression of photorespiration by elevated CO_2 concentration is an increase in the quantum yield of CO_2 assimilation (i.e. in the slope of the relation between assimilation rate and quantum flux density) and a reduction in the compensation quantum flux density, leading to the more efficient use of light by shaded leaves (Pearcy & Björkman 1983).

Stomatal conductance

In general, stomatal conductance declines in relation to an increase in ambient CO_2 concentration over a few minutes, but there is little information to discriminate between this short-term response and any long-term physiological acclimation. Reduction in the number of stomata per unit area of leaf has been observed in one tree species after 123 days at elevated CO_2 concentration but not in another (Oberbauer *et al.* 1985), and Woodward (1987) claims to have detected a reduction in stomatal density of eight tree or shrub species near Cambridge over the past 200 years by making comparisons with herbarium specimens. Whether the latter is the result of developmental acclimation or genetic adaptation is, however, unclear.

Stomatal sensitivity to ambient CO_2 (figure 4) shows wide variation in tree seedlings. In general, conifers are less sensitive to CO_2 than broadleaves, but sensitivity varies with light, temperature and water stress and, in some cases, may have been induced inadvertently by the application of stress (Eamus & Jarvis 1989).

Stomata sense the CO_2 concentration in the intercellular spaces rather than in the ambient air (Mott 1988) and as a result, stomatal conductance is affected by both the rate of assimilation, because it influences C_i, and by the ambient CO_2 concentration. However, stomata also respond independently of assimilation to other variables such as quantum flux density and water-vapour saturation deficit, with the result that at normal ambient CO_2 concentrations, a change in stomatal aperture leads to a change in C_i, whereas a change in C_i, as a result of a change in the rate of assimilation, has a rather smaller effect on stomatal

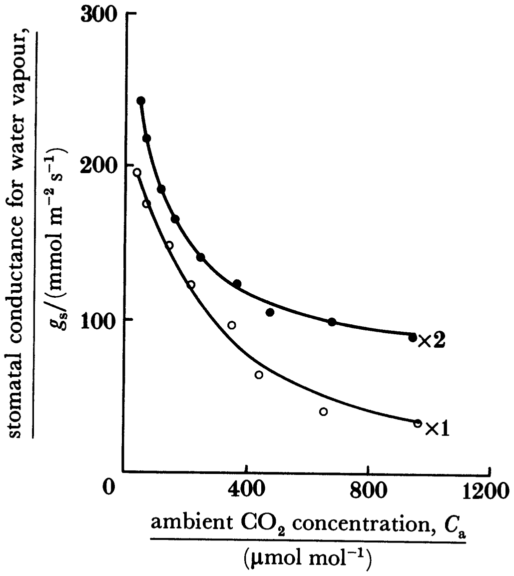


FIGURE 4. The average relation between stomatal conductance for water vapour (g_s) and the ambient CO_2 concentration for leaves of *Betula pendula* on plants grown for two months in current (×1) ($n = 7$) and double the current (×2) ($n = 4$) atmospheric CO_2 concentration. Measurement conditions as in figure 3. Unpublished data of A. P. Sandford, A. J. Brenner and P. G. Jarvis.

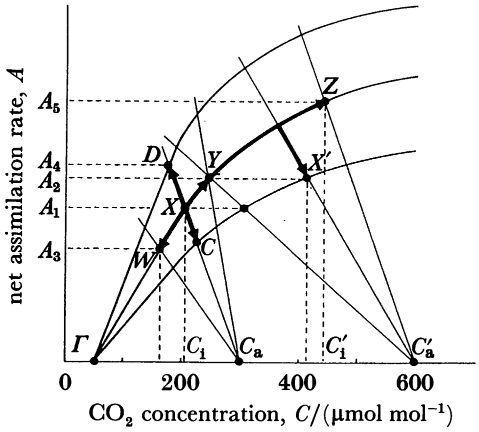
conductance (Jarvis & Morison 1981). Thus, at elevated ambient CO_2 concentrations, C_i does not rise as much as would be expected if the stomata did not close and, consequently, the increase in assimilation rate is less than might have been anticipated.

The combined effects of a reduction in stomatal conductance and a reduction in Rubisco activity lead to a smaller increase in assimilation rate in response to an increase in ambient CO_2 concentration in acclimated leaves than would be expected from a consideration of unacclimated leaves with unresponsive stomata at the present day CO_2 concentration (figure 5).

Water use efficiency

An increase in CO_2 concentration increases the rate of assimilation and decreases the stomatal conductance. In leaves well coupled to the atmosphere, a reduction in stomatal conductance leads to a near proportional reduction in transpiration rate (Jarvis & McNaughton 1986). Thus, in growth chambers and assimilation chambers or cuvettes, a rise in CO_2 concentration leads to an increase in water use efficiency (moles of CO_2 assimilated per moles of water transpired) on both counts. Even in species in which stomatal conductance changes little, there is still an increase in water-use efficiency on account of the increase in assimilation.

This is generally true for trees in the field because both individual trees and stands of trees are generally extremely well coupled to the atmosphere. The only major exceptions are seedlings and young trees in a dense understorey or with a multi-layered canopy above. In the understorey of moist tropical forest, for example, CO_2 concentrations are high (500–1000 μmol mol^{-1}) even today, on account of the respiration of soil, litter and wood (see, for example, Medina *et al.* 1986), and water-vapour saturation deficits are very small, relative to the atmosphere above (Shuttleworth *et al.* 1985). In these circumstances, assimilation by seedlings



to show the possible consequences of an increase in ambient CO_2 concentration for assimilation rate, taking into account likely effects on stomatal conductance. The line ΓZ is an A/C_i function as in figure 2. The line $C_a D$ depicts the stomatal conductance that intersects at point X to give the assimilation rate A_1. If the stomata open or close somewhat the intersection moves to Y or W giving the new assimilation rates of A_2 or A_3, respectively. If Rubisco activity increases or decreases then assimilation moves onto the lines ΓD or ΓC, respectively, with higher (A_4) or lower assimilation rates. A rise in the ambient CO_2 concentration to 600 µmol mol^{-1} with no change in Rubisco activity or stomatal conductance would increase the assimilation rate to A_5. Reductions in both could bring the assimilation rate back to A_1, or anywhere within the area defined by $C_a'Y$, $C_a'Z$ and YZ.

is enhanced by the high CO_2 concentration, although strongly light-limited for much of the time (Kwesiga *et al.* 1986), and transpiration is very insensitive to changes in either stomatal conductance or saturation deficit, and is small except when the sun penetrates to the forest floor (Jarvis & McNaughton 1986).

Carbon dioxide at the stand and forest scales

For practical reasons, direct measurements of the effects of a controlled increase in CO_2 concentration on processes in forest stands are extremely difficult, if not impossible, to make; as yet there are no directly measured data and little likelihood of any in the immediate future. Thus, at the present time, the likely effects of an increase in CO_2 concentration can only be estimated through the use of models from measurements of processes and variables made on unacclimated stands at present day CO_2 concentrations, and from measurements on seedlings and young trees acclimated to increased CO_2 concentrations in artificial surroundings.

Measurements have been made of the exchanges of water vapour and carbon dioxide by a range of plantation and woodland canopies in current atmospheric conditions (Jarvis *et al.* 1976; Jarvis 1986; Verma *et al.* 1986; Baldocchi *et al.* 1987) and these data can be used to test models of the influence of environmental and stand variables on the carbon dioxide balance and water use efficiency of stands. Several suitable models for this purpose exist. One, codenamed MAESTRO (Grace *et al.* 1987; Wang 1988), is straightforward to run for an existing crown structure, stand structure and set of environmental conditions and can indicate answers to the question: what would be the consequences for the assimilation, transpiration and water use efficiency of a stand of a doubling of the ambient atmospheric CO_2 concentration?

In attempting to answer this question, it is difficult to know what aspects of acclimation to increased CO_2 concentration to take into account. It is clear from the preceding section that acclimation of the photosynthetic and stomatal parameters at the leaf scale should be considered, but it is far from clear at present what other features of tree or stand structure and processes, such as the distribution of leaf area density, rates of soil respiration and decomposition processes, etc. may also be subject to acclimation. In figure 6, CO_2 assimilation by the canopy of a stand of *Picea sitchensis* at the current ambient CO_2 concentration, calculated using appropriate leaf parameters in an assimilation sub-model based on that of von Caemmerer & Farquhar (1981), is compared with estimates of canopy assimilation in an atmosphere of double the current CO_2 concentration, again using appropriate parameters. The parameters used were determined for seedlings grown in controlled environment rooms at current and twice the current ambient CO_2 concentrations so that the simulation compares current CO_2 concentration with current tree parameters against doubled CO_2 concentration with appropriately changed parameters. The use of parameters measured on seedlings acclimated in controlled environment rooms, although convenient, must be regarded as suspect. An alternative currently being tried in pollution studies with *Pinus taeda* (R. O. Teskey & P. H. Dougherty, personal communication), would be to expose whole branches of mature trees to different CO_2 concentrations in chambers, *in situ* in the canopy, for one or more growing seasons, and to measure parameters on the foliage, which is likely to be at least partly acclimated and also rather more appropriate in other respects.

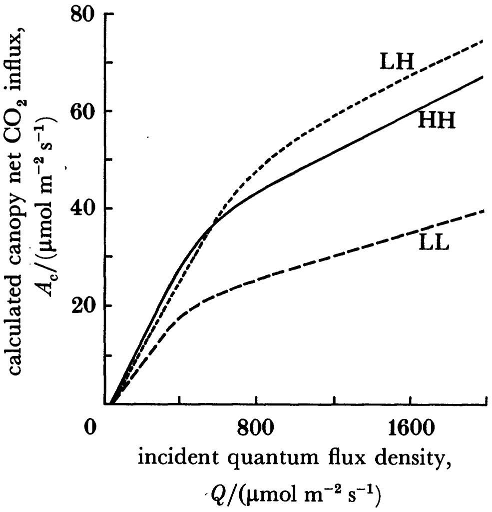


FIGURE 6. The relation between the total net CO_2 influx to a stand of *Picea sitchensis* calculated by using the canopy model MAESTRO with appropriate parameters in the CO_2 and water-vapour exchange routines for the current atmospheric CO_2 concentration (L–L) and double the current atmospheric CO_2 concentration (H–H). The line L–H shows the result if parameters for the current atmospheric composition are used with a doubling in the atmospheric CO_2 concentrations. The solar beam fraction was assumed to be 0.5, the leaf area index 9.0, the solar zenith angle 45°, the air temperature 20 °C and the water vapour saturation deficit 1.0 kPa.

Figure 6 shows that canopy assimilation is likely to be increased by a doubling of the atmospheric CO_2 concentration, but not as much as would be expected if the parameters for the unacclimated trees were used in the calculations for double the atmospheric CO_2 concentration. Changing the parameter set or the CO_2 concentration did not have a large effect on the degree of co-limitation within the canopy, indicating that it is the influence of crown structure on light interception, particularly the area of leaves and the distribution of leaf area density, that ensures that the majority of the leaves operate in the co-limited region.

Such predictions cannot be verified directly but depend for their acceptance on adequate verification of the model against measurements of canopy functioning in the current

CO_2 environment with respect to other variables. MAESTRO, for example, has been shown to predict accurately the radiation environment beneath the canopy of stands of *Pinus radiata* and *P. sitchensis* (Wang 1988), and consequently may be applied with some degree of confidence.

Experiments on seedlings have shown that a doubling of the ambient CO_2 concentration may compensate to a degree for a reduction in the quantum flux density (see, for example, Tolley & Strain 1984). If an increase in atmospheric CO_2 concentration compensates for shading of the lower leaves in the canopy and thereby reduces leaf senescence, the sustainable leaf area will be increased, more radiation will be absorbed, and there may be a further increase in CO_2 assimilation and growth. That the growth of forest may increase in relation to the increase in CO_2 concentration, as a result of increases in both the assimilation flux density and the leaf area concentration, seems likely but is speculative.

At the stand scale, we must necessarily also be concerned about the consequences of an increase in CO_2 concentration on mineralization processes in the soil and on nutrient cycling through the system because these processes may ultimately limit the extent to which photosynthetic efficiency can be increased or leaf populations maintained. Similarly, an increase in stand leaf area will lead to an increase in both the amount of precipitation intercepted by the canopy and evaporated directly to the atmosphere and the transpiration loss of water (Jarvis & McNaughton 1986), so that the availability of water may act to limit the projected increase in growth resulting from the increase in CO_2 concentration. This point is further complicated because there may be increases in both water use efficiency and in leaf area per tree, with opposing effects upon total tree water use. More complex models of stand processes are required to take these possible feedbacks into account.

Effects of forests on atmospheric CO_2

Forests accumulate large amounts of carbon in woody branches, stems and litter. The standing crop of dry matter may typically vary from 100–500 t ha^{-1}†. A stand of 320 t ha^{-1} of dry matter of typical composition will have taken up approximately twice that amount of CO_2 during its period of growth, thus reducing the content of the atmosphere by that amount.

Measurements of the net CO_2 flux made about the canopy show that during the growing season, net assimilation of CO_2 from the atmosphere by forest reaches a maximum during the course of the day of around 20 (±10) μmol m^{-2} s^{-1} (figure 7), whereas losses of CO_2 by respiration from the stand at night may range from about 10% of the daytime fluxes in young stands to 50% in old growth stands that have a net exchange of zero over 24 h (Jarvis *et al.* 1976; Jarvis 1986, 1987; Verma *et al.* 1986; Baldocchi *et al.* 1987). High temperatures and low humidities reduce the CO_2 influx by increasing stand respiration and decreasing canopy conductance, (figure 8), and water stress causes a similar reduction. The daily course of net CO_2 assimilation from the atmosphere by agricultural crops and many other kinds of vegetation falls within the same range of values.

On a regional scale, the effect of these rates of uptake on the atmospheric CO_2 concentration can be estimated from a CO_2 mass balance of the convective boundary layer (CBL). Stable conditions overnight often result in high concentrations of CO_2 of 400–600 μmol mol^{-1} in the

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† 1 hectare (ha) = 10^4 m^2.

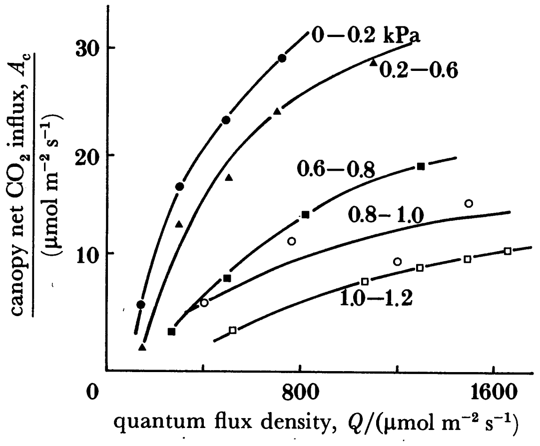

Figure 7. The relation between the net CO_2 influx from above to a stand of *Picea sitchensis* (A_c) and the incident quantum flux density (Q). The data shown were classified with respect to the water vapour saturation deficit of the air, which is strongly correlated with air temperature. Each point is the median of 6–20 mean hourly measurements. Adapted from Jarvis *et al.* (1976).

surface layer close to the vegetation. As the sun rises and fluxes of heat, water vapour and CO_2 are generated at the surface, the overnight inversion disperses and the CO_2 concentration in the CBL is reduced by the vegetation. If we assume, for simplicity, an average daytime CO_2 flux density of 10 μmol m^{-2} s^{-1}, the total daytime influx will be of the order of 450 mmol m^{-2}. As the day develops, in unstable conditions the CBL may grow from a few metres to hundreds of metres in depth, driven by the fluxes of heat and water vapour at the surface (see André, this symposium). Thus, as CO_2 is removed by the vegetation, entrainment through the capping inversion at the top of the CBL adds warmer, drier air containing CO_2 at the current seasonal atmospheric concentration (McNaughton 1989). If the CBL grows during the day to a depth of 1000 m, from which a total of 450 mmol m^{-2} CO_2 are removed, the average daytime reduction in CO_2 concentration throughout the CBL will be 10 μmol mol^{-1}. The concentration will be uniform throughout the mixed layer but there will be a substantial vertical gradient in the surface layer so that the maximum daytime reduction of the CO_2 concentration near the leaf surfaces within the vegetation may be up to ten times as large, or 100 μmol mol^{-1}, depending on the degree of coupling of the vegetation to the atmosphere (Jarvis 1985). This drawdown in the CO_2 concentration by vegetation is usually measured relative to the atmospheric concentration at a reference level just a few metres above the vegetation surface and, does not take into account the reduction in concentration across the surface layer above or throughout the mixed layer, and hence is generally considerably underestimated (McNaughton & Jarvis 1983). Thus, on a regional scale, there is frequently a substantial daily oscillation in the CO_2 concentration from, say, 500 μmol mol^{-1} in stable conditions at night to 300 μmol mol^{-1} in unstable conditions during the daytime close to the leaf surfaces, and correspondingly smaller oscillations occur some distance above the vegetation.

Measurements of CO_2 influx to forest stands are few and restricted to short periods of a number of days during the main part of the growing season, usually in better than average weather. There are insufficient measurements of this kind from even one site to enable computation of seasonal fluxes. Estimates of seasonal changes in CO_2 flux on a regional scale must, of necessity therefore, be made using much coarser methods. Recently, Fung *et al.* (1987)

have partitioned estimates of soil respiration and net stand CO_2 assimilation month by month on the basis of seasonal variation in the normalized difference vegetation index (NDVI) determined by remote sensing for 32 different vegetation types in 4° × 5° grid boxes, to obtain the seasonal exchanges of CO_2 shown in figure 8. Over the seasons, assimilation and respiration of temperate and boreal evergreen forest generally follow temperature synchronously so that there is scarcely any period of net carbon loss (figure 8*d*). Young trees of spruce and pine in Norway and Scotland, for example, have a positive net carbon balance in every month of the year on average (Hagem 1947, 1962; Bradbury & Malcolm 1978). For deciduous forest, on the other hand, substantial asynchrony occurs in the spring and autumn, particularly the former when stand respiration may substantially exceed assimilation, and this can lead to significant periods of considerable net carbon loss (figure 8*c*). By contrast, in the tropics, where seasonal variation in environmental variables is generally small, there is little seasonal variation in either assimilation or respiration rates so that the net flux of CO_2 also shows little seasonal variation, and in climax forest, where the fluxes of respiration and assimilation are approximately equal, little departure from zero (figure 8*a*).

This comparison shows the way in which seasonal variation in assimilation and respiration is likely to lead to an annual oscillation in the regional net CO_2 flux between atmosphere and vegetation. The seasonality of temperature and radiation in particular, generates the oscillation and this is exaggerated by asynchrony between respiration and assimilation, largely resulting from the phenology of leaf growth.

The amplitude of the measured oscillations in atmospheric CO_2 concentration is small near the Equator and in the Southern Hemisphere, but increases to about 17 μmol mol^{-1} at latitude of *ca.* 75° N (figure 8) (Komhyr *et al.* 1985). By combining the seasonal CO_2 fluxes of the different vegetation types with a three-dimensional tracer model, Fung *et al.* (1987) made predictions of the seasonal oscillations in the atmospheric CO_2 concentration as a function of latitude. Figure 9 shows that the model of seasonal CO_2 influx and efflux by different kinds of vegetation also predicts the change in amplitude of the annual CO_2 oscillation with latitude quite adequately (Fung *et al.* 1987). The increase in amplitude of the oscillation at high latitudes can be attributed to the more extensive areas of vegetation in the Northern Hemisphere as compared with the Southern Hemisphere, associated with large seasonal variations in day length, quantum flux density and temperature, together with seasonal changes in the standing crop of the vegetation and a degree of asynchrony between respiration and assimilation (Fung *et al.* 1987).

A large part of the oscillation can be attributed to the northern, temperate and boreal forest. Figure 10 shows that at Point Barrow (71° N) approximately 50% of the oscillation can be attributed to the boreal forest, whereas at Mauna Loa (20° N) the boreal forest may account for about 30% of the total amplitude (D'Arrigo *et al.* 1987). These calculations suggest that the CO_2 dynamics of forest in the Northern Hemisphere have a major role in determining the annual seasonal oscillation in atmospheric CO_2 concentration. Unfortunately, however, there is no means of determining whether the estimated fluxes used in the calculations are appropriate, because at present there are no appropriate field measurements being made of the net CO_2 exchange of forests or other areas of vegetation.

Since 1976, the amplitude of the CO_2 concentration oscillation in the Northern Hemisphere has increased by about 10%, or close to 1% per annum. The oscillation at Mauna Loa has, for example, increased from 6.0 μmol mol^{-1} in 1976 to 6.6 μmol mol^{-1} in 1986, an increase in

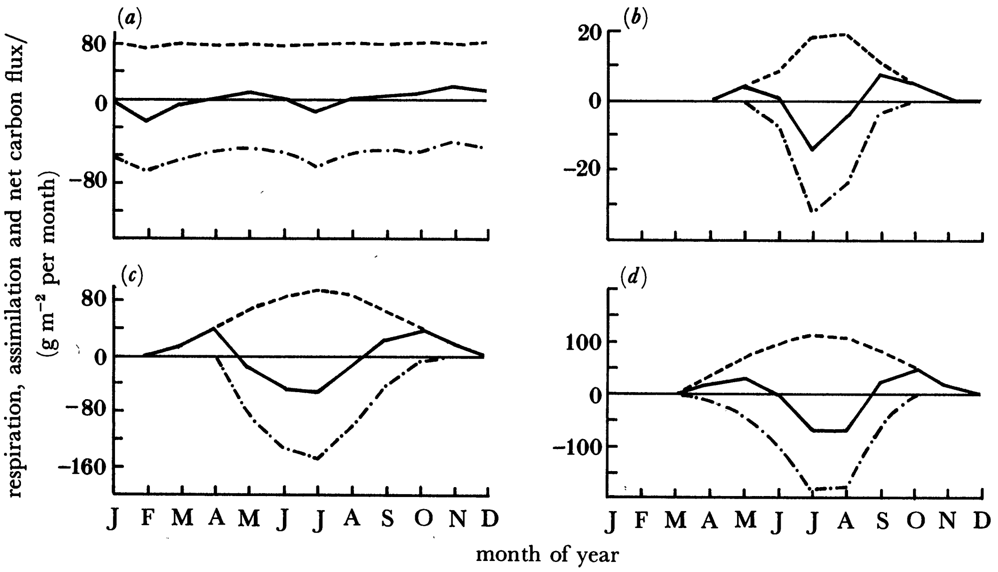

FIGURE 8. Examples of monthly fluxes of carbon (grams per square metre per month), using an exponential relation to describe the dependence of CO_2 assimilation on the remotely sensed NDVI for: (*a*) tropical rainforests, 6° S, 60° W; (*b*) tundra, 70° N, 160° W; (*c*) deciduous forests, 54° N, 35° E; and (*d*) evergreen forests, 54° N, 95° W. Respiration (positive is shown by (---), assimilation (negative) by (-.-.-.) and the net carbon flux by (——). From Fung *et al.* (1987).

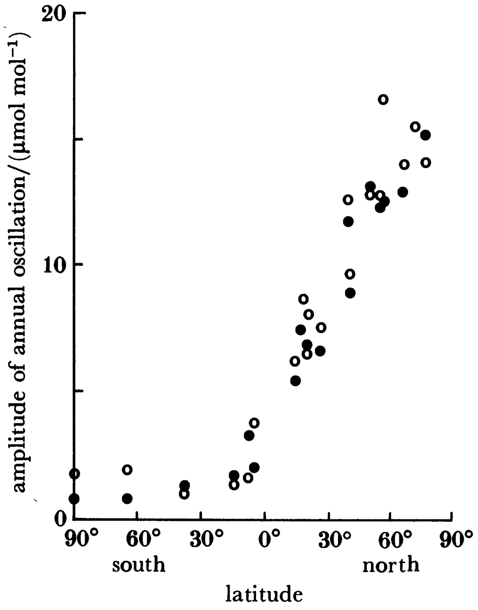

FIGURE 9. A comparison between the measured (○) and calculated (●) peak-to-peak amplitudes of the annual CO_2 oscillation at the earth's surface in relation to latitude by using data like that in figure 8 for 4° latitude × 5° longitude model grid boxes. From Fung *et al.* (1987).

amplitude equivalent to 0.8 Gt ha^{-1} of carbon since 1976 (Revelle & Kohlmaier 1986). In the years just before 1976 there was a hiatus in the atmospheric CO_2 concentration record as a result of the oil crisis, and there is less evidence for such an increase in amplitude in the period preceding the oil crisis in 1973. Over the 23 years 1961–1984, there has been an average increase of 0.8 % per year at Mauna Loa and 1.1 % per year at Point Barrow (G. H. Kohlmair,

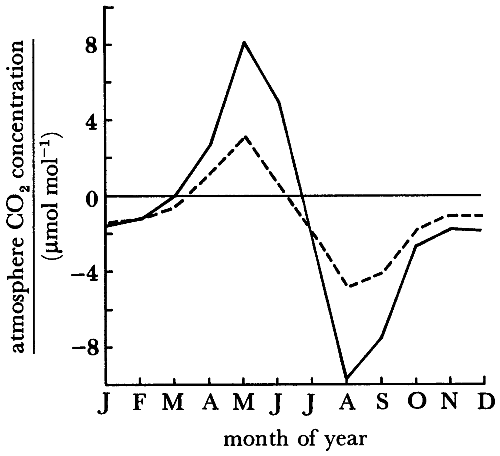

FIGURE 10. The calculated annual oscillation of atmospheric CO$_2$ at Point Barrow Alaska (71° N, 157° W) including (——) and excluding (---) the temperate and boreal forests. From D'Arrigo *et al.* (1987).

R. Revelle and C. D. Keeling, unpublished report 1985). The reason for this increase in amplitude over the past ten years is at present unclear, but on the basis of the above demonstration of the involvement of boreal forest, we may suppose that an increase in amplitude does reflect an increase in the rate of assimilation by the temperate and boreal forest.

An increase in the annual oscillation of 1 % represents a fluctuation in the amount of CO$_2$ in the atmosphere that is equivalent very approximately to an increase in 1 % of the annual net productivity of the temperate and boreal forests. Thus a small increase in forest productivity could be sufficient to account for the increase in the oscillation.

An increase in assimilation by these forests could result from one or more of the consequences of the rise in atmospheric CO$_2$ concentration. It could, for example, result from the rise in CO$_2$ concentration itself leading to an increased rate of assimilation at the leaf scale. Allowing for a CO$_2$ compensation concentration of the forest of about 150 μmol mol^{-1} (Jarvis 1985), an increase in ambient CO$_2$ concentration of 15 μmol mol^{-1} could be expected to lead to a 7 % increase in the rate of assimilation. This fertilizing effect of CO$_2$ might also be supplemented by the addition of significant amounts of nitrogen in the precipitation (10–20 kg ha^{-1} per year) as a result of the global increases in pollution, and both effects may lead to long-term increases in leaf area of the vegetation. There is some evidence for increase in leaf area in the recent measurements of NDVI but the record only goes back eight years and consistent calibration over the period is a problem. A global increase of temperature over the past 10 years of 0.25 °C, as demonstrated by Jones *et al.* (1988), could also be expected to increase assimilation by a small percentage, and although respiration would also be increased, a degree of asynchrony between the two would lead to an increase in amplitude of the oscillation.

If the atmospheric CO$_2$ concentration is so sensitive to the physiological activities of vegetation, particularly forest, proper consideration must be given to the possible role of vegetation in ameliorating the rise in atmospheric CO$_2$ concentration. A forest accumulating dry matter of average composition with respect to fats, proteins, carbohydrates and lignin at a rate of 5 tonne ha^{-1} per year, the approximate average for the U.K. (Jarvis 1981), would assimilate CO$_2$ at a rate of *ca.* 10 tonne ha^{-1} per year (Jarvis & Leverenz 1983), removing carbon from the atmosphere at 2.7 t ha^{-1} per year. Consequently, an area of such forest of 2 Gha would be able to assimilate the 5–6 Gt per year of carbon currently being added to the global atmosphere annually by the burning of fossil fuels and the possible oxidation of soil and wood organic matter. The approximate area of Europe is 1 Gha (10×10^6 km^2). Thus a new, young, actively growing forest twice the area of Europe, could, in principle, assimilate all of the CO_2 produced through combustion and oxidation at the present rate. This could not, however, proceed indefinitely.

If the eventual standing crop of dry matter reached 400 t ha^{-1} (218 t ha^{-1} of carbon), such a 2 Gha forest would be able to absorb 5–6 Gt per year of carbon for *ca.* 80 years. As a forest approaches maturity, however, the annual respiration increases, so that eventually a steady-state is achieved, the total standing crop becomes constant and there is no further increase in the amount of CO_2 being sequestered each year. If the forest is left unmanaged, the trees will eventually die at different times and be replaced naturally: assimilation of CO_2 and its oxidation will go on at the same annual rate, and there will be no further net gain of CO_2 to the forest or net exchange with the atmosphere. Thus, every 80 years or so, it would be necessary to establish an additional new forest twice the size of Europe. This is clearly an untenable projection.

Alternatively, if the forest is managed so that as the trees mature they are harvested and replanting occurs, the total biomass over the area will remain constant, but the forest will be growing all the time. This prospect carries with it the corollary that the timber produced must not, on any account, be oxidized and that means that it must be utilized in some way so that the risk of it burning is negligible. Most of the wood products in our society are of relatively recent origin, wood harvested more than 300 years ago mostly having burned or decayed. It seems unlikely that large, annual crops of timber could be treated or stored in such a way that there was absolutely no risk of their combustion. One possible location to store them might be the bottom of the sea: another might be to put them in the coal mines! In either case, no additional energy should be consumed in the process, as this would further exacerbate the increase in atmospheric CO_2 concentration!

CONCLUSIONS

A doubling of the present atmospheric CO_2 concentration is likely to occur by the end of the next century and will have many effects on trees and forests.

The role of CO_2 as a substrate in photosynthesis has been extensively investigated and is well understood at the cellular scale, but the details of its action as an activator and regulator of Rubisco are only being elucidated at present.

Many measurements at the leaf scale of CO_2 assimilation in relation to ambient CO_2 concentration show a marked stimulation of CO_2 uptake, but few such measurements have been made on fully acclimated plants or trees. There are useful biochemically based models of CO_2 assimilation at the leaf scale, but there is little information on which to base parametrization of these models for fully acclimated leaves. Because CO_2 regulates stomatal aperture to some extent many observations have been made of the effects of raising the ambient CO_2 concentration on stomatal conductance. The results are very variable and in some trees, particularly conifers, stomatal conductance seems rather unresponsive to changes in ambient CO_2 concentration. However, lack of a mechanistic model of stomatal action makes explanation difficult. The possible role of CO_2 in regulating other physiological processes such as leaf growth is unexplored.

There have been several experiments to investigate the effects of increase in atmospheric CO_2 on the growth of seedlings and young trees. The results are very varied in magnitude of response and the experiments generally suffer from several inadequacies. In particular, the experiments are virtually all short term (less than twelve months) on very young trees that are often pot-bound, with growth restricted by the lack of active sinks and in nutrient-deficient condition. There is a considerable need for long-term experiments in which growth is not artificially restricted by unsuitable, experimental conditions.

The experimental approach is not practicable with much older trees, stands and forests. The effects of CO_2 on processes at the stand scale can only be assessed through models. Adequate models of water vapour and CO_2 exchange exist at the canopy scale and can be used to demonstrate the likely effects of an increase in atmospheric CO_2 concentration on canopy processes. However, models of stand processes taking into account feedbacks within the stand, such as the interactions between leaf composition and rates of decomposition, are not available. At the larger scales of forest and region, a very complex network of processes requires to be taken into consideration and there is quite insufficient information about the effects of CO_2 on these processes to permit reasonable predictions.

An alternative approach is to look at the effects of forests on the atmosphere and hence to deduce whether the atmosphere may also be affecting the forests. The amplitude of the seasonal oscillation in atmospheric CO_2 concentration is increasing and seems to indicate that the temperate and boreal forests are an increasingly large sink for atmospheric CO_2. However, the concentration of CO_2 in the atmosphere continues to rise at a rapid rate and it seems unlikely that the area of global forests could be expanded sufficiently to have a significant impact on the rise in atmospheric CO_2 concentration.

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Discussion

J. I. L. Morison (*Department of Meteorology, University of Reading, U.K.*). Commenting on the increased amplitude of the seasonal cycle of global CO_2 concentration observed in recent years Professor Jarvis has attributed this speculatively to the direct effect of CO_2 on biosphere fixation rates or to the increased nitrogen inputs mentioned by D. Fowler (this symposium). Equally, it should be recognized that climatic changes already occurring could introduce asymmetry into the CO_2 fixation and production of the biosphere. For example, workers at the Climate Research Unit at the University of East Anglia have identified that recent years have been warmer.

P. G. Jarvis. I agree that it is quite likely that the reported rise in temperature by Jones *et al.* (1988) of *ca.* 0.25 °C over the past eight years could well contribute towards the increase in amplitude of the seasonal CO_2 oscillation.

W. G. Chaloner, F.R.S. (*Department of Biology, Royal Holloway & Bedford New College, Surrey, U.K.*). Professor Jarvis has commented on the problem of time-scale in assessing the capacity of plants to adjust or acclimate to a raised level of CO_2. I invite him to consider what kinds of *adaptation* might occur if elevated CO_2 levels prevailed long enough to select, as it were, ecotypes particular to that environment. One might speculate that higher CO_2 might favour a lower stomatal index in a given plant population. Might this in turn give marginally higher water-stress tolerance? I only raise this to question whether acclimation experiments give an adequate picture of what long-term changes might bring about.

P. G. Jarvis. There have been only three acclimation experiments with young trees lasting more than 12 months that I am aware of, and all three have been unsatisfactory because the plants became pot-bound or suffered heat stress. I agree with the implication of Professor Chaloner's question that short periods of acclimation of a few months may give a very inadequate guide to long-term acclimation and eventual adaptation. In a recent report on this subject Dr Derek Eamus and I referred to the plants in all the experiments done so far as *acclimating* rather than acclimated and in none of the experiments does the question of adaptation arise.

M. G. R. Cannell (*Institute of Terrestrial Ecology, Edinburgh, U.K.*). Does elevated CO_2 decrease the activity of Rubisco – its affinity for CO_2 – or does the plant produce less Rubisco? How does nutrition affect the negative impact of elevated CO_2 on Rubisco activity?

P. G. Jarvis. There are only a few studies in which long-term effects of a doubling of ambient CO_2 concentration on Rubisco have been investigated, and none on trees that I am aware of. Some recent investigations by Rowan Sage (Sage *et al.* 1989) on herbaceous plants show that several of the above alternatives may occur in various combinations, for example a reduction in amount of Rubisco with either an increase, a decrease or no change in activation state. I know of no experiments in which Rubisco activity has been related to elevated CO_2 in combination with different rates of supply of nutrients.

J. Roberts (*Institute of Hydrology, Wallingford, U.K.*). I should like to raise another issue with respect to plants adapting to high CO_2 environments. Do not seedlings, understorey plants and young saplings in any case grow in high CO_2 conditions that occur at the forest floor?

P. G. Jarvis. Yes, this is certainly true in tropical forest. Close to the forest floor (i.e. within a centimetre or two) in both temperate and tropical forest, the CO_2 concentration is several thousand micromoles per mole and within the litter the concentration may be much higher. In temperate forest, the concentration falls steeply with height above the ground because of the quite good coupling to the atmosphere above, so that seedlings are not really growing in a CO_2-enriched atmosphere during the daytime. (In stable conditions at night the concentration is very much higher throughout the stand volume.) However, in multi-storeyed, tropical forest the air near the ground is very poorly coupled to the atmosphere above and, as Ernesto Medina has shown, seedlings grow in an atmosphere of increased CO_2 for most of the time. This CO_2 comes from the decomposition of organic matter, much of it from the canopy above and thus represents an internal recycling that leads to large $\delta^{13}C$ values in the seedlings such as $-40\,\%$ (Medina *et al.* 1986).

H. G. JONES (*AFRC Institute of Horticultural Research, Wellesbourne, U.K.*). Professor Jarvis mentioned the difficulty of using information from experiments where CO_2 concentrations are only altered for short periods for the prediction of vegetation responses to altered atmospheric CO_2 concentrations. In particular, he concentrated on acclimation of the photosynthetic system, but can he comment on the importance of other possible developmental responses to CO_2 such as altered leaf area and altered phenology?

P. G. JARVIS. Dr Jones has touched here on an important and as yet unresolved scientific question. There is no doubt that leaf area is enhanced in many experiments in which the ambient CO_2 has been doubled and a 'direct' effect of CO_2 on leaf growth has been postulated more than once. It is very difficult to tell from experiments done so far whether an increase in leaf area is purely and simply the result of an enhanced supply of substrate resulting from a higher rate of photosynthesis, or whether there are actually direct morphogenetic effects of CO_2 on the rate and duration of leaf production, number of cell divisions, and size of cells in the leaves, etc. Suitable experiments to discriminate between these two possibilities have not, so far as I am aware, been done.

There is abundant evidence, however, that increase in the ambient CO_2 concentration does increase the root:shoot ratio if not accompanied by an increase in rate of nitrogen supply. This is compatible with current models of assimilate partitioning in plants that relate alteration to root and shoot to the relative rates of supply of carbon to the leaves and nitrogen to the roots. An increase in the rate of supply of carbon for photosynthesis has effectively the same result as a decrease in the rate of supply of nitrogen to the roots.

R. AMTMANN (*German Military Geophysical Office, Mont Royal, F.R.G.*). Looking at the Mauna Loa time series, some scientists suggest that the most prominent relative peaks of this time series can be explained by the El Niño/Southern Oscillation phenomenon. Does Professor Jarvis think that it is necessary to take this phenomenon into account or is it possible to explain the occurrence of these major peaks by the natural variability in the photosynthetic activity of the global forests alone?

P. G. JARVIS. I am unable to give an adequate reply to this question.