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THE IMPACT OF ELEVATED CARBON DIOXIDE LEVELS ON MARINE AND COASTAL ECOSYSTEMS

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1 Historical levels of carbon dioxide.

At one time, at the start of life, the atmospheric carbon dioxide content was as high as 30% (Lovelock and Whitfield, 1982). A CO_2 concentration between 200 and 400 ppm has been present during the last 1 billion years (Degens _et al_., 1984).

1.1 Holocene

20,000 yr ago, CO_2 levels, as calculated from trapped gas bubbles in ice, were 160 ppm (Delmas _et al_., 1980) or 190-230 ppm (Neftel _et al_., 1982), (Fig 1). 18,000 yr ago full glacial conditions existed. Shackleton _et al_., (1983) derived a value of 260 ppm, for that time, from ocean sediment cores. The discrepancy between these data illustrates the difficulty in dating in the first place. At the close of the ice age atmospheric CO_2 rose 60 ppm in 100 yr (Broecker _et al_., 1985), a time-division refinement which would be hard to ascertain in different cores.

While the climate around 6000 yr BP was significantly different from today, the global mean temperature was estimated as being within 1 ^{o}C of todays mean temperature. The differences in climate at that time were local and seasonal and showed large variations in precipitation in some areas and regions of higher as well as lower temperatures (Webb and Wigley, 1985). This period derives its importance from the calculated 5% lower (in January) and 5% higher (in July) solar radiation values, due to changes in the earth's orbit and inclination.

1.2 Pre-industrial.

The level of the pre-industrial atmospheric carbon dioxide levels in the atmosphere has been estimated from a number of biological and geological records i.e. tree rings (Peng _et al_., 1983) (245-270 ppm), sclerosponges (Druffel and Benavides, 1986) (280 ppm), ice cores (e.g. Neftel _et al_., 1982, Friedli _et al_., 1986) (280-290 ppm) and ocean sediment cores (e.g.

Duplessy, 1986).

1.3 Future scenarios.

The last decades have been an unusually interesting time for climate studies. In the early 1950s, there was concern lest the warming trend of the first half of the century would persist (Gribbin & Lamb, 1978). In the early 1970s the prevailing view was that the earth was moving towards a new ice-age (e.g. Dansgaard et al., 1975 (Fig 2) Flohn, 1974). Many articles speculated about the impact of a 1-2 °C cooling on agriculture as the observed 0.4 degree cooling had reduced the growing season (in the UK) by 10 days (Starr & Oort, 1973). By the late 1970s and early 1980s that view had shifted 180 degrees, once again, to the belief that the earth's atmosphere was being warmed as a result of increasing CO_2 loading (Stewart & Glantz, 1985). The implication of the above is not only that the acceptance of a future global warming is rather new, but more importantly that the available data in the early 1970s seemingly supported, or did not exclude, the possibility of a future global cooling (Fig 3). These data should not be discarded. There remains good factual support for both opposing views, although a selective choice in data, to support an opinion, appears to occur (Idso, 1983). Nevertheless, there seems to be a cautious general agreement now on the period when the signal of a climatic change might be expected to become discernible in the natural variation: 2020-2040, 30 to 50 years from now. A few expect proof of the continuous cooling, more, and especially modelers, expect proof of the "Greenhouse Effect".

The one and only topic on which everybody agrees is that the atmospheric carbon dioxide is rising rapidly, the major period of increase starting in the mid 1940's. The future levels of the atmospheric carbon dioxide concentrations are dependent on emissions and sinks. The distribution of carbon on earth is summarized in Table I. As the anthropogenic influence on the size of the sources creates the problem, a number of scenario's have estimated future levels. These estimates are based on the expectations of fossil fuel demand, the impact of land-use changes, including deforestation or biotic growth, and the fraction that is retained in the atmosphere. The most pessimistic scenario (Siegenthaler & Oeschger, 1978) calculates an atmospheric CO_2 level of more than 2000 ppm to be reached in 2060. The scenario's are summarized by Perry (1982) (Fig 4). The scenario's of IIASA (International Institute of Applied Systems Analysis) are generally accepted as the most realistic, although they also accept a low and a high scenario (Häfele, 1981).

Table I. Carbon in sedimentary rocks, hydrosphere, atmosphere and biosphere. (after Stumm & Morgan 1981)

	10^{18} mol C	Total on Earth units of atmospheric CO_2.
Atmospheric	0.054	1
Sediments		
Carbonate	5100	94000
Organic carbon	1000	18500
Land		
Organic carbon	0.1	1.8
Ocean		
$CO_2 + H_2CO_3$	0.019	0.35
HCO_3^-	2.9	54
CO_3^{3-}	0.36	7
Dead organic	0.4	7
Living organic	0.0007	0.01

The effect of carbon dioxide on global temperature and indirectly on sea level remains an area of dispute and will remain so, provided no clear separation in signal and noise (signal to noise ratio) of the available data is forthcoming. One thing however is clear; there is no proof yet that the calculated and predicted surface warming, which should be detectable now, has occurred (Madden & Ramanathan, 1980, Wigley & Jones, 1981, Idso, 1983).

2 Carbon dioxide and the sea.

2.1 Ocean circulation.

Warming, as a result of doubling the atmospheric CO_2 concentration, will increase with latitude. Especially in the polar regions, the areas of downwelling, the mean temperature is expected to increase from 1 °C (Washington & Meehl, 1982) to 15 °C (Manabe & Wetherald, 1975) (Fig 5). But a definite signal is even in this most sensitive area not yet discernible (Fig 6). This will reduce the temperature gradient that drives ocean circulation. Not only will the overall circulation rate be reduced but, the episodic events that produce the coldest bottom waters will be less frequent. Baes (1982) expects the reduced circulation to lower net biological productivity of the oceans and, since the formation and export of detritus from surface to deep waters will not be similarly reduced, the organic carbon content of the upper ocean should decrease. Total dissolved carbon (TC) and pCO_2 of the surface water will therefore increase. CO_2 should then be released from the surface of the ocean into the atmosphere. The increased pCO_2 renders the sinking waters more corrosive to calcium carbonate, promoting dissolution of deep sea sediments and a rise in alkalinity. The total balance of reduced deep-water production in combination with a higher pCO_2 of the sinking water is at this moment, as a long term prognosis, only speculative.

2.2 Chemistry of carbonate speciation

The inorganic chemistry of carbon in the oceans is quite well understood. Atmospheric (gaseous) carbon dioxide dissolves in water to form hydrated CO_2 and carbonic acid (H_2CO_3), represented in the reaction:

$$CO_2 + H_2O \Longleftrightarrow H_2CO_3.$$

Two additional reactions can occur in which H_2CO_3 loses first one and then a second hydrogen ion (H^+) to form the bicarbonate ion (HCO_3^-) and the carbonate (CO_3^{--}) ions:

H_2CO_3 <==> H^+ + HCO_3^-.
HCO_3^- <==> H^+ + CO_3^{--}.
or:
CO_2 + H_2O <==> H_2CO_3 <==> H^+ + HCO_3^- <==> $2H^+$ + CO_3^{--}.

Of the three inorganic carbon species in the ocean, bicarbonate, carbonate and carbonic acid/hydrated carbon dioxide take-up 95%, 3% and 2% respectively. The buildup of $[CO_3]$ leads to the precipitation of calcium carbonate following:

Ca^{2+} + CO_3^{--} <==> $CaCO_3$.

This process is largely under biological control.
The total of the carbon species in solution is, for convenience, frequently presented as TC (Total Carbon, moles kg^{-1}).

The partial pressure of CO_2 (pCO_2) in surface waters can differ by as much as 90 mu-atm (both positive and negative) (Keeling, 1968). A, short-lived, reduction of pCO_2 to 125 mu-atm has been observed during plankton blooms in the Bering Sea (Codispoti _et_ _al_., 1982). However, in general the ocean surface water is in "equilibrium" with the carbon dioxide content of the atmosphere (Baes, 1982). The pressure deficit is, in average, 20 mu-atm. This equilibrium is artificial if the ocean is taken as a whole. The equilibrium is sustained because of biological processes and the supersaturation with respect to $CaCO_3$ of surface waters, also ascribed primarily to biogenic control. Based on the average concentrations TC amounts to 2.33 mM kg^{-1}. Oceanic water below 2000 m , in a fully mixed ocean, would be undersaturated with respect to $CaCO_3$, because of the effect of pressure on the solubility of calcite (the least soluble form). This horizon occurs at 5000 m in the actual situation of the North Atlantic (Brewer, 1983). After upwelling and subsequently warming of this deep water pCO_2 would be 1200 mu-atm and consequently CO_2 would be released into the atmosphere, producing a several fold increase of atmospheric CO_2 concentrations. The release of CO_2 from the ocean, under present-day conditions, is restricted to the tropics.

This process does not occur globally because the CO_2 is consumed in photosynthesis, hence compartmentalized, and ultimately transported downwards as detritus. Photosynthesis requires nitrogen and phosporus in the ratio 16 to 1. In deep water the two nutrients have this ratio, but in warm surface waters the concentration of both is reduced virtually to zero (Fig 7). In cold surface waters the concentration can reach the values for deep water because then insolation acts as the limitation for production. As a consequence the most productive waters are found at moderately high latitudes where insolation and circulation is sufficient to utilize the available nutrients, or in upwelling areas (west coasts of continents) in the (sub-) tropics.

2.3 Changes in pH.

The effects of increased atmospheric CO_2 on the carbonate system of the surface waters can be approached as a theoretical, thermodynamical system in which equilibria determine changes and concentrations or, the biological activity, inducing major changes, is also taken into account. The first, seemingly simple, set of calculations has not yet produced an unequivocal estimate of the effect of doubling the atmospheric CO_2 on the chemistry of ocean surface waters. The differences might be small, but acidification has a major impact when approaching some treshold value, especially in nutrient-rich waters. Stumm & Morgan (1981) calculated a lowering of pH 0.279 pH units, under equilibrium conditions, after doubling of the partial pressure of CO_2. This represents an increase in $[H^+]$ by a factor of 1.9. Holm-Hansen (1982), estimated a decrease of 0.5 pH units as the result of doubling atmospheric CO_2, while Baes (1982) reached a decrease of 0.2 pH units. The general agreement is now on 0.3 pH units (Sibley & Strickland, 1985), provided alkalinity does not change (Brewer, 1983). Alkalinity is not affected by the uptake of atmospheric CO_2.

Alkalinity = excess of positive charges over the anions of strong acids (net charge balance) (Brewer, 1983).

$[Alk] = [Na^+]+[K^+]+2[Ca^+]+2[Mg^+]+\dots. -[Cl^-]-2[SO_4^{--}]-[NO_3^-]-\dots.$

and can also be defined as (Pytkowics et al., 1977):
$[Alk] = [HCO_3^-] + 2[CO_3^{--}] + [BOH_4] + [OH^-] - [H^+]$.

However, the alkalinity is subjected to changes if ions of strong acids or bases are removed from the water. This occurs in biological processes (Table II).

The profiles of TC (Fig 8) in the upper ocean indicate that CO_2 has been removed, producing calcite supersaturation. This removal is caused by biogenic processes and therefore determined by limiting factors (e.g. insolation, nutrients, temperature). The removal of CO_2 in photosynthesis increases the alkalinity also. Increased uptake of atmospheric CO_2 will lower the alkalinity and pH, and hence the degree of supersaturation of calcite and aragonite.

Table II. Processes affecting alkalinity (After Stumm & Morgan, 1981).

Photosynthesis and respiration:	
$nCO_2 + nH_2O \Longleftrightarrow (CH_2O)_n + nH_2O$	no change
$106\ CO_2 + 16\ NO_3^- + H_2PO_4^{--} + 122\ H_2O + 17\ H^+ \Longleftrightarrow [C_{106}H_{263}O_{110}N_{16}P_1] + 138\ O_2$. (algae)	increase
$106\ CO_2 + 16\ NH_4^+ + H_2PO_4 + 108\ H_2O \Longleftrightarrow [C_{106}H_{263}O_{110}N_{16}P_1] + 107\ O_2 + 14H^+$	decrease
Nitrification:	
$NH_4^+ + 2O_2 \longrightarrow NO_3^- + H_2O + 2H^+$	decrease
Denitrification:	
$5CH_2O + 4NO_3^- + 4H^+ \longrightarrow 5CO_2 + 2N_2 + 7H_2O$	increase
Sulphide oxidation:	
$HS^- + 2O_2 \longrightarrow SO_4^{--} + H^+$	decrease
$FeS_2 + 15/4\ O_2 + 7/2\ H_2O \longrightarrow Fe(OH)_3 + 4H^+ + 2SO_4^{--}$	decrease
Sulphate reduction:	
$SO_4^{--} + 2CH_2O + H^+ \longrightarrow 2CO_2 + HS^- + H_2O$	increase
$CaCO_3$ dissolution:	
$CaCO_3 + CO_2 + H_2O \Longleftrightarrow Ca^{2+} + 2HCO_3^-$	increase

Whitfield (1982) argues that, in pessimistic scenarios of future CO_2 emissions, undersaturation in aragonite might occur in latitudes above 50^o.

2.4 Diurnal and spatial variation in pH.

CO_2 uptake in photosynthesis increases the pH during daytime. The respiration and decomposition (also during daytime) release CO_2 and therefore lower the pH measurably. The resulting diurnal fluctuation is superimposed on the changes caused by increased CO_2 uptake by the sea from a high CO_2 atmosphere. A lower pH as a result of an increase in $[CO_2]$ can be brought about by biological respiration, chemical oxidation, decrease in temperature or increase in pressure. The diurnal variation in pH is depending on the availability of nutrients and the local microenvironmental conditions (e.g.temperature, insolation, stratification, turbidity, mean pH). The diurnal fluctuation is approximately 0.3 pH units in the oceans (Liss & Crane, 1983) which have a range from 7.5 to 8.5 (Calabrese & Davis, 1966) or 7.8 to 8.3 (Dietrich *et al.*, 1980) and a mean of 8.0 (Skirrow, 1975) while a pH of 8.2 would be in chemical equilibrium with todays atmospheric CO_2 pressure (Stumm & Morgan, 1981).

Deep oceanic water has a lower pH (approximate pH=7.7). When upwelling occurs, especially in summer conditions, a sharp spatial gradient from pH 7.7 to 8.2 can develop over a short distance perpendicular to the coast (Park, 1969).

2.5 Heavy metals and pH.

Growth rate changes (inhibition or stimulation) are related to cupric (Cu^{--}) ion activity (in analogy to pH expressed as pCu, the negative logarithm of the cupric ion activity), and not to the total copper concentration (Steemann Nielsen & Wium-Andersen, 1970). The cupric ion activity can be altered, independently of total copper concentration by

changes in the pH, influencing the degree of complexation, and the concentration of chelators, the latter sometimes produced and retained extracellularly (polypeptides) by the organism itself as a protective measure. A chelator detoxifies the water by binding certain toxic metals, but it also increases the availability of essential metal ions (especially iron) in forms that are biologically active (Jackson & Morgan, 1978). CO_3^- , OH^- , SO_4^{--} , Cl-, and $B(OH)_4$ are the main natural complexating ions. The effect of pCu on an estuarine diatom (*Thalassiosira pseudonana*) was studied by Sunda and Guillard (1976)
(Fig 9). The results are summarized in Table III.

Comparable dose-effect combinations were found for other diatoms and some green planktonic algae.

The range of pCu in natural seawater is from 10.5 - 9.0, with a mean of 9.7, indicating that in the absence of chelators the natural levels of copper are toxic to at least some species of plankton. Chelators are particularly absent in upwelling waters and, conversely, coastal water have a relatively high content. Increases in the pH stimulates complexation of Cu^{--} , hence a decrease in the pH increases the cupric ion activity. McKnight and Morel (1979) reported a 1:1 decrease of pCu with pH (in fresh water).

Table III. The effect of changes in the Cu-concentration on algal growth.

pCu	effect
14.6	40% reduction of growth due to nutritional deficiency
13.3 - 10.6	Maximal growth.
10.6 - 8.6	Delayed inhibition of growth, no distortion.
8.6 - 8.3	Inhibition of growth, morphological distortion.
< 8.2	Immediate inhibition of growth rate.

The effect thereof is dependent on the susceptibility of the planktonic species. A decrease of the pH from 8.2 to 7.7, the effect of doubling atmospheric CO_2, will decrease pCu from 9.6 to 9.2, sufficient to double the inhibitory effect of Cu^{--} on algal growth (in some species). Sunda and Guillard (1976) concluded that changes in the pH of seawater could be an important factor controlling cupric ion toxicity to phytoplankton. However, most eukaryotic algal species release measurable amounts of, mostly weak, copper-complexing agents. Strong copper-complexing agents (e.g. hydroxamates) were released by Cyanophyceae, and thought to be associated with the prokaryotic nature of the blue-green algae. The ligands are predominantly released during periods of slow growth or when the algae are in a stationary phase (in batch-cultures), resembling the conditions during an algal bloom in natural waters (McKnight and Morel, 1979). The success of the detoxification than becomes dependent also on the rate in which these organic molecules are metabolized by bacteria.

The dependence of toxicity on the pCu and not on the total copper concentration was also demonstrated for the dinoflagellate *Gonyaulax tamarensis*. Cells of this species were 100% nonmotile at a pCu of 9.7, while at pCu 10.4 only 50% were nonmotile. Nonmotile cell do not divide or grow (Anderson & Morel, 1978). The small range indicates that a toxic level of Cu^{--} could be induced rather quickly.

The degree in which the local populations will be affected (through changes in the pH) is not precisely known, because the amount of organic chelators, the input of fluviatile (anthropogenic) copper, the absorption complexes in the sediment/silt load, and the species sensitivity are all interacting. Furthermore, the effect of a diurnal variation in pCu, which will occur as a result of changes in the pH caused by photosynthesis / respiration sequences will add to the complexity in solving the question arising. Noted should be that the two effects are temporally separated. The environment will be most toxic during periods of respiration (darkness) when the pH is lowered. If there is a pH effect, not sufficiently countered by excess organic chelation capacity, than the threshold for toxicity will be reached, and the effect is negative. One more example of feedback mechanisms of which the resultant impact is as yet unknown. A lowering of the pH stimulates the availability of free CO_2, the carbon species which is taken up preferentially. But, than also the pCu will be lowered, negating to some degree the stimulation of productivity to an unknown balance.

2.6 Effect on primary production.

Plankton, microphytobenthos, epiphytes, macroalgae and (marine) phanerogames constitute the primary producers of the (marine) intertidal community. Changes in CO_2 content of the ambient water, governed by a reduction of the pH (acidification), and lengthening of the growing season could add up to an increase of the primary production.

An effect of CO_2 enrichment on diatom populations in fresh water was the lowering of the sinking rate at lower pH values and during periods of exponential growth (Jaworski *et al.*, 1981). A decrease of the pH causes a shift in carbon speciation towards higher CO_2 concentrations, the carbon species assimilated preferentially. A process linked to photosynthesis regulates the specific gravity of phytoplankton (Bienfang, 1981) and higher sinking rates therefore are also associated with nutrient depletion (Eppley *et al.*, 1967). The effect of increasing atmospheric CO_2 on marine plankton populations will therefore be twofold. Stimulation of photosynthesis as a result of enhanced CO_2 availability and increase of the population size because of a higher buoyancy of the cells. The stimulatory effect will be mitigated by the reduction of the light penetration depth.

However, to maintain the required acid/base conditions in the organism will cost energy, which than is no longer available for growth. In eucaryotic cells, various pH values can be maintained within the different membrane-bound organelles. Procaryotic cells do not have this compartimentalization, and hence the question of lowered pH in sea water will have special significance for blue-green algae and bacteria. Cyanophyta usually require alkaline growth conditions, and the pH of 7.6

is approaching the lower limit for growth (Holm-Hansen, 1982). The implications of this effect of carbon dioxide increase in the atmosphere can be quite large as many species of cyanophyta contribute to the production of an ecosytem because of their position in the nitrogen cycle.

2.7 Dissolution of biogenic carbonates.

There are several crystal forms of $CaCO_3$, namely calcite, aragonite and vaterite. Calcite is most frequently found in oceans and sediments, followed by aragonite. Vaterite is rare and has been found only in arthropode skeletons. Near-surface oceanic waters are supersaturated with regard to calcium carbonate and this supersaturation is rendered metastable because the growth of nuclei is inhibited by Mg ions, organic molecules and phosphate ions (Pytkowicz et al., 1977). In some marine environments, like the Skagerrak for instance, an extensive dissolution record of biogenic calcareous material is produced by a limited degree of carbonate undersaturation. However, the chemical dissolution apparently does not impose serious problems for the marine environment and its inhabitants. Etch patterns have been observed on apical ends of shells of gastropods but the dissolution rate is insignificant for these large animals (Alexandersson, 1976). The effect on microscopic organisms, e.g. coccolithic algae, has not been studied from this point of view.

The deep ocean is undersaturated, and over half of the biogenic carbonates, produced in planktonic and macroalgae (Borowitzka and Larkum, 1976) and animals, are redissolved during and after settling. Other carbonates (e.g. $MgCO_3$, $SrCO_3$) occur but are relatively unimportant. High pressure, low temperatures and a high CO_2 content promote the dissolution of the aragonite and calcite. The redissolved carbonate is returned to the surface by upwelling.

The solubilities of the various carbonates increase in the order; low magnesium calcite, aragonite, high magnesium calcite. Solubility product calcite ($0.554\ 10^{-6}$), aragonite ($0.098\ 10^{-6}$) (Borowitzka, 1977). The carbonate of calcified tissue mainly occurs in the two crystal forms calcite and aragonite, of which the latter goes into solution at pH 6.3 (Borowitzka & Larkum, 1976). The arrest of algal calcification has been demonstrated below this pH, and the calcification rate is reduced below pH 6.5-7.0 (Borowitzka & Larkum, 1976). In this process any influence of increased carbon dioxide is therefore not expected.

2.8 Effect on secondary production.

The pH effect on marine invertebrates has received little attention as a change in pH is expected to be small due to the buffer capacity of sea water. Nevertheless, the increase in atmospheric CO_2 will result in a decrease of the pH by 0.3 units. The pH approaches than the values (pH = 7.7) for which shell dissolution was reported in the Japanese pearl oyster (Pinctata fuscula) (Kuwatani & Nishii, 1969). The high primary production in nutrient rich Dutch coastal waters and the associated high rate of respiration will cause a relatively high diurnal fluctuation. The decrease is less pronounced as the increase in well oxygenated waters. Nevertheless a deleterious, although probably minor, effect of the pH on aragonite, after the adjustment of the sea to double CO_2 concentrations, can not be discounted offhand. Furthermore, the US Environmental Protection Agency has recommended, for open waters, a maximum allowable deviation of 0.2 pH units from the natural variation (Knutzen, 1981). A new equilibrium with atmospheric CO_2 (if doubled) would surpass this limit.

Although the pH of the open ocean, today, usually ranges from 7.5 to 8.5 (the higher values due to CO_2 uptake in photosynthesis), the pH in tidepools, bays and estuaries may decrease to 7.0 or lower due to dilution and production of H_2S. These inshore areas constitute the major portion of the habitat of commercial bivalves (i.e. Mytilus edulis). There is therefore some reason for concern.

Some concern about the effect of pH changes especially on small (planktonic or juvenile) organisms directly, in a high productivity environment like the Wadden Sea, will be appropriate. The CO_2 partial pressure and pH of the water can have marked effects on overall body metabolism. Carbon dioxide has been used to anaesthetize copepods. Death is caused in fish larvae of some species, in laboratory experiments, by a lowering of the pH to 7.7., a value within reach after doubling of the atmospheric CO_2 concentration (Holm-Hansen, 1982). However, the changes in speciation and concentration of soluble metals, in a polluted environment like the Wadden Sea, will affect the community probably sooner. It might be clear that the size of the problems, because of all the unknowns, will require a major research effort to elucidate all implications of the ongoing "global experiment".

Marine production, on a global scale, is threatened much more profoundly by the possible effect of ocean warming. Warming will increase with latitude and therefore reduce the temperature gradient that drives ocean circulation. The overall circulation rate will be reduced and patterns might change. Less cold bottom water will be produced. The reduced ocean circulation is expected to lower the biological production of the ocean. Lower rates of photosynthesis imply lower rates of CO_2 uptake, hence the increase of CO_2 partial pressure in oceanic waters. This will reduce the gradient between the two major compartments, atmosphere and ocean. Possibly and eventually the ocean might become a source of carbon dioxide (Baes, 1982). To illustrate the possible effect of global warming on the food-web and ultimately on the production of harvestable stocks, it should be stressed that primary production is not the key-factor. In Antarctic waters the rate of primary production is only about 50% higher than in oligotrophic areas. Nevertheless harvestable stocks are very much higher in the Antarctic waters, where food-webs are much shorter, compared to oligotrophic seas. The nature of the food-web is to a large extent dictated by the species composition of the phytoplankton crop. Nutrient-rich waters tend to have large cells. Nutrient-poor waters are characterized by nanoplankton and flagellates (Holm-Hansen, 1982).

It should be taken in consideration that autotrophic life in the ocean is most important in maintaining a viable earth. In a lifeless ocean, chemical processes and thermodynamic equilibria would result in a partial pressure of approximately 1200 mu-atm, depending on temperature. The surplus would be released to the atmosphere, increasing the present-day atmospheric concentration severalfold. Photosynthesis reduces the partial pressure of CO_2 in the ocean now in average to 20 mu-atm below ambient atmospheric pressure, while sustained differences of 90 mu-atm are observed (Baes, 1982). Additional supply of nutrients will offset the above scenario.

3 Carbon fixation pathways.

Carbon dioxide uptake of a plant is essentially a diffusive process. The gradient, and consequently the rate of diffusion is dependent on the difference in concentration between internal (C_i) and external (ambient, C_a) levels of carbon dioxide. This gradient can be enhanced if the internal concentration is made low. A concentrating mechanism has this effect. Some plants possess this capability.

3.1 The C_3 pathway.

Initial photosynthetic CO_2 fixation occurs via one of the two cyclic pathways; C_3 (initial stable product is a three-carbon glycerate) and C_4 (initial stable product is a four-carbon acid). The reductive pentose phosphate cycle (RPP cycle, Calvin cycle, C_3 cycle) is the basic biochemical pathway whereby carbon dioxide is converted to sugar phosphates during the process of photosynthesis. This pathway is ubiquitous in all photoautotrophic green plants. It occurs in all eukariotic photosynthetic cells and in all cyanobacteria. CO_2 is incorporated in sugars by the enzyme ribulose 1.5 biphosphate carboxylase/oxygenase (RUBISCO). This enzyme is important, comprises up to 40% of the cellular protein and acts as a carboxylase in photosynthesis. Plants wich fix exogenous inorganic C via RUBISCO lack, by definition, a CO_2 concentrating mechanism.

The photosynthetic carbon oxidation (photorespiration), a C_2 cycle (glycolate pathway) coexists, in C_3 plants, with the C_3 cycle and is also catalysed by RUBISCO. This enzyme than acts as a oxygenase. The competition between the two substrates (CO_2 and O_2) for this enzyme directs the flow of carbon (Fig 10). Because of its competitive nature, O_2 inhibition is strongly dependent on CO_2 concentration and, conversely, apparent photosynthesis (CO_2-uptake) is strongly affected by the O_2 concentration. Respiration has several functions. It is a source for glycine and serine synthesis for protein. The greatest importance of photorespiration in C_3 plants is as a metabolic system for balancing photosynthetic energy production with CO_2 availability (Tolbert & Zelitch, 1983).

The activity of the carboxylating enzyme per unit leaf area largely determines the CO_2 assimilation rate at any CO_2 concentration. However, in the long run, the concentration of this enzyme is affected by the CO_2 concentration (Wong, 1980).

3.2 The C_4 pathway.

In some higher plants (C_4 and CAM plants) there is an additional pathway (PEP cycle, Hatch & Slack cycle, C_4 cycle) which incorporates carbon dioxide first in four-carbon acids (predominantly malic and aspartic acid, via oxaloacetic acid). The name C_4 plant denotes a plant with the C_4 cycle and a specific type of leaf morphology, characterized by mesophyl cells in which the initial CO_2 fixation occurs. The four-carbon acids are subsequently transferred towards the bundle sheath cells where they are decarboxylated. The released CO_2 is refixed in the RPP cycle.

The C_4 cycle is not an alternative to the RPP cycle but an efficient carbon concentrating mechanism. It does not result in any net reduction of CO_2. The reduction of CO_2 to form sugarphosphates has to be performed in the C_3 cycle, elsewhere in the leaf. In C_4 plants the C_3 and C_4 cycle are separated spatially (Fig 11).

A modification of this C_4 pathway is the crassulacean acid metabolism (CAM). In CAM plants the C_3 and C_4 cycle are separated temporally. The initial fixation of CO_2 into a four-carbon acid occurs during the night.

The four-carbon acids are stored in the cell. The release of the CO_2 from the acids and refixation of the CO_2 in the C_3 cycle takes place during the day, within the same photosynthetic cell. The main advantage of this mechanism is the reduction of waterlosses, very advantageous in arid environments. Only a few aquatic macrophytes (e.g. isoetids) possess this pathway, but in the marine and brackish environment this pathway is of very little importance. The ecological implications of this acid metabolism will not be elaborated on further.

The C_4 cycle utilizes excess ATP to maintain a higher level of CO_2 in the environment of the carboxylation enzyme of the RPP cycle (RUBISCO). The intercellular CO_2 concentration (C_i) at the RPP carboxylation site can be as high as 1.5 mbar in C_4 plants, under present atmospheric conditions. Since the discovery of the C_4 pathway it has become well established that this pathway enables the plant to photosynthesise at a higher rate under conditions (e.g. light) where, in the absence of this mechanism, the photosynthetic rate would be limited by the CO_2 concentration in the intercellular spaces (Ehleringer & Björkman, 1977).

4 Aquatic Plant Communities.

Plant assemblages.

a. microscopic algae:
  - prokaryotic or eukaryotic,
  - free floating (phytoplankton), or
  - attached (epiphytes, phytobenthos),
  - fresh, brackish or marine habitats.

b. macroalgae:
  - fresh, brackish or marine habitats.

c. higher plants (macrophytes, vascular aquatic plants):
  - submersed, floating-leaved or emergent,
  - fresh, brackish or marine habitats.

a. Microscopic algae, phytoplankton and epiphytes, are the largest group, both in number of individuals as well as number of species, within the aquatic plant assemblages.

b. Macroalgae are poorly represented in fresh waters, however they form the main component of most coastal marine benthic ecosystems, especially on hard substrata. The primary characteristics of CO_2 metabolism, CO_2 uptake and photosynthetic pathways are similar in plants from all types of aquatic habitats.

c. Vascular aquatic plants from the temperate marine environment are primarely submersed angiosperms of which the largest group (seagrasses) are stricktly marine although within some of the seagrasses a marked degree of fresh water tolerance exists.

Freshwater aquatic plants will be excluded from this report.

4.1 Pathways of CO_2 fixation by aquatic organisms.

Photosynthetic CO_2 assimilation in terrestrial plants can be divided in 4 major groups (see Chapter 3-3.2): C_3, C_4, C_3/C_4 and CAM. The different pathways appear to be partially correlated with environmental factors, particularly O_2, temperature and water availability. CAM fixation is largely associated with water conservation in succulent species in arid regions. Its occurrence in aquatic environments (Littorella, Isoetes & Crassula) appears to be a concequence of the secondary CO_2 conservation function of the CAM assimilatory pathway.

The assessment of the effects of increased atmospheric CO_2 on the physiology, productivity and ecology of aquatic plants is more complicated than in terrestrial plants. Aquatic plants are found in a variety of habitats and are grouped according to their morphology, size, mode of attachment (if any) and watertype. The difficulties in the evaluation of the effects is aggravated by the fact that atmospheric CO_2 is absorbed and dissolved in water, where it enters the carbonate system and forms HCO_3^- and CO_3^{--}. The final concentration of a carbonate species is dependent on the chemical properties of the watertype itself. The effect of the speciation of the carbon source is relative to the ability of the plant to utilize more than one carbon species. Many aquatic plants using RUBISCO as their initial carboxylase counter the limitations on CO_2 supply via the operation of biophysical CO_2 concentrating mechanisms which are based on active transport of HCO_3^-, CO_2 or H^+ at the plasmalemma (Prins et al., 1982a, 1982b).

Photosynthetic CO_2 fixation is always 'aquatic', in that the carboxylases function in aqueous media (Raven et al., 1985).

RUBISCO of aquatic plants always has relatively high CO_2-saturated specific reaction rates in comparison to RUBISCO of terrestrial C_3 plants, when assayed at the same O_2 concentrations. The kinetics of RUBISCO of the aquatic plants are thus more similar to those of terrestrial C_4 plants than to those of terrestrial C_3 plants (Raven et al., 1985).

4.2 Phytoplankton.

In non-marine environments CO_2 shortage might limit phytoplankton production, provided all growth-factors (e.g. nutrients, light, etc.) are optimal. In marine waters, CO_2 limitation of plant growth is rarely considered because of the large quantities of carbon (as carbon dioxide and carbonates) available and the much more profound influence of nutrients and light. The number of studies into the effect of enhanced CO_2 levels is also quite limited, for the same reasons. Small et al. (1977) studied the response of the marine diatom Skeletonema costatum and the marine chrysophyte Isochrysis galbana (a flagellate) to high (0.15%) levels of CO_2 and did not find changes in growth rates, final population yield and other parameters of production, after the plants were acclimated (after one cell division), although an initial response (negative, because of the step-wise lowering of the pH) was observed. In this study the nitrate content was set to ultimately limit the yield. The insensitivity to minor changes in the pH, and resultant changes in available CO_2, was also observed in the coccolithophorid Criscosphaera elongata (Swift and Taylor, 1966). However, in a semi-continuous culture in large vessels, Laing and Helm (1981) observed a stimulation of the algal production of

Tetraselmis suecica when CO_2 supply was adequate to maintain a pH 7.8 and a decrease in the cell division rate with increasing pH (Fig 12). Please note the distribution of datapoints around pH 8. This study was performed in enriched seawater. It appears that stimulation of algal growth will follow increased CO_2 levels if nutrient levels are not limiting. Actively growing phytoplankton has a 4 times lower sinking rate compared to those that ceased growing (Fig 13) (Eppley et al., 1967). This can act as a positive feedback in oceanic waters, but will also induce progressive light limitation in nutrient rich coastal and estuarine habitats. The sinking rate is most affected by growth reduction that results from P-limitation (Bienfang, 1981). The sinking rate has a diurnal pattern, but any relative change in this pattern is not envisaged. The implication for a natural ecosystem, as in the Dutch estuaries and Wadden Sea, would be a more rapid growth and steeper production curves at the beginning of the growth season as compared to the current pattern. This will largely be balanced by lower winter and hence spring water-temperatures as envisaged (Palutikof et al., 1984b) to result from climatic change. The yield, as particulate organic carbon, of the system will, in all likelihood, not be affected because nutrient and light levels eventually will curtail production. Nitrate limitation can be mitigated, possibly causing shifts in species composition, as many algae can fix nitrate from dissolved nitrogen and thus ease nutrient shortage in surface water (Degens et al., 1984). The limitation of primary production in the sea, as caused by nutrient shortage, is largely dependent on phosphate (P). Phosphorus can not be supplied biologically. The C/P ratio in phytoplankton is about 100/1 (the so called Redfield-ratio).

The production cycle in temperate waters varies in time of onset, amplitude and spread and, can shift by weeks between years. Spawning of fish and invertebrates precedes the peak in primary production. The timing of the events can match or mismatch (Cushing and Dickson, 1976). If lower spring water temperatures, caused by the lower wintertemperatures (Palutikof et al., 1984a), delay spawning more than the start of, a possibly stimulated, primary production than it can be postulated that the time lag between the two might become narrower. This would lower the chance of a mismatch to occur. Which would enhance secondary production. On the other hand, in many species spawning is triggered by non-temperature environmental signals (lunar-cycle, rainfall, day length) (Bardach & Santerre, 1981). Only species stimulated by day length could experience a mismatch as day length will not change. And this possible mismatch might be mitigated again because hatching of the eggs and processes leading to metamorphosis might accelerate. Post-larval stages of aquatic animals are strongly influenced by temperature. But it should be remembered that estuarine species are adapted to a highly variable environment, a counteracting factor in the impact of carbon dioxide on these communities (Bardach & Santerre, 1981).

An increase in the C/N ratio, which would make the phytoplankton less valuable as a food source, is not indicated (Small *et al*., 1977) and is not to be expected as nitrogen is rarely limiting. Most species have a capability of nitrogen fixation.

However, the possibility that species composition will change can not be ruled out without further study, as this is expected to occur in fresh-water phytoplankton (Wetzel and Grace, 1983). The effect of such response on the food chains in the marine environment is totally unknown as detailed studies into this are lacking. Studies that would be virtually impossible and would have only a very limited value, for predictive purposes, as the environment is so patchy, diverse and subjected to anthropogenic influences.

4.3 Phytoplankton feedback.

The surface of the unfrozen ocean, covering 70% of the planet, is relatively dark and has the potential to absorb over 90% of the incident solar energy. The incident solar energy appears to be one of the components in a "bio-controlled thermostasis of the planet", a term coined by Bates *et al*. (1987). In the "circular" sequence of events key-positions are taken by sulphur metabolism and primary production as a cause for a cloud-albedo feedback with insolation and temperature.

The ocean emits reduced sulphur gases, mainly dimethylsulphide (DMS), produced by phytoplankton in the photic zone. DMS is oxidized to methane sulphonic acid and sulphate. Sulphate aerosols have a minor cooling effect on the atmosphere through backscatter. Sulphate particles, however, serve as cloud condensation nuclei, which in turn alter the optical properties of the clouds. An increase of 0.02% of cloud albedo would decrease the Earth's surface temperature by 1.3 °C, equivalent to a change in the solar constant of -0.7% (Charlson et al., 1987). The DMS flux is correlated with primary production and hence insolation. The sequence is thought as part of a possible global biological system which influences the amount of solar radiation reaching the surface (Bates et al., 1987) but the tuning and the patterns in correlation have to be unravelled yet, but a insolation / primary production / sulphur emission / cloud formation / increased albedo / reduced insolation feedback loop appears to be a feasible concept for which indications exist (Fig 14).

The picture that emerges is that of a bewildering array of possibilities. The presently occurring shifts and changes gird weeks. The slow and gradual, almost unmeasurable, changes that might result from more CO_2 and a different temperature regime will, for a long time yet to come, disappear in the variability that results from "weather".

4.4 Macrophytes.

Water is, generally speaking, not a suitable habitat for abundant macrophyte life. Vegetation usually does not show a high organization level, the species number is low and the structure is limited (Segal, 1982). Dissolved free CO_2 is used preferentially by most aquatic plants and even used exclusively by some (Steemann-Nielsen, 1947, Prins et al., 1982a, 1982b) but bicarbonate ions are used by many algae and higher plants, especially in hard water and in the sea (Bristow, 1969).

Marine aquatic macrophytes include three algal Divisions: Chlorophyta (greens), Rhodophyta (reds) and Phaeophyta (browns), as well as several angiosperm genera (seagrasses).

4.4.1 Macroalgae.

The determination of the carbon fixation pathway in marine algae has been attempted many times, but the results are rarely conclusive. It is entirely possible that a species resembles a terrestrial C_3 plant in some responses (e.g. O_2 inhibition, high CO_2 compensation point) while other properties (e.g. enzyme characteristics) suggest a C_4 assimilation (Bowes, 1985).

Most benthic marine algae are capable to utilize HCO_3^- as a substrate for photosynthesis, but the influence of an eventual preferential uptake of CO_2 remains to be quantified for most macroalgae. The study of this aspect is rather complicated due to the increase of the pH which is associated with photosynthesis. The quantitative status of carbon supply in culture media is almost invariably obscure (Jaworski et al., 1981). A change in the pH immediately alters the distribution of the available carbon species (Fig 15). In Rhodymenia palmata a clear optimum, at pH 7.4, in photosynthesis was shown (Fig 16) (Colman & Cook, 1985), but as the rate of photosynthesis was larger than the rate supply of CO_2 (from conversion of HCO_3^-) it was nevertheless concluded that this was a pH effect. An increase of the pH almost instantaneously reduces the amount of available CO_2 by chemical processes. Joliffe & Tregunna (1970) concluded that Phorphyra and Desmarestia from the US Pacific coast required CO_2 as a substrate for photosynthesis. These species would gain some profit from a lowering of the pH as this increases the availability of CO_2. The other species in their study (Alaria, Costaria, Enteromorpha, Gigartina, Nereocystis, Sargassum and Ulva assimilated HCO_3^- (Thomas & Tregunna, 1968, Joliffe & Tregunna, 1970). Representatives of many of these genera are important benthic marine algae in the coastal waters of The Netherlands also. These species will hardly be favoured by the expected changes. However, preferential uptake of CO_2 over HCO_3^- is a widely occurring phenomenon. A slight beneficial effect therefore can not be discounted. On the other hand, changes in temperature, will anyway be of much more importance, especially for intertidal species. This aspect is outside the scope of this report (see another volume in this series).

4.4.2 Seagrasses.

Seagrasses have for decades become less and less important as contributors to the productivity of the ecosystem as a major decline has occurred. In the Dutch Wadden Sea only relict populations of Zostera marina remain but the second species Zostera noltii is expanding in some areas. The concentration of CO_2 in natural seawater is approximately 15 uM while that of HCO_3^- is approximately 2.5 mM. The photosynthetic pathway in seagrasses is also an area of dispute, for the same reasons as presented above for macroalgae. HCO_3^- is the main carbon species utilized by seagrasses but they assimilate CO_2 as well. The fixation of bicarbonate is an indication of the C_4 pathway but the observed inhibition of photosynthesis, in some seagrasses, by O_2 is a typical feature of the C_3 pathway hence the details have to be studied more (Downton et al., 1976, Beer et al., 1977, Bowes, 1985). These observations concerned tropical seagrasses and are not expected to be different in the temperate species. Nevertheless, seagrasses respond favourably to increased availability of CO_2 as is shown by the stimulated rate of photosynthesis as CO_2 becomes more available (Fig 17) (Beer et al., 1977).

Freshwater aquatic macrophytes can derive up to 95% (depending on the species) of their carbon from sediments. The CO_2 diffuses within the shoot from the unilluminated sediment to the illuminated shoot (Den Hartcg & Segal, 1964). It appears that seagrasses lack this capability and they derive only a very small quantity from their carbon through uptake from sediments (Raven et al., 1985).

5 Effects of CO2 on plants.

Carbon dioxide is the ultimate substrate for photosynthesis, which provides all the chemical energy and raw materials needed for all other growth processes and biological activity on earth. Photosynthesis governs the plant and under field conditions photosynthesis may be limited by environmental or by genotypic- phenotypic characteristics of which the most important are listed in Table IV (Etherington, 1974).

Table IV. Variables of the plant and the environment which influence the performance.

Environmental variables:

1. Energy.
   a. Quality, quantity and duration of photosynthetically active radiation.
   b. Quantity and duration of infrared radiation, influencing heating and water-loss effects.
   c. Other photomorphogenic and photoperiodic effects.
2. Carbon dioxide supply, concentration and leaf ventilation.
3. Air and leaf temperature.
4. Soil water potential and quantity.
5. Mineral nutrition.
6. Seasonal cycle.
7. Pathological condition.

Genotypic - phenotypic variables.

1. Leaf diffusion resistance.
   a. Stomatal and cuticular.
   b. Internal.
2. Carbon fixation pathway.
3. Composition of the photosystem.
4. Chloroplast shape, structure and distribution.
5. Leaf structure, anatomical and optical.
6. Plant leaf area.
7. Leaf display, angle, phyllotaxy, spacing and overlapping.
8. Concentration of photosynthesate and translocation rate.
9. Endogeneous rhythms (i.e. in stomatal aperture).
10. Leaf age.
11. Developmental stage.
12. Adaptation.
13. Factors relating to environmental conditions e.g. plant water potential, nutrient status, temperature etc..

While CO_2 might be regarded as a pollutant in the context of the implications of an increased "greenhouse effect", elevated levels of CO_2 can be directly beneficial to plant productivity in those species where present ambient atmospheric CO_2 concentrations (C_a) are evidently limiting photosynthesis, provided other factors (e.g. light, nutrients, water, temperature) are optimal. Blackman (1905) considered temperature, light and the supply of nutrients as limiting factors. He suggested that the rate of photosynthesis increased with an increase in the value of any one of those factors, as long as that factor was rate limiting and that it ceased to be dependent on this factor when one of the other factors became limiting (Fig 18). This concept is, as being too simplistic, more and more abandoned recently, although it apparently continues to be a prerequisite for the design of experiments. In most natural ecosystems the productivity is, at least partially, limited by other factors than the supply of carbon dioxide. No environmental factor operates alone. All factors, abiotic and biotic, in the actual environment of an organism are active and modify the response to a change in this environment (holocoenosis) (Strain, 1985).

Therefore, and because of the ability to adapt to changes, exposure to prolonged elevated CO_2 levels resulted in some species in adaptations which reduced net photosynthesis. In these and in many of the species possessing a carbon concentrating mechanism the direct fertilizing effect of increased CO2 will be negligible. These statements are as yet premature. The following summary of, and introduction into, these aspects of plantphysiology, should elucidate the conclusion.

A wide range of possible effects of the CO_2 increase has been hypothesized and includes plant competition, community composition, plant water-use efficiency, quantum yield efficiency, ecosystem water-yield, nutrient status, carbon sequestering and plant-animal interactions. The responses of plants to elevated CO_2 and the interactions or feedbacks are summarized in Fig 19 and in more detail presented in Fig 20.

5.1 Biological effects of increased atmospheric CO_2. Plant level.

5.1.1 Global distribution and fixation pathways.

The advantages of the CO_2 concentrating mechanism of the C_4 photosynthesis are maximal under conditions of high light intensities, high temperatures and limited water supply, conditions prevalent in habitats in subtropical regions. In the temperate and more cooler climates, C_4 plants occur infrequently and are considered to be relatively rare, but are common in some habitats (e.g. Spartina spp. in salt marshes). The occurrence of C_4 grasses is best correlated with night temperatures during the growing season (Caldwell et al., 1977). They have spread into regions where they are subjected to extreme winter temperatures, but not into regions where the mean minimum temperature is below 8 ^oC during the warmest month (Long, 1983). The occurrence of the C_4 dicotyledons is best correlated with evaporation during the summer. Low temperatures might modify the kinetics of the pathway, but there appears to be no fundamental reason why the C_4 pathway photosynthesis should exclude a species from cool regions (Caldwell et al., 1977).

In general, and in present day ambient CO_2 concentrations, the assimilation rate of C_4 species is in the range 60-100 mg CO_2 dm^{-2} h^{-1}, while the rate of C_3 is much lower at 10-30 mg CO_2 dm^{-2} h^{-1} (Kindl & Wöber, 1975). The potential relative production of C_3 and C_4 crop species in relation to latitude is illustrated in Fig 21. Other physiological factors, associated with the C_4 pathway, are than beneficial.
In a closed system, without any additional supply of CO_2, C_3 plants reduce the atmospheric CO_2 concentration to 40-70 ml l^{-1}, the CO_2 compensation point, while C_4 plants are capable to absorb virtually all available CO_2.

Carboxylation efficiencies of C_4 plants are high. CO_2 saturation occurs above 130 ppm intercellular CO_2 concentration. Since the stomata regulate the intercellular CO_2 pressure at or just below this saturating concentration, only a small increase of net fixation will occur after an increase of ambient CO_2 concentrations, under most conditions.

Net photosynthesis in a C_3 plant, at the present CO_2 concentration of the atmosphere, is inhibited 30-50 % by the atmospheric oxygen because of the photorespiration. At 600 ppm CO_2 in air photorespiration decreases to 10-35%, hence a production increase as compared to the present situation (Fig 22a,b). C_3 plants dispose of excess photosynthetic capacity (ATP, NADPH) by photorespiration. Up to 50% of the CO_2 newly fixed into carbohydrate is reoxidized back to CO_2 in photorespiration processes during the day. Because of the large amount of photorespiration or excess energy, plants have a potential for increased photosynthesis in a higher CO_2 atmosphere.

Part of the energy, wasted in photorespiration, will be used to increase productivity.

In the absence of a mechanism to concentrate CO_2 in C_3 mesophyll cells, the rate of net photosynthesis, when light, or more precisely photon flux density, is not limiting is largely dependent on the rate of CO_2 diffusion from the intercellular air-space to the carboxylation site. Any increase in the ambient CO_2 concentration which increases the CO_2 gradient across the cell will therefore stimulate the rate of carboxylation and reduce the proportion of carbon lost in photorespiration, hence will increase production of biomass (Colman & Espie, 1985). The ratio C_i/C_a is linear in many species under otherwise constant environmental conditions (Fig 23, Morison & Gifford, 1983)), but can be subject to changes if the stomatal conductance responds to other stimuli than C_i (Pearcy & Björkman, 1983).

In high CO_2 environments, as in C_4 plants, the oxidation of existing carbon compounds will be restricted. C_4 pathways raise intracellular CO_2 concentration at the carboxylation site so much that they nearly overcome the photosynthetically CO_2 limiting level of present day atmospheric CO_2 concentrations. The effect of elevated C_a on plant productivity, in a comparison of the two pathways, are often presented as in Fig 24. This kind of generalization originates mainly from crop response studies and is valid for many species, but this dose-effect curve cannot be used to predict the effect of an increased C_a on photosynthesis in all plants. The range of net photosynthesis in C_4 plants overlaps the range determined for C_3 plants considerably. The differences in the response within one genus (Euphorbia) are illustrative (Fig 25).

Stimulation of photosynthesis by increase of atmospheric CO_2 could lead to increased starch accumulation in the chloroplast when sucrose synthesis is already in excess (Guinn & Mauney, 1980) and acts as a negative feedback mechanism. The possible subsequent deformation of the chloroplast, if accumulation continues, might reduce photosynthesis severely (Fig 26).

Comparative studies, based primarily on gas exchange characteristics of single leaves in C_4 halophytes (shore plants; plants capable of thriving on salt-impregnated soils (Holmes, 1979)) present the C_4 species in a favourable light compared to their C_3 counterparts, although net photosynthetic rates in the C_4 halophytes may still be much less than reported for C_4 agronomic species such as corn and sugar cane. The question must still be raised as to how these C_4 halophyte species perform in their natural habitat, and whether or not they are indeed superior to the C_3 halophyte species.

5.1.2 Quantum yield efficiency.

The amount of carbon dioxide taken up by the vegetation depends largely on the amount of photosynthetically active radiation intercepted by its foliage. A typical rate for uptake (for a cereal crop) is 42 g m^{-2} day^{-1}, of which 33.g m^{-2} day^{-1} is taken up from the atmosphere and the remainder comes from soil respiration. Values as high as 70 m^{-2} day^{-1} have been reported for maize. A growing crop thus absorbs the equivalent of all CO_2 in the lower 50-100 m of the atmosphere, requiring efficient turbulent diffusion (Legg, 1985).

Besides the effect of increased cloudiness, due to elevated levels of evaporation, on insolation, which is as yet unknown, light regime and light quality will remain unchanged, for all practical purposes. The effect of the increased ambient atmospheric CO_2 therefore will depend on changes in canopy structure and the physiological effect of increased internal CO_2 on quantum yield efficiency (moles CO_2 fixed / mol quanta absorbed). The quantum-yield in the present atmospheric conditions with respect to CO_2 and O_2 at 30^0 C are identical for both C_3 and C_4 plants (+ 0.053 mol CO_2 / absorbed Einstein) (Ehleringer & Björkman, 1977) (Fig 27).

C_4 photosynthesis has a higher energy requirement. Two additional high-energy bonds (ATP) are used in the fixation of CO_2 for the regeneration of the CO_2 acceptor (phosphoenolpyruvate). ATP (and NADPH) generation is light dependent, hence the C_4 photosynthetic pathway might result in a lower efficiency of light utilization at low light intensities. A lower quantum efficiency for CO_2 fixation would be an important disadvantage in shaded habitats. Under present atmospheric conditions with regard to oxygen, the O_2 inhibition of the quantum yield in C_3 plants offsets the additional ATP requirement of the C_4 pathway at 25-30 ^oC.

Under conditions of sufficient soil moisture, a C_3 plant will have greater potential for C gain at low temperatures, while C_4 plants appear to be rather insensitive to temperature (Fig 28). The quantum-yield of a C_3 plant is strongly dependent on both the intercellular CO_2 concentration and leaf temperature (Fig 29). Photosynthesis continues to increase with the rise of the concentration of CO_2 and the sensitivity to high temperatures of a C_3 plant is partially offset by the increased CO_2 concentration, enabling stimulated photosynthesis at higher leaf temperatures (Fig 30). The relative stimulation of the photosynthesis in combination with high CO_2 levels is accentuated by higher leaf temperatures. These changes in quantum-yields are due to changes in the O_2 inhibition. The quantum-yield of a C_4 plant is independent of the intercellular CO_2 concentration, which is high due to the concentrating pathway, over a wide range of temperatures. The independence is a direct result of the suppression of photorespiration.

5.1.3 Temperature.

When otherwise similar C_3 and C_4 plants compete, temperature is an important determinant of the outcome. Hofstra and Hesketh (1975) found net photosynthesis per unit leaf area of _Atriplex_ _nummularia_ (C_4) to be quite inferior to corn (also C_4) at several temperatures, however Jones _et_. _al_. (1969) found _A_. _nummularia_ to be superior to corn when net photosynthetic rates per unit leaf were measured for whole plants under field conditions. Apparently _A_. _nummularia_ could carry on photosynthesis at approximately

67% of the maximum rate for individual leaves whereas Zea mais was functioning in the field at approximately 35% of maximum leaf rates.

Dormancy of seeds and buds plays a role, but the earlier, more rapid growth of a C_3 species during the spring when temperatures are still cool, was the factor that appeared to account for the differences in performance of C_3 and C_4 species (Fig 31) (Pearcy et al., 1981). This mechanism can create a niche separation in mixed stands, as resource utilization will be separated in time (Kemp & Williams, 1980). As a result the maximum standing crop in monotypic meadows of Puccinellia maritima (C_3) and Spartina anglica (C_4) are temporaly separated (Fig 32) (Long, 1983). This will significantly enhance the competitive advantage of the C_3 pathway in a higher CO_2 environment. However, with the increase of atmospheric CO_2, the temperature is also expected to rise significantly. The C_4 species than regains some of its competitive advantage over the C_3 species as the photosynthetic capacity of a C_3 plant can be greatly reduced by temperature. For two important salt marsh species from the Dutch coasts (Spartina anglica and Puccinellia maritima) the net photosynthetic rate of Spartina becomes higher above 11 ^{o}C compared to Puccinellia (Fig 33; Long, 1983). However, many C_3 and C_4 plants show an acclimation response which results in a shift in the optimum temperature toward the temperature at which the plant has been most recently acclimated (Mooney et al., 1977, Kemp & Williams, 1980).

5.1.4 Water-use efficiency (WUE).

WUE is the ratio between net CO_2 exchange rate to transpiration rate, also indicated as the P/T (photosynthesis to transpiration) ratio. These two seemingly unrelated characteristics are both closely related to the conductance of the stomata for water vapor and are therefore largely dependent on the same property of the plant (Raschke, 1979; Fig 34). Typical water-use values are 300 g H_2O / g DW for C_4 and 600 g H_2O / g DW for C_3 species (Kindl & Wöber, 1975).

Stomata open when exposed to light. The stomata become narrower and the stomatal resistance increases (or the stomatal conductance decreases) when the ambient CO_2 concentration (C_a) increases. The stomatal aperture is modified by the relative humidity of the surrounding air. This effect counteracts the opening response to high light and high temperatures. The magnitude of the stomatal responses to a higher C_a varies greatly among species.

In most C_3 and C_4 plants stomatal conductance changes in response to a change in the C_a in such a way that the ratio C_i (internal CO_2 concentration) to C_a remains more or less constant (Fig 35). The values differ depending on the pathway. In C_3 species the ratio C_i/C_a ranges from 0.6 to 0.8, while in C_3 species this ratio amounts to 0.3-0.5. As stomatal conductance decreases, in response to increased CO_2, transpiration decreases proportionally in both C_3 and C_4 plants and provided other conditions remain unchanged, both will show an increased WUE. The stomatal closure and the resulting decrease of the transpiration might lead to higher leaf temperatures under high energy load. Heat damage of the leaves might than occur (Fig 36). In this aspect C_4 species are the least susceptible, an adaptation which effectively acts as a feedback mechanism.

Stomatal conductance can be manipulated experimentally and hence many of the prognoses are deduced from these experiments. Recently, Woodward (1987) showed the stomatal numbers to be sensitive to increases in CO_2 too, in a controlled environment. An increase of the CO_2 concentration from the pre-industrial value of 280 ppm to the present day concentration of 340 ppm caused a decrease in the stomatal density (number of stomata per unit leaf surface) of 67% in the leaves that had been initiated and developed during the treatments. A correlation between stomatal density and C_a can be found, in nature, in an altitudinal range (Woodward, 1986). More important for the assessment of the impact of changes in ambient CO_2 levels is the observation that a decrease in the stomatal density (40%) also has occurred, gradually and linearly with the increase of atmospheric CO_2 (21%), during the past 200 years (Woodward, 1987) (Fig 37+38). This information was gathered from the inspection of leaves of herbarium specimen. However, the experiments were extended to assess the response to higher levels of CO_2. Unexpectedly, the stomatal density did not respond to CO_2 levels exceeding the current level. The implication of this observation for the response to future changes, in the control of leaf gas exchange and hence WUE, is not known. Possibly an as yet not elucidated adaptive mechanism to gradual changes in natural populations. My conclusions rely quite heavily on this study as it illustrates the capacity of nature to adjust to changes. An as yet speculative implication would be that the natural selection has been in the direction of limiting water stress and not, as is inferred from many studies, to increase productivity.

The intercellular CO_2 concentration (C_i) reflects the interrelationships between photosynthetic rate and stomatal conductance. Photosynthetic water use efficiency is closely related to C_i. Thus, if C_i/C_a remains constant as mostly occurs in both C_3 and C_4 species, than at constant temperature and humidity, P/T is proportional to C_a for both C_3 and C_4 plants. Since C_i/C_a is lower in C_4 species, the constant of proportionality ($1-C_i/C_a$) may be two or more times larger than for a C_3 species. Under water limited conditions the CO_2 enhancement of growth in C_4 species may be greater than in C_3 species. If the stomata respond to maintain C_i constant, then the photosynthetic water use efficiencies of both C_3 and C_4 plants will increase in parallel (Fig 39). The photosynthetic WUE of C_4 plants will always be higher, but the relative improvement will be much greater for C_3 plants. Thus, with increasing C_a, the photosynthetic WUE of both C_3 and C_4 plants are likely to increase, but the relative improvements will depend on how stomata and consequently C_i, respond. However, Pearcy et al. (1981) showed, in an experiment in which the environmental conditions under optimal water supply allowed both species (a C_3 and a C_4 plant) to perform equally, that yield and performance were reduced in the same degree after reduction of the water supply. They argue that the importance of photosynthetic differences expressed prior to canopy closure are problably most important in deciding how the relative performance of the species will be, as yield is essentially the decisive parameter in ecosystem functioning.

Environmental factors that influence C_i/C_a will have a strong effect on the responses of photosynthetic WUE to increasing C_a. Species differences in the responses to these factors will be important (Fig 40). Predictions indicate that an increased CO_2 concentration will substantially increase the amount of biomass produced per water expended. Increased C_a should substantially increase plant productivity wherever water supply exerts an important limitation to growth, but under severe drought stress the final effect of a high C_a on productivity might be negligible.

The ratio WUE_{660}/WUE_{330} in a number of crop species is approximately 2.0 (Wong, 1980). The effect can be achieved by reduction in transpiration and increase in photosynthetic rates. One generalization can be made. C_4 plants show little response of photosynthesis to increasing CO_2 concentration above 340 ppm, but show considerable decrease in stomatal conductance which results in increase in photosynthetic WUE mainly because of reduction in transpiration. In contrast, C_3 plants increase photosynthesis considerably but the stomatal conductance is reduced to a lesser degree. However, any prediction deducted from the carbon fixation pathway can only be a generalization. WUE improvement in relation to C_a in some C_3 species is higher than the improvement in some C_4 species.

An improved water status of a leaf under increased CO_2 may increase the rate of leaf expansion and the rate of canopy development. Since elevated C_a probably leads to improved water status, an increase in the xylem water potential and an increased supply of photosynthetic products, rates of leaf expansive growth should be accelerated. The growth of leaves is most important in determining productivity when the canopy is incomplete and a substantial portion of the incident light is not intercepted by the plant. In this situation canopy development and biomass accumulation are approximately exponential.

Faster canopy development in elevated CO_2 increases not only canopy CO_2 uptake but also canopy transpiration. Nevertheless, increased CO_2 concentration should still have a beneficial effect on WUE. The transpiration rate per unit leaf area is significantly lower in plants grown in elevated CO_2 environments, but virtually indistinguishable if expressed on a per plant basis (Fig 41). Thus, the ultimate result of increased CO_2 on the transpiration rate of a fully developed plant community, especially under drought stress, remains as yet unclear.

The climate model of Manabe & Wetherald (1980) did not calculate a change in soil moisture, due to a climatic change, for the latitudes north of 48^0 North (Fig 42). Hence, water availability might remain unchanged. The modeling of Revelle & Wagoner (1983) resulted in an estimated 40-70% decrease in streamflow in the western USA. However, Aston (1984), Idso & Brazel (1984), Wigley & Jones (1985) predicted, on basis of hydrological modelling, taking into account the reduction of evapo-transpiration, an increase in stream-flow (Fig 43) or enhanced ecosystem water surplus. Idso & Brazel (1984) reached positive values between 40 and 60% for drainage basins in Arizona. A change in the same order of magnitude but with a different sign! The response of the vegetation, provided water was limiting, on the precipitation / evaporation ratio is not taken into account in any of these studies. Hence, the net effect of all changes, associated with higher CO_2 levels, on water availability to plants is as yet rather uncertain. The plants need less water while the availability of water might increase. The occurrence of drought stress than might be limited simultaneously by the two related mechanisms. The reduced water-stress might then stimulate community biomass, which in turn increases evapotranspiration, closing the circular argument. The effect of reduced evapotranspiration on water-surplus is largest in arid areas, where C_4 plants, less susceptible to drought, are frequently dominant. The uncertainty is compounded by the observations that the positive effect of high CO_2 levels on leaf area development can be reduced almost completely if a soil-water deficit develops (Fig 44) (Morison & Gifford, 1984) but also that a greater relative CO_2 stimulation of growth or yield occurs under drought-stress conditions (Cure, 1985). Obviously, much more research is required.

5.1.5 Growth form: determinate vs. indeterminate.

The magnitude of the effect of increased CO_2 might be influenced by the growth form of the species. Growth forms that are indeterminate and have a large potential "sink" for photosynthates are considered more likely to show stimulation of photosynthesis with elevated CO_2 than species that are determinate and have only limited potential for further growth (Oechel & Strain, 1985). Under competitive circumstances larger plants tend to become larger and smaller plants relatively smaller until some are eliminated. Such trends may often be traced back to the influence of seed weight. Seedlings with larger than average food resources are most likely to become dominant in the population. This process of increasing dominance of large individuals can be mitigated or accelerated by the response of the plant, determined in part by the photosynthetic pathway, to increasing levels of carbon dioxide.

One area of concern in ecological studies is predicting the potential growth responses for plants in an ecosystem context where nutrients may limit the potential for growth and where changes in WUE may alter patterns of moisture limitation on growth. Species with different carbon fixation pathways may react differently in the rate of transpiration with respect to soil-moisture availability. Further, elevated C_a does not necessarily lead to increased growth. Plant processes using assimilated CO_2 have evolved at lower CO_2 levels. With elevated levels of CO_2, sucrose supply may increase and nutrient deficiencies may severely limit growth (Tolbert & Zelitch, 1983).

Enhanced leaf development can become a problem if the absorptive root area shows a relatively lower increase than the leaf area. However, studies of root growth generally show that in an elevated atmospheric CO_2 concentration most plants allocate proportionally more of the extra carbon below ground. Species with bulbs, rhizomes, corms or tubers will respond favourably to increased CO_2. Differential allocation of carbon to various organs, while atmospheric CO_2 increases, will cause changes in competitive behaviour that will be very important in natural ecosystems. Plants that produce relatively larger roots may gain an advantage in obtaining soil water and nutrients. On the other hand, an increased root-to-shoot ratio changes the balance of respiring to photosynthesizing tissue. If total plant respiration increases faster than total plant net photosynthesis, plant carbon balance will be affected negatively.

Plants grown under high CO_2 concentrations frequently show higher rates of height growth (Sionit *et al.*, 1985). Perennial plants and annual plants with indeterminate growth became taller at higher CO_2 concentrations (Paez *et al.*, 1984). Determinate annuals have been shown to increase in height at a faster rate under high CO_2, but the final height attained was not affected. For many temperate plants, however, rates of height growth and canopy development in the spring may be more important than the final size in determining competitive success. Plants that start growing earlier and exceed their competitors in rate will eventually interfere with light availability to the slower growing plants.

The variability in the response to increased CO_2 availability can be very high in (some ?) species as was demonstrated by Wulff and Miller-Alexander (1985). This intraspecific variation suggests that selective changes may occur quickly in a population. And also, that any effect induced by elevated levels of CO_2 can become unimportant if the offspring of another individual responds relatively more favourable to another change (e.g. temperature).

5.1.6 Partitioning, changes in shoot/root ratio.

Root growth and microbial activity, whereby nutrient availability increases, is stimulated by increased atmospheric carbon dioxide (Rosenberg, 1981, Goudriaan and Ketner, 1984). In species where a substantial amount of the biomass is stored in below-ground organs, the stimulatory effect of CO_2 fertilization on biomass allocation into these parts is relatively high. The increase of yield by doubling CO_2 was 50% in sugarbeets (*Beta vulgaris*) (Ford and Thorne, 1967), 75% in potato (*Solanum tuberosum*) (Collins, 1976), 100% in konjak (*Amorphophallus konjac*) (Imai and Coleman, 1983) and even reached 150% in casava (Manihot esculenta) (Imai et al., 1984).

5.1.7 Negative feedbacks by accumulated metabolites.

Growth depends on the export of photosynthetic products from leaves to growing regions, "sinks", of the plants. In a number of species export from leaf sources increases linearly with increased net CO_2 uptake. If new "sinks" are not generated by growth, leaf photosynthesis may decrease and the initial enhancement of growth will be reduced.

Observations suggest that in some plants, high levels of CO_2 produce an imbalance of N assimilation. The effect of such unbalanced growth on the quality of the plants as a food source (Lincoln et al., 1982, 1984) and seed viability remains to be investigated for many species (plants and grazers), their interactions and the ultimate impact on an ecosystem. Glucose can produce a stimulation of NO_3 uptake, the reduction of which has a high energy requirement (as does the reduction of sulphur compounds). Sucrose starvation arrests the cell cycle in meristematic regions (Farrar, 1985).

Many of the results are obtained in experiments where the plants were subjected to short-term increases in C_a. The response may change after long-term exposure. Tissue & Oechel (1987) found that the sedge Eriophorum vaginatum, a tundra tussock species had similar photosynthetic rates when photosynthesis was measured at the growth CO_2 concentration (Fig 45). The loss of photosynthetic capacity might be attributed to a reduction in the level of RUBISCO. The lower carboxylation capacity would tend to bring the carboxylation rate in line with the electron transport capacity, as long as this does not change as well (Pearcy & Bjorkman, 1983). This observation essentially illustrates that it might be entirely possible that an increase of the CO_2 levels at the slow rate as is observed (MacDonald, 1982) and predicted in a number of scenario's, might have no effect what so ever on photosynthesis, because the fertilizing effect might be balanced by decreased activities of enzymes and transport-chains, decreased levels of enzymes, physiological restrictions and evolutionary adaptation.

5.1.8 Flowers, seed numbers, seed size.

More reproductive structures will be formed in a high CO_2 environment, because of the increased number of branches and growing tips, which result from a reduction in apical dominance. These will give rise to more flowers if the appropriate environmental and hormonal stimuli are present (Sionit _et al_, 1981). Effectively the same effect is achieved by reduced floral abscission (Rogers _et al_., 1983a,b). A reduction in apical dominance has been observed also by Paez _et al_., 1980. However, this effect was only observed during the initial growth of the normal as well as the high CO_2 experimental plots. The accelerated maturation was the sole cause of the initial change in apical dominance. At maturity, there were no differences in the number of branches or fruits produced at the different CO_2 levels. Life cycles of most C_3 species (and some C_4 species, e.g. maize) are speeded up and differences seen early in life cycles do not always translate into more biomass or more reproductive output at the end of the growing season (St. Omer & Horvath, 1983; Garbutt & Bazzaz, 1984; Bazzaz _et al_., 1985). Conversely, there are some indications that life cycles of some C_4 species (e.g. Sorghum) might even slow down (Carter & Peterson, 1983), but Bazzaz _et al_. (1985) attributed that observation to faulty experimental design. The plants were not allowed to complete the life cycle.

Seed size may increase in a higher CO_2 environment, but decreasing seed sizes have also been observed (in _Plantago lanceolata_; Wulff & Miller-Alexander, 1985). Although larger seeds may germinate more slowly (lower volume to surface ratio), larger seeds can produce seedlings that develop faster. But, large seeds may disperse less easy. The effects of these counteracting responses on community structure have to be elucidated yet. However, most agricultural (greenhouse) species will increase the reproductive output as CO_2 increases (Kimball, 1983). Reproductive success is essential for species survival in a natural ecosystem. Even a very strong competitor in vegetative growth and persistence will not survive in the long run without some recruitment of new individuals in the community (Oechel & Strain, 1985).

5.1.9 Tillering.

One of the most important effects of a higher CO_2 level may be an increase in tillering (branching) rates. In the sedge Eriophorum vaginatum, for example, the tillering rate increased almost sixfold at 680 ppm CO_2 compared with 340 ppm CO_2, despite relatively little changes in other growth parameters (Tissue & Oechel, 1987). Increasing the carbohydrate supply by growing plants under more elevated CO_2 concentrations and better environment apparently activates meristem production and development leading to tiller appearance (Oechel & Strain, 1985). Increased allocation to asexual reproduction is not universal. The mean dry weight of stolons per plant increased in arctic populations of Saxifraga flagellaris at elevated CO_2, but decreased in alpine populations (Billings et al., 1983a, 1983b). This points out that the variability in the response patterns also applies to different ecotypes of the same species.

Elevated CO_2 has been shown to affect the phenology and senescence of plants. Annuals may develop more quickly under elevated CO_2, reaching full leaf area, biomass and flower and fruit production sooner than plants at ambient CO_2 levels (Paez et al., 1980, 1983, 1984) In a competitive situation, early leaf and seed production could shift the population dynamics and competitive relationships. Winter annuals from the California chaparral developed faster but also died earlier as atmospheric CO_2 increased. There is also evidence of delayed senescence of some species under elevated CO_2. The arctic cotton grass Eriophorum vaginatum retained maximal photosynthetic capacity later into the fall when grown at high CO_2 (Tissue & Oechel, 1987).

5.1.10 Shading and selfshading.

Leaf biomass density was estimated to be about 300 g C m^{-2} for forest, grassland and agricultural area. Typically leaves contain about 20-40 g C m^{-2} leaf area, so that annually about 8-15 m^2 of leaf area is produced per m^2 ground area (LAI = leaf area index, m^2 leaf per m^2 ground). A LAI of 3 is sufficient for complete light interception, hence the net primary production is saturated with respect to biomass (Goudriaan and Ketner, 1984). In most plant populations, especially if a closed canopy occurs, the light level within the canopy will be limiting photosynthesis considerably. The potential enhancement of photosynthesis due to increased levels of CO_2, can than not be taken advantage of.

5.1.11 Palatibility and value for consumers.

Herbivore grazing has a profound effect on plant productivity and could reduce the anticipated production increase. The leaves of plants growing in elevated CO_2 regimes have an increased supply of carbohydrates available. A hightened carbohydrate content can lower the relative protein content of the food-source, a response observed in many crop species (e.g. Patterson & Flint, 1982; Sionit, 1983; Lincoln _et al_., 1984). This enhanced production of carbohydrates is generally restricted to C_3 species. The resultant higher C/N ratio reduces the nutritive value of the food source to herbivores. Two responses, and the intermediate proportions thereof, might develop. Unchanged intake of food, resulting in a decrease of the growth rate, because of nitrogen deficiency, or increased feeding without changes in growth rates.

Lincoln _et al_., (1984) studied the response of herbivorous insects to leaves of a C_3 plant grown in a high (650 ppm) CO_2 environment. The C/N ratio of the leaves increased 9%, and the relative leaf nitrogen content decreased 11%. The herbivores increased the consumption rate by 81% in this experiment but the growth rate nevertheless was reduced by 12%. Hence, the almost doubled grazing rate could not compensate for the reduced nitrogen content and conversion efficiency.

Because the change in growth rates is only minor as compared to the feeding rate it might be expected that the effect of an increase in atmospheric CO_2 on population density (through larval growth-rates) is also of minor consequence. The response of an insect to increased ambient CO_2 concentrations is the opposite of the response of a plant. The insect has to open the spiracular valves to vent metabolic excess CO_2 (and to inhale oxygen). The gradient C_i/C_a is reduced in a high CO_2 environment. Spiracular valve opening has therefore to occur more frequently or has to be prolonged. The insect will then, in analogy with plants, loose more water. This negative influence on the insect water balance will, at least partially, be offset by the higher water content of the ingested phytomass grown in an atmosphere with a higher CO_2 content. The total balance of all these synergistic or conflicting aspects of increasing CO_2 levels on plant/herbivore interactions, especially on community or ecosystem level is as yet unknown. The balance will be different for many predator-host combinations (e.g. the carbon pathway of the host plant is of importance). It might be deducted that insect herbivores of C_4 plants will experience water stress sooner in a high CO_2 environment which in turn might influence fecundity, hence possibly reducing population sizes and so offsetting the advantage of C_3 plants in a community.

5.1.12 Production.

Commonly 25-50% of the carbon in sucrose is lost by respiration within 24 h of its acquisition, and typically a mesophyte (plants from temperate climates with normal amount of moisture) will respire up to 70% of the carbon it has acquired during its lifetime (Farrar, 1985). Yet, photorespiration is not included in these figures. Dark respiration, a continuous process and not restricted to darkness, is a complex of three types of processes; (1) metabolism of carbon compounds; (2) electron transport and (3) recycling of phosphorylated and reduced products (ATP, NADH, NADPH). Sucrose is the major substrate.

The respiratory network will normally catalyse the partial oxidation of sugars to CO_2, and the remainder of the carbon is withdrawn from the network as a variety of carbon skeletons for biosynthesis (e.g. aminoacids, polysaccharides). An increased ambient CO_2 pressure implies an increased resistance to CO_2 efflux from non-photosynthetic tissues or in darkness. Recycling of ADP is held to be the major brake on respiration, an energy providing process. The response of plants to CO_2 fertilization suggests that increased internal CO_2 concentrations do not influence respiration negatively, an effect which could occur if the processes were sensitive to shifts in the chemical equilibrium. The processes are catalysed. Respiration associated with growth is a function of the supply of substrate while respiration associated with plant maintenance is independent of the supply of substrate.

For salt marshes composed of _Spartina patens_, _Distichlis spicata_ and _Scirpus olneyi_ 60% of the net seasonal community carbon gain was lost at night or during spring and autumn when the rate of CO_2 assimilation was low. During the period of maximum production this loss through respiration was reduced to 34% of the daily uptake (Drake & Read, 1981). This assimilatory/respiratory balance of the community as a whole leaves 40% of the production available for export or accumulation.

Kimball (1983) has analysed 430 observations on the influence of higher C_a on agricultural yield. Considering all the mature agricultural crops, the relative yield increase was 1.36 (Fig 46). Experiments with noneconomic plant species, single or in community environments, into the effect of long-term increased CO_2 levels, have been neglected until now (Wittwer, 1985). The tundra study (Tissue & Oechel, 1987) is the only exception while recently research has been undertaken on marsh ecosystems (Drake _et al_, 1985, 1986).

A parameter, the biotic growth factor (b) for the effect of increases in the atmospheric CO_2 concentration is introduced by Oeschger _et al_, (1975). This parameter, the ratio (b) is the fractional increase in the rate of CO_2 fixation to the fractional increase in partial pattern of CO_2 allocation the value of 0.27 has been used. In cotton (C_3) (b) ranged from 0.41 to 1.03 and in maize Wong (1980) the phosphate limitation, via 0.3 under nitrogen limitation to 0.7 under optimal supply of nutrients in greenhouse experiments (Goudriaan and de Ruiter, 1983). In cotton the response (b) was dependent on the nutrient level (Fig 47) but the response decreased with higher CO_2 levels. The same was true for the C_4 plant, but at the highest CO_2 levels the effect of nutrient limitations was only minor.

The total set of responses to changes in the two major variables; increasing atmospheric carbon dioxide and climatic change is a mixture of responses, checks and balances, structured as;

If ..., then ..., and possibly also ..., but ....

As might have become clear from the previous, the intraspecific and interspecific variability prohibits firm conclusions on plant responses to gradual increasing levels of atmospheric CO_2. Nevertheless, and stressing the caution that should be applied, I will conclude this chapter with a summary as presented by Idso (1983), probably the most outspoken in advocating the beneficial effect of CO_2 fertilization (Table V).

Table V. Summary biological effects of CO2. Individual plant level (Idso, 1983).

Increased levels of atmospheric CO_2 will generally lead to:
- increases in plant leaf area;
- increases in specific leaf weight;
- increases in the number of branches, meristems, tillers;
- increases in fruit / seed numbers;
- increases in fruit / seed size;
- better germination of seeds and spores;
- earlier production of flowers;
- accelerated maturity;
- higher dark fixation of CO_2;
- increases in plant tuberization;
- increases in symbiotic mycorrhizal activity.

5.2 Community level.

5.2.1 Production agricultural crops.

The CO_2 fertilization effect on agricultural crops is an area of dispute. The response of some species is well known from greenhouse experiments which were generally performed during short periods or in favourable and well regulated conditions (Rogers et al., 1983b). Cultivars that are already close to their maximum potential yields show only a minor effect of CO_2 enrichment (Kendall et al., 1985). The measured responses can not be extrapolated to the real-world field environment. A long term CO_2 fertilization effect has not yet been observed, in spite of a 25% increase in atmospheric CO_2 (Wigley, 1984). However, modeling (Palutikof et al., 1984a) of the effect of climatic change into the yield of agricultural crops in the United Kingdom, resulted in a negative impact for most species. This was attributed to changes in temperature and precipitation. It can be argued that negative effects will in the long run be offset, by breeding of adapted strains, technological counter measures (Cooper, 1982) and crop management (Rosenberg, 1982).

5.2.2 Grasses.

The low vegetation of the Alaskan coastal tundra, dominated by sedges and grasses, did not respond to doubling of the atmospheric CO_2, as nutrients were limiting in the natural habitat (Billings et al., 1984). In their experiments addition of nitrogen stimulated growth, however, the combined effect of nitrogen and CO_2 addition was not different from the response to nitrogen fertilization alone. It should be stressed that natural ecosystems were studied (in microcosms) which illustrates the very limited value of an extrapolation of the results obtained in greenhouse experiments to natural ecosystems which are in balance with the total set of constraints and stimuli. This is further elucidated by other experiments performed by this research-group. In Billings et al. (1983a,b; 1984) they reported also that a rise in temperature had a negative effect on CO_2 uptake of the community. This was attributed to stimulated rates of decomposition and soil respiration (Peterson et al., 1984).

5.2.3 Effects on trees.

A "natural" ecosystem where the possible fertilizing effect of CO_2 has been assessed comprises forests. Because it can serve as an analogy to salt marshes, solely in the aspect of naturalness, some results are included.

The short term response of the dominant species (Pinus ponderosa) in the coniferous forest of the western United States to increased atmospheric CO_2 (150 ppm above ambient) was a 84% rise in net photosynthetic rates (Green & Wright, 1977). The responsiveness was not altered by high temperature or decreasing water potential. The response was reduced, but not eliminated, in plant damaged by air polution oxidants.

The scaling-up of physiological responses, determined in small-scale and short term greenhouse experiments, is especially difficult in forest response modeling. The mixture of different species with possibly species-unique responses, and mixed age stands would produce many variables. Shugart and Emanuel (1985) therefore argue that the fertilizing effect of CO_2 on forests will be minor, especially eventual effect than will be of a lesser importance than the impact of climatic changes that might occur concurrently. It should be noted however, that the deposition of N (acid rain) from anthropogenic sources, especially in Northern forests, creates a situation in which enhanced CO_2 could very well be fertilizing. The increasing trend in the amplitude of the CO_2 signal is attributed for a large part to growth enhancement of northern boreal forests, which account for 30% of the amplitude as observed on Mauna Loa (D'Arrigo et al., 1987). The effect on tree growth as deduced from tree-ring width is still debated (LaMarche et al., 1984, Wigley et al., 1984). The enhancement has not yet been conclusively proven nor can it be discounted and is possibly dependent on the site of observation. Reduced tree growth, attributed to air-pollution and the possible increase in mid-latitude temperature, seems to be the rule at present (Solomon, 1986).

5.2.4 Salt marshes.

The great problem for salt marsh plants is to obtain CO_2 without the loss of water vapour through respiration. Although water as such is never lacking in salt marshes, it must be desalted at significant physiological cost. It is not energetically competitive for a plant to loose water through its stomata, yet the stomata must be open to receive CO_2.

The effects of increased CO_2 on the responses of individual plants as presented previously originate from controlled experiments in laboratories. Of the species occurring in the saline and brackish terrestrial vegetation of the Wadden Sea only two (Lolium perenne and Trifolium repens), from brackish pastures (TI in Table VI) have been studied in a competition experiment (Overdieck et al., 1984) in a high CO_2 environment, during two years. The results are illustrative for the restrictions that should be applied to an extrapolation of greenhouse experiments, with crop species, to natural vegetations. In the first vegetation period 50% and 72% respectively more total phytomass had accumulated in the 600 ppm glasshouse than in the glasshouse with ambient air. In the second vegetation period the increase in phytomass dropped to 13% and 17% respectively. However, the grass declined dramatically in both greenhouses as compared to the open-field control, while the differences between the greenhouses (CO_2 experiment) had disappeared. On the other hand, Trifolium repens benefitted from the carbon fertilization.

Spartina anglica (C_4) is a dominant species in halophytic pioneer communities (SS in Table VI), where it occurs in an association with Salicornia spp., and in the low salt marshes together with Puccinellia maritima (C_3). The effect of increased CO_2 on Spartina anglica and Puccinellia maritima is currently under investigation (Rozema, pers. comm.). The research on Spartina alterniflora on the Atlantic Coast of the USA was initiated much earlier and some of the results are considered applicable to the European salt marshes, at least to draw the attention to the many existing uncertainties.

Table VI. Distribution of major vegetation types of the Wadden Sea islands and Dutch mainland coastal areas, in ha, calculated from "Landscape and vegetation map of the Wadden Sea islands and mainland coastal areas, K.S. Dijkema, 1976.

	SS	ST	SP	SF	TU	TO	TI	TOTAL
Mainland								
Friesland	780	-	980	360	52	-	1320	3492
Groningen	1185	80	1550	280	-	-	66	3507
North-Holland	-	-	-	31	-	-	-	31
West Frisian Islands								
Texel	20	-	150	60	-	150	-	380
Vlieland	6	-	27	16	-	-	12	61
Terschelling	260	-	740	270	-	220	41	1531
Ameland	56	-	65	270	21	34	15	461
Schiermonnikoog	190	-	160	260	97	270	-	977
Rottum	91	-	44	-	-	22	-	157
Griend	-	-	7	-	-	-	-	7
TOTAL	2588	80	3723	1807	170	696	1540	10604

SS = Halophytic pioneer communities with *Spartina anglica* and *Salicornea europaea* within daily tidal range and on beach plains.
ST = Halophytic pioneer community with *Aster tripolium* on mud flats.
SP = Halophytic grasslands and dwarf shrub vegetation with *Puccinellia maritima*, *Limonium vulgare* and *Halimione portulacoides* on low salt marshes and beach plains.
SF = Halophytic grasslands with *Festuca rubra*, *Juncus gerardii* and *Agrostis stolonifera* on high salt marshes, brackish marshes and beach plains.
TU = Open communities with *Spergularia marina*, *Glaux maritima*, *Agrostis stolonifera* and *Juncus anceps* on beach plains and in young dune slacks.
TO = Closed grasslands with *Ononis spinosa*, *Lotus corniculatus*, *Agrostis stolonifera*, *Carex distans*, *Juncus maritimus* and *Scirpus rufus* on transitions between salt marshes or beach plains and young dune slacks or dunes.
TI = Brackish pastures with *Lolium perenne*, *Trifolium repens* and *Elymus repens* on the highest (grazed) salt marshes, often protected by low summer-dike.
Source: Dijkema & Wolff, 1982.

In ecosystems, growth and productivity are limited by many factors in addition to CO_2, and interactions among all these factors are possible. In a comparison between net photosynthesis in the laboratory and net photosynthesis in the field, Drake (1984) recorded a 8-fold reduction from the laboratory rate to the marsh community rate in <u>Spartina alterniflora</u>, due to the limitations imposed by the environment and the canopy. The ecological significance of the differences between the C_3 and C_4 pathway, relative to the tidal marsh habitat are not evident from field carbon exchange measurements. No differences in photosynthetic rates between a pure C_4 community (90% <u>Spartina</u>, 10% <u>Distichlis spicata</u>) and a mixed C_3/C_4 community were apparent. The greater biological potential of the C_4 species for photosynthesis under optimum conditions was offset by the greater effect of leaf N deficit in C_4 than in C_3 plants in the actual marsh environment.

The communities of the tidal mud- and sand flats (SS, Table VI) cover approximately 26 km^2 of the Dutch Wadden Sea. The observed annual production of these communities range between 390 & 600 g m^{-2} yr^{-1} . The effect of increased CO_2 on <u>Salicornia</u> spp. is unknown. Productivity in this part of the marsh is not limited by soil nitrogen (Dijkema, pers. comm.) and hence a minor increase in production might be expected if only the increases in the ambient temperature (C_4 plants benefit more) and CO_2 are taken into account. However, the rise of the sealevel can have a profound effect since the saline mudflats, covered by the Spartinetum and/or Salicornietum, have a vertical range of 0.9m. A relative sea level rise of lm, as is expected according to some scenarios, would destroy these communities provided no rise of the substrate level occurs simultaneously.

The low salt marsh, covering approximately 60 cm vertically, will be affected by changes in community structure and community productivity because of the rise in ambient CO_2. The saline low salt marsh is dominated by two communities (Puccinellietum & Halimionetum). The low salt marsh covers 37 km^2 of the coasts of the Dutch part of the Wadden Sea (SP, Table VI). The annual production of these communities ranges from 460 to 550 g

m^{-2} y^{-1} but a production of 1030 g m^{-2} y^{-1} was recorded in the Eastern Scheldt (Wolff *et al.*, 1979). See also Table VII. The low salt marsh, in the Wadden Sea, is dominated by *Puccinellia maritima* which species reaches a cover of 100% in floristic-sociological classifications (Dijkema, 1983). *Spartina anglica* is second in abundance except in the variants with *Halimione portulacoides* or *Aster tripolium*. *Puccinellia maritima* is a C_3 species and this community of the low marshes might change in structure. *Puccinellia* will benefit more, because of the pathway, from a rise in ambient CO_2. This enhancement of the production will be compounded because the soil N concentrations are limiting. C_4 plants are proportionally more affected by decreases in leaf nitrogen. However, the expected increase of the temperature will stimulate *Spartina* more. The relative magnitudes of the responses in these two species would determine the direction of the changes if sea level rise would not interfere.

Apparently, C_4 species are expanding their range or have at least been observed more frequently in grasslands during the last years. This is attributed to the rise in temperature which has occurred during this period. The three observations; temperature rise, CO_2 level rise and increased distribution of C_4 plants might be indicative for the possibility that temperature is the more influential stimulus. This is as yet purely speculative as N deposition (acid rain) could enhance C_4 production as well.

Elevated CO_2 levels promote the growth of roots in agricultural crops and reduce the shoot/root ratio. If *P. maritima* responds in such a way, the species may be capable to expand its range into higher regions of the marsh. In this and other species the changes in the microenvironment might counteract.

Increased shoot/root ratios because of flooding, and conversely decreased shoot/root ratios due to the stimulation of root growth by elevated levels of atmospheric CO_2. At this stage, however, it appears unlikely that the proportional dominance of *S. anglica* and *P. maritima* will change.

Table VII. Production (g DW m^{-2} y^{-1}) of salt marsh species and communities. A = above-ground; B = below-ground; ann. = annual production; max. = maximum observed production; * = studies in The Netherlands.

Association or species					Source
Plantagini-Limonietum	A	ann.	390 - 600	*	Ketner, 1972
	B	max.	1515	*	Ketner, 1972
Juco-Caricetum	A	ann.	290 - 460	*	Ketner, 1972
Juncetum gerardi (Baltic)	A	ann.	400 - 436		Wallentinus, 1973
Spartina patens	A	ann.	630		Valiela et al., 1976
	B	max.	6200		Valiela et al., 1976
	B	ann.	2600		Valiela et al., 1976
	A	ann.	6043		Hopkinson et al., 1978
	A	ann.	4160		Hopkinson et al., 1980
S. alterniflora	A	ann.	420		Valiela et al., 1976
	A	ann.	130 - 700		Kruczynski et al., 1978
	A	ann.	130 - 3000		ref. in Kruczynski, 1978
	A	ann.	2660		Hopkinson et al., 1978
	A	ann.	1380		Hopkinson et al., 1980
	B	max.	6600		Valiela et al., 1976
	B	ann.	3500		Valiela et al., 1976
	B	max.	2200		Smith et al., 1979
S. cynosuroides	B	max.	1300		Gallagher & Plumley, 1979
	A	ann.	1360		Hopkinson et al., 1978
	A	ann.	1130		Hopkinson et al., 1980
S. anglica	B	ann.	6000 - 6300	*	Vink-Lievaart, 1983
S. townsendii	A	ann.	720	*	Wolff et al., 1979
Juncus roemerianus	B	max.	1360		De la Cruz & Hackney, 1977
	A	ann.	240 - 950		Kruczynsli et a;., 1978
	A	ann.	240 - 2100		ref in Kruczynski, 1978
	A	ann.	3416		Hopkinson et al., 1978
	A	ann.	3300		Hopkinson et al., 1980
Halimione portulacoides	B	ann.	8000 -12500	*	Vink-Lievaart, 1983
Triglochin maritima	A	ann.	180	*	Wolff et al., 1979
	B	ann.	3500 - 4800	*	Vink-Lievaart, 1983
Elytrigia pungens	A	ann.	1010	*	Wolff et al., 1979
	A	ann.	1010	*	ref. Joenje & Wolff, 1979
	B	ann.	4400 - 7600	*	Vink-Lievaart, 1983
Limonium vulgare	A	ann.	230	*	Wolff et al., 1979
Puccinellia maritima	A	ann.	300 - 430	*	Wolff et al., 1979
Puccinellietum maritimae	A	ann.	410 - 500	*	Ketner, 1972
	A	ann.	1030	*	ref. Joenje & Wolff, 1979
Salicornia virginica	A	ann.	600		Zedler et al., 1980
Salicornietum	A	ann.	200 - 400	*	Joenje, 1974
Salt marshes Wadden Sea	A	ann.	400 - 500	*	Alberda, 1974
Juncetum gerardi	A	ann.	430		Wallentinus, 1973
Juncus gerardii (USA)	A	ann.	620 - 4450		Linthurst & Reimold, 1978

Not only because of the possible feedback as suggested above but more because a temperature increase, which is envisaged, will stimulate Spartina more than the estimated enhancement of the C_3 species (Puccinellia).

Summary of possibilities.

C_3. Increased growth rates of plants. Increased water content of plants. Reduced C/N ratio. Increased grazing of herbivores. Herbivores earlier waterstressed but water content of food is raised. Depressed plant productivity.
Or; Protein deficiency, reduction in numbers and/or viability of offspring. Reduced population size. Reduced grazing. Additional increase of plant production.

C_4. Relative low increase in growth rates and water content. C/N ratio less susceptible. No increased herbivory. No compensation for water stress in the food source. Reduced viability and fecundity. Reduction in number of grazers. Enhanced plant productivity.

However, the interactions between the components of these aspects of ecosystem functioning are largely (virtually) unknown, but increased herbivore feeding is the most likely effect of CO_2 enrichment, provided the nutritive value changes negatively.

The as yet unpredictable response of ecosystems to the occurring changes in their environment is also recognized by Idso (1983), one of the most outspoked advocates of the imminent beneficial (for man) impact of increasing atmospheric carbon dioxide (table VIII).

Table VIII. Summary biological effects of CO2. Community level (Idso, 1983).

Total community biomass will increase. A reliable estimate of the magnitude of the increase in natural ecosystems is not possible.

Community composition will change. The variability in responses between species having the same pathway prevents predictions of what species will become dominant if the species composition changes and what if the existing species composition remains unchanged. But, in communities in which some species have the C_4 pathway of photosynthesis and others have the C_3 pathway, the C_4 species will decline relatively, provided no temperature effect will occur.

Life cycles of most species will accelerate. Changes in timing of flowering and seed production may affect animal pollinators and consumers. The combined effect of increasing temperature and hence duration of the growing season and CO_2 increase is as yet unpredictable.

6 Summary and conclusions.

It should be stressed that the conclusion reached, is not concerned with climatic change *per se*, but solely reflects the assessment of the possible impact of gradually increasing carbon dioxide levels in the atmosphere. A few remarks should preceed this conclusion.

The role of carbon dioxide in plant and ecosystem functioning has been largely ignored in research other than agricultural and especially greenhouse crop yield experiments.

The physiological response of a plant, as determined in relatively short-term experiments, has too frequently been scaled up without proper scientific evidence or confirmation. Evolutionary adaptations, the origin of ecotypes, phenotypes and the long-term effects of feedback mechanisms have largely been ignored, partly because of the difficulties and imponderables involved in the design of conclusive experiments, partly because some aspects would need very long-term observations.

Nevertheless, any observation is, essentially, taken on face value, without judgement of contradictory results. However, the little information that has been obtained in studies into the response of natural populations, has received precedence.

Summary.

Most results are obtained in experiments where the experimental CO_2 concentration was changed, from ambient, to the experimental level instanteneously. These plants were in all aspects adapted to these ambient levels and the response to the change was determined. However, the changes in atmospheric CO_2 will proceed very slowly and gradually. Plants and plant populations have a long time (many generations) and the capacity to adapt to new environmental stimuli. The few studies in which long-term observations were made showed this.

In only one species (*Spartina anglica*) the C_4 pathway is ascertained. Of the two other salt marsh species from the Dutch coasts that might have this pathway (which is not yet conclusively determined) only *Halimione* is an important species. The soil-characteristics requirements are rather typical and soil and temperature constraints have already a large influence. Nevertheless this species is apparently already expanding its range. This is attributed to the slight change in temperature that is thought to have occurred in the last decade. The species is a successful competitor as it recolonizes a suitable area, within a few years, after death due to severe frost. The consequences of the, possible, C_4 pathway will not be of much importance.

A competive situation, in which the photosynthetic pathway might be of influence for the outcome exists between *Puccinellia* and *Spartina*. *Puccinellia* could gain some profit from increasing CO_2, but temperature and waterlogging will affect this species also more. The final impact is dependent of the relative magnitudes. But, it is expected that the sea level rise, increasing temperature and carbon dioxide will balance to a large extend.

The salt marsh is a harsh environment, reflected in species paucity. Large environmental fluctuations already occur (temperature, soil aeration, water stress), to which the plants have adapted. The variability is also reflected in the large interannual variation in productivity. CO_2 fertilization might ease the stress, but it is not expected that the range in production will change notably.

Below ground biomass might increase. However, the rate of mineralization will change also, although it is not yet known if this rate will change in the same relative magnitude. If below ground biomass, or soil organic content, continues to increase it will effectively lower the amount of available nutrients. As nutrients are frequently limiting, it might as well occur that the production is negatively effected.

The direction of plant adaptation might go in the direction of limiting water stress. This does not imply an increased production of structural carbohydrates, which also is limited by light and nutrient supply.

The impact on aquatic organisms is an area of more concern. pH decrease and the resultant increase in concentrations of toxic heavy metal ions (in the reactive form) could reach levels in which an effect will be experienced by some organisms. This might mitigate the likely stimulation of primary production as CO_2 uptake is preferred mostly. It is therefore not expected that total production will change much as warming and the resultant changes in upwelling and mixing will rduce nutrient availability. However, species composition might change and this could have an impact on the foodweb.

Conclusion.

The impact of rising levels of atmospheric carbon dioxide on halophytic ecosystems will be minor, and probably inconsequential, compared to the impact of sea level rise and climatic change.

The impact of rising levels of atmospheric carbon dioxide on the ocean could have consequences for the functioning of this ecosystem. The possible deleterious effects will be delayed for some decades, but research into the effects should be undertaken soonest, most of all because of the size of the system involved and the irreversibility of some, possible but not yet proven, effects on a global scale.

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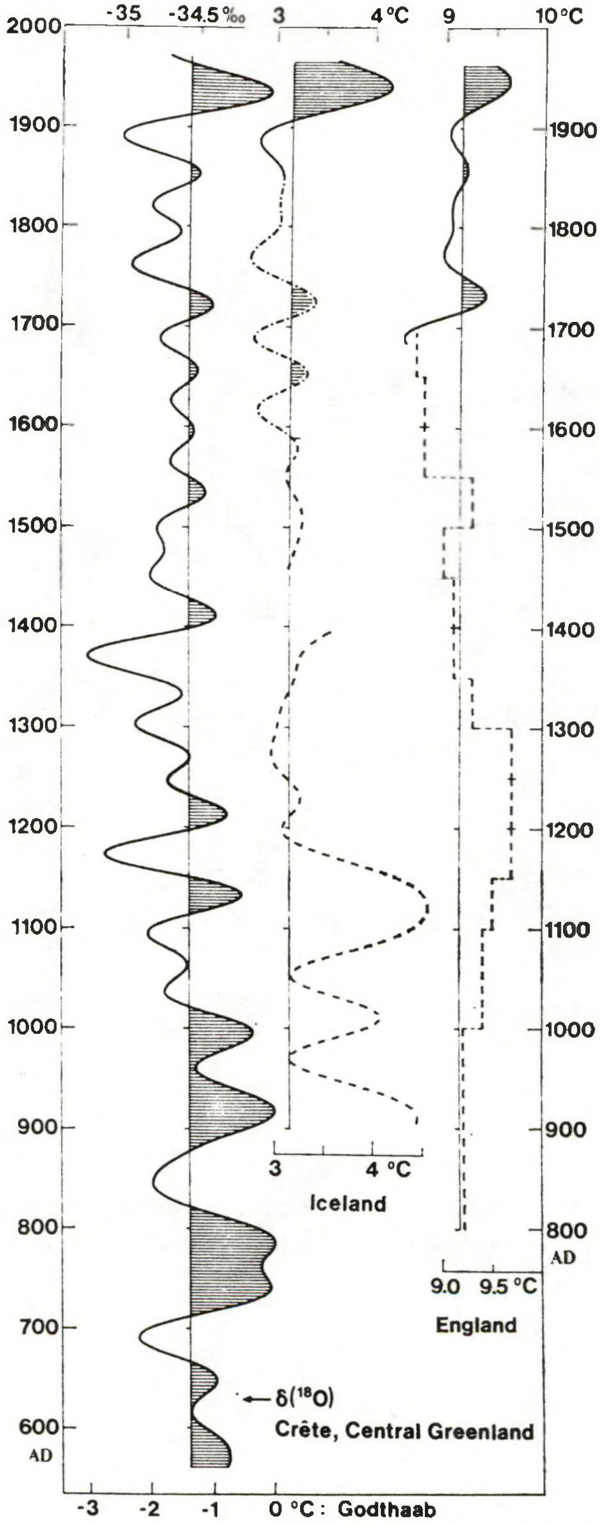


Fig 2. The temperature record of some localities in the Northern Hemisphere as reconstructed from ice-cores and direct observations. The expectation of a natural cooling period now is deducted from these and comparable data (after Dansgaard et al., 1975).

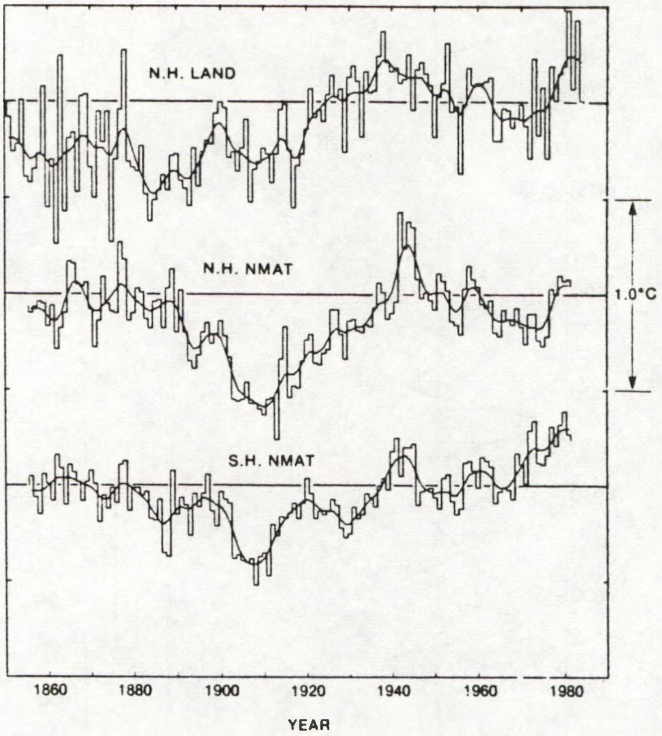


Fig 3. Comparison of Northern and Southern Hemisphere surface air temperature fluctuations. NMAT = nighttime marine air temperatures. (from Wigley *et al.*, 1985).

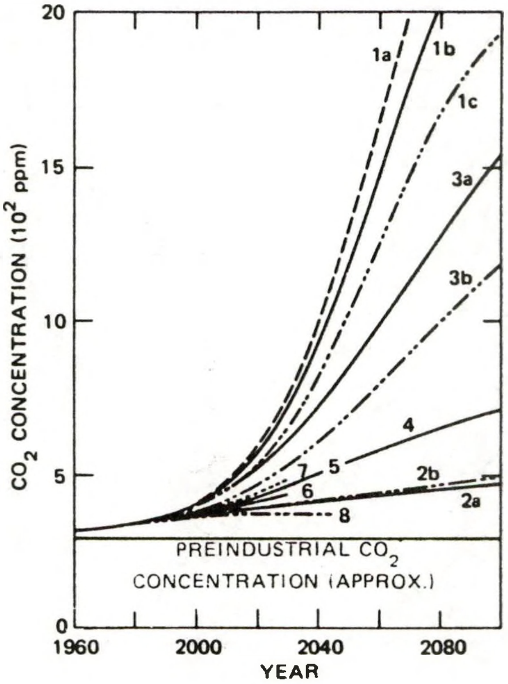


Fig 4. Projected atmospheric CO_2 concentrations for various scenarios. 1. Siegenthaler & Oeschger, 1978; Upper limit. a. biosphere growth factor = 0; b. biosphere growth factor = 0.2; c. airborne fraction (AF)= 0.55. 2. Siegenthaler & Oeschger, 1978; Lower limit. a. biosphere growth factor = 0; b. biosphere growth factor = 0.2 and AF= 0.55. 3. Keeling & Bacastow, 1977; a. model result; b. AF= 0.55. 4. Rotty & Marland, 1980; AF= 0.55. 5. IIASA High Scenario, AF= 0.55. 6. IIASA Low Scenario, AF= 0.55. 7. IIASA High Scenario, High Coal Variant, AF= 0.55. 8. Lovins *et al.*, 1980, AF= 0.55. (after Perry, 1982).

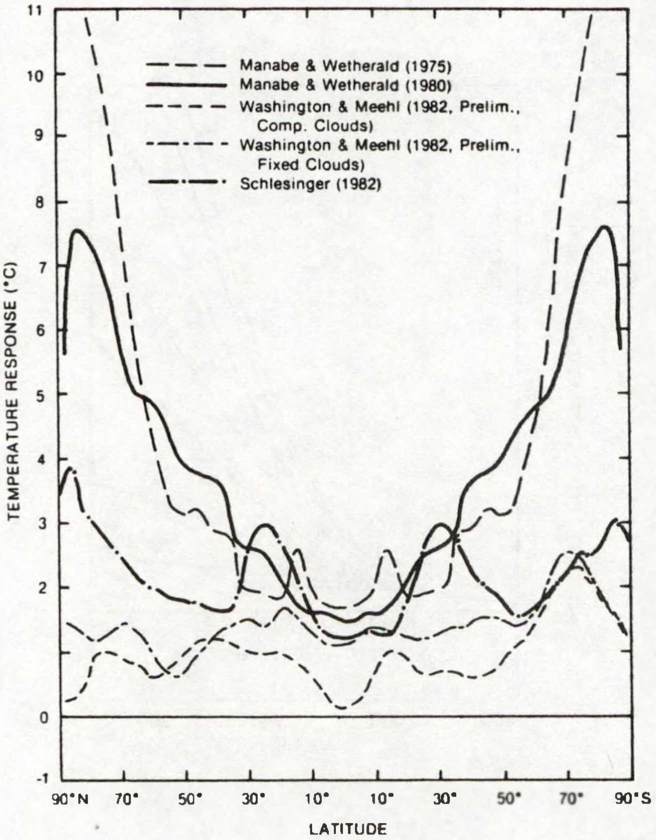


Fig 5. Equilibrium response of temperature in various general circulation models versus latitude. (from Hoffert & Flannery, 1985).

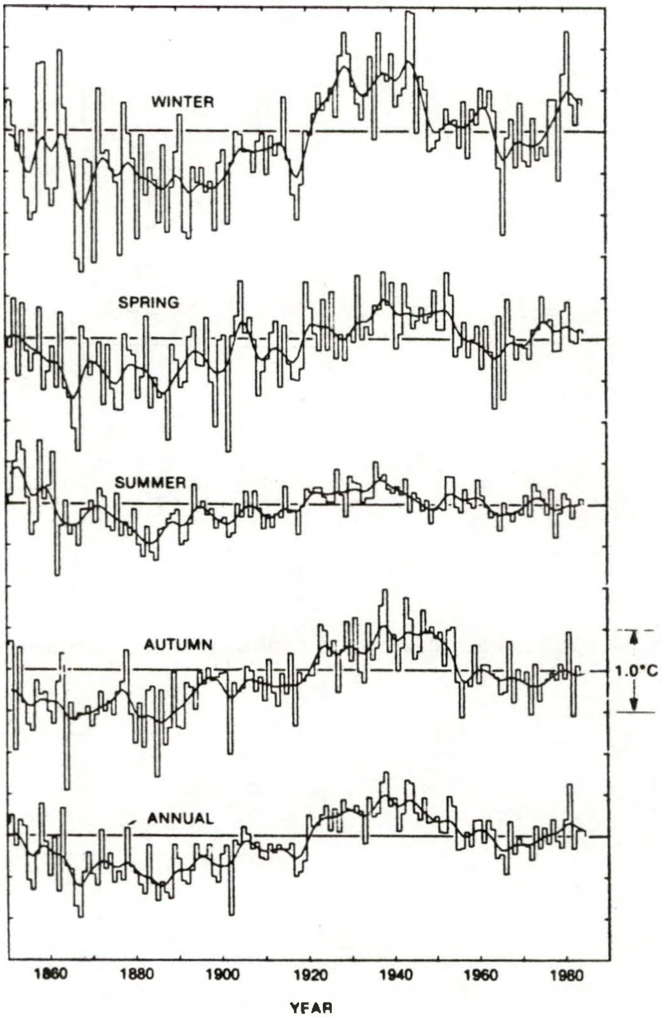


Fig 6. Arctic (65^o-90^oN) surface air temperature fluctuations by season. (from Wigley et al., 1985).

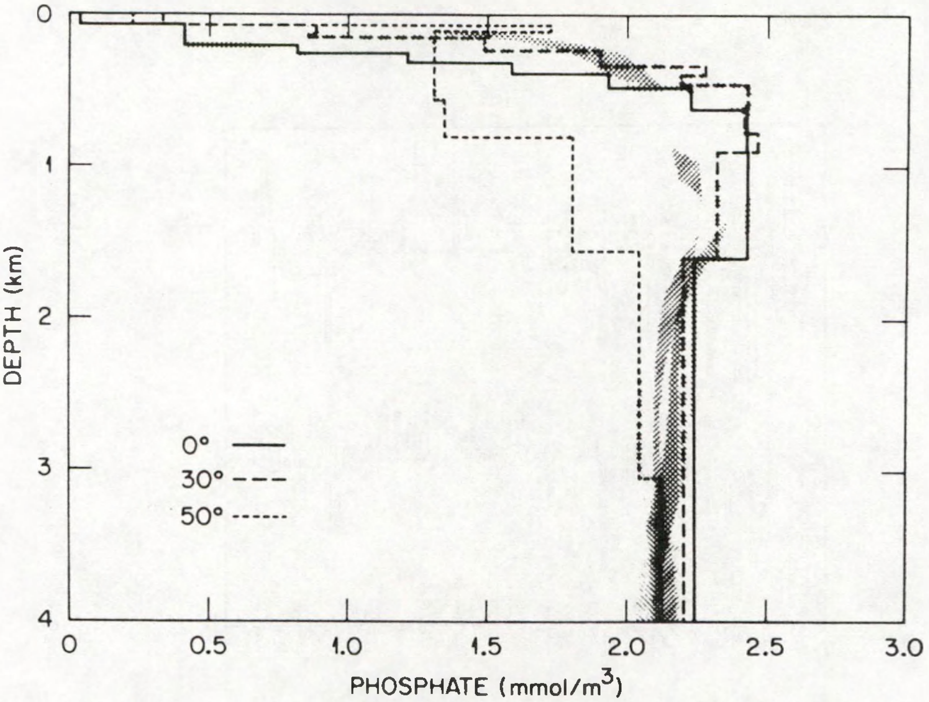


Fig 7. Depth profile of oceanic phosphate concentration.

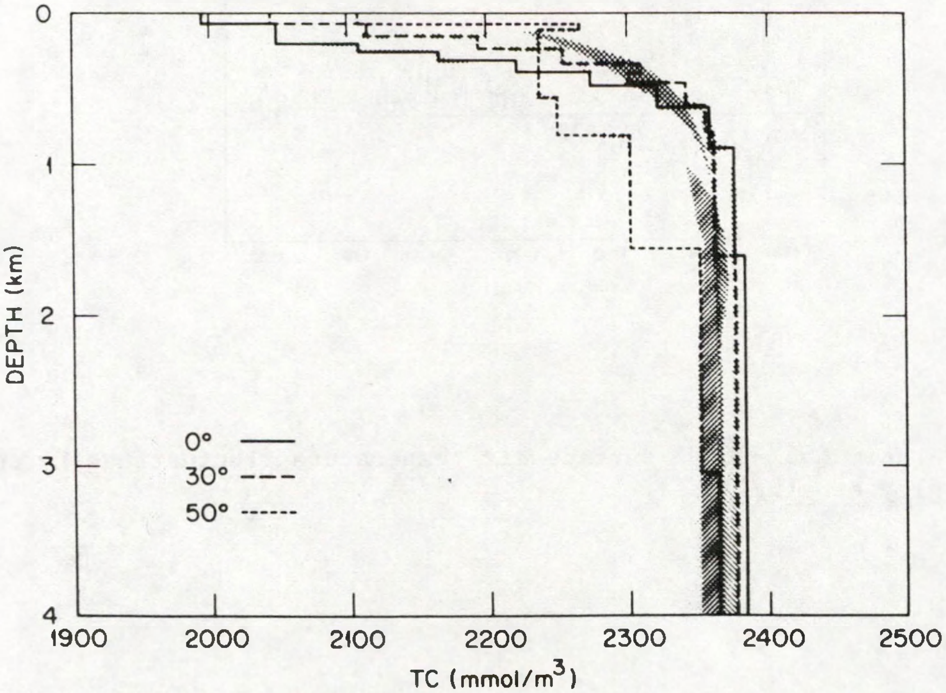


Fig 8. Depth profile of oceanic total carbon concentration.

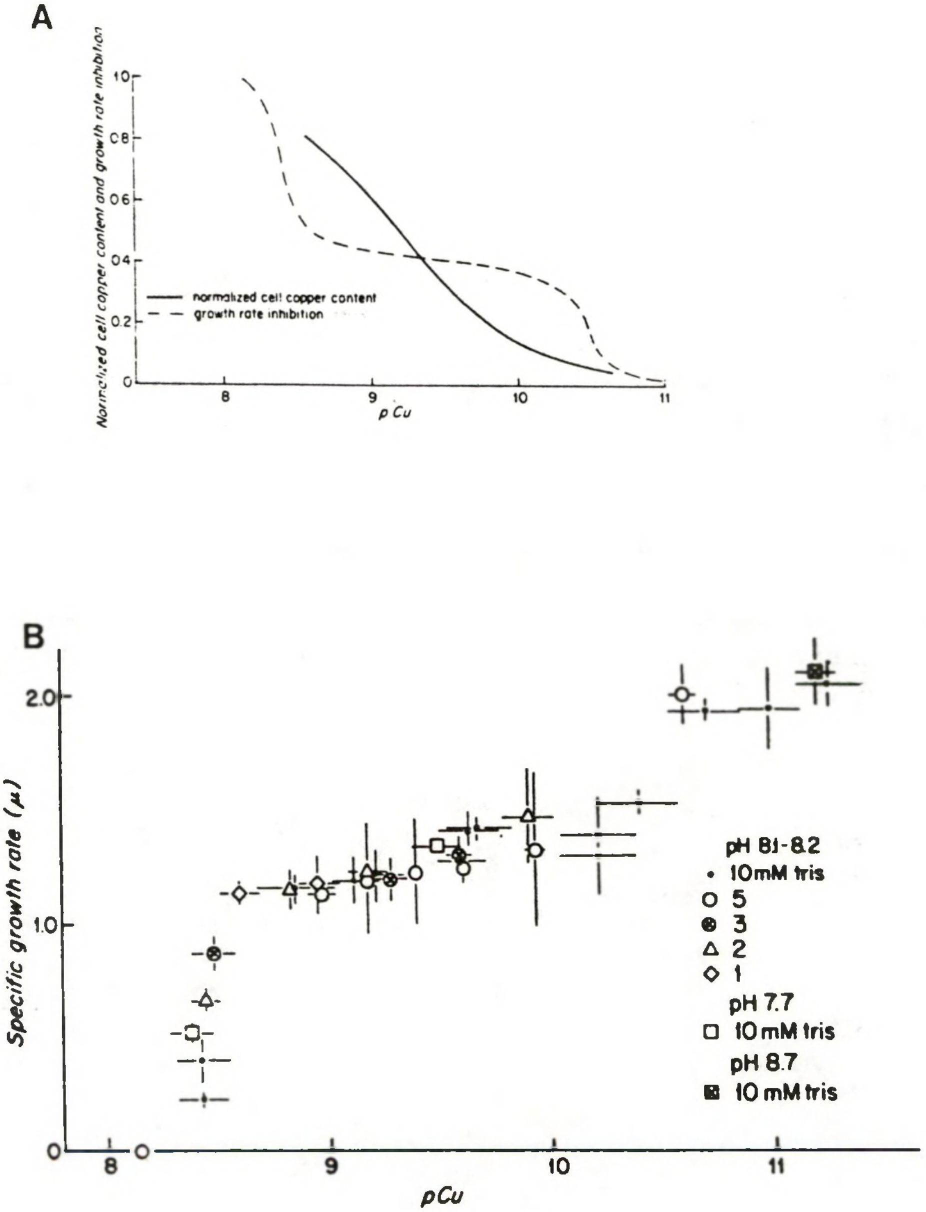


Fig 9. A. Growth rate of the estuarine diatom Thalassosira pseudonana as related to pCu, and (B) growth rate inhibition relative to the growth rate in the pCU range 11-13. (after Sunda & Guillard, 1976).

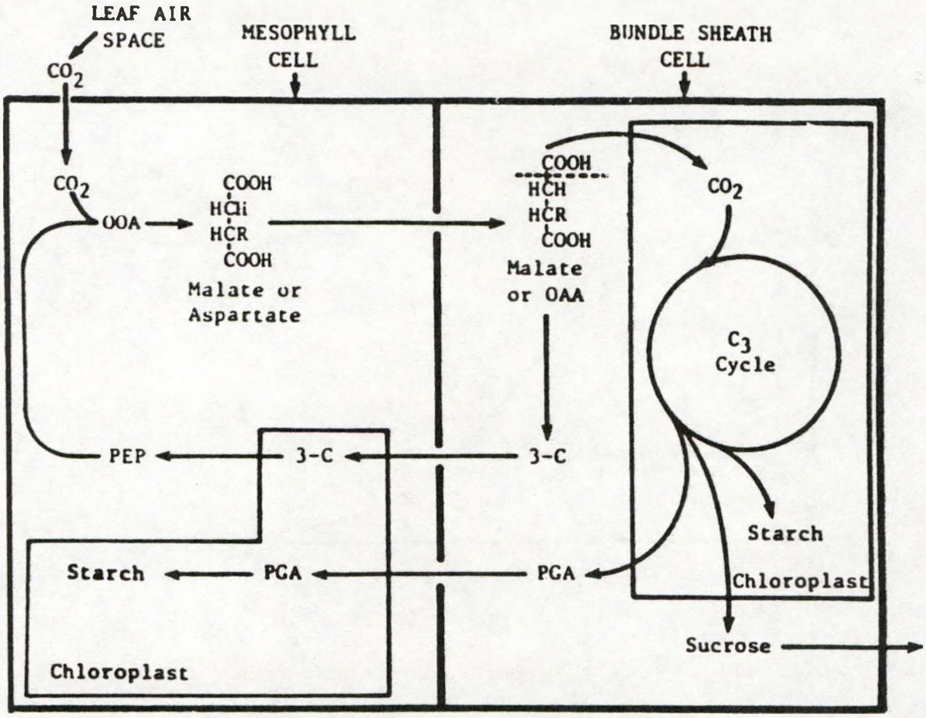


Fig 10. Schematic relationship of photosynthesis (C_3-cycle) to photorespiration (C_2-cycle). (after Tolbert & Zelitch, 1983).

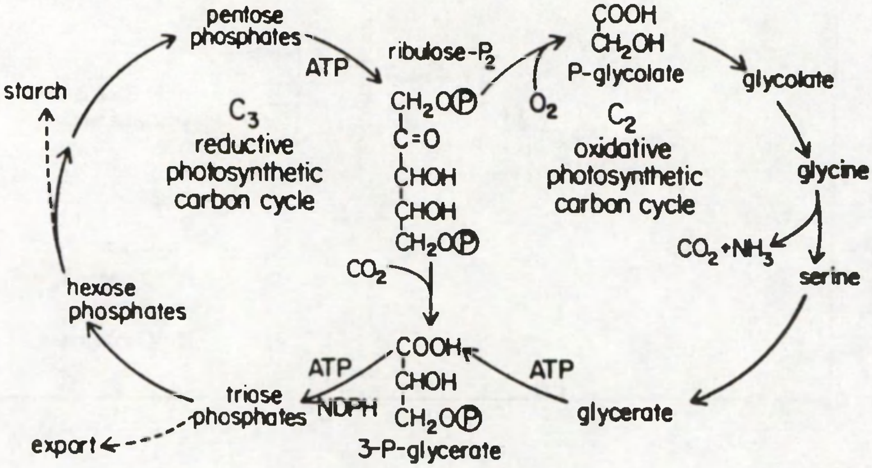


Fig 11. Reactions of the C_3 and C_4 cycle for CO_2 fixation in C_4 plants. CO_2 is fixed in the mesophyll cells into C_4 acids and after transfer and decarboxylation of these acids reafixed in the bundle sheath cells. (after Tolbert & Zelitch, 1983).

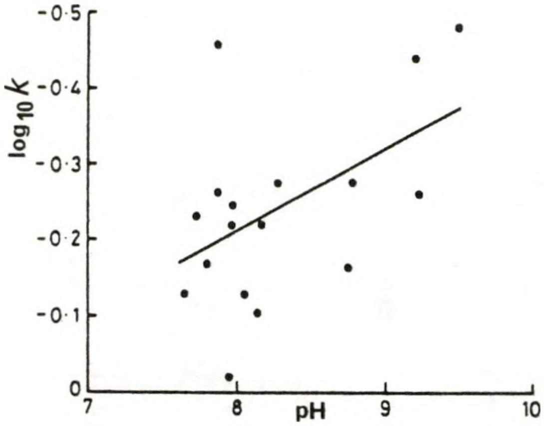


Fig 12. The relationship between the daily cell division rate (K) and pH of the alga Tetraselmis suecica. (after Laing & Helm, 1981).

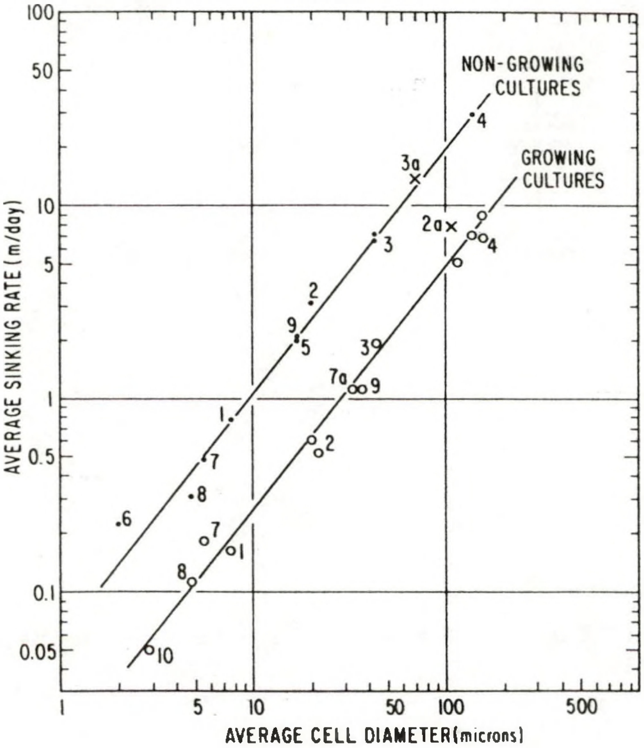


Fig 13. The relation between the average sinking rates and the average cell diameter in growing and non-growing cultures of 10 species of unicellular marine diatoms. (after Eppley et al., 1967).

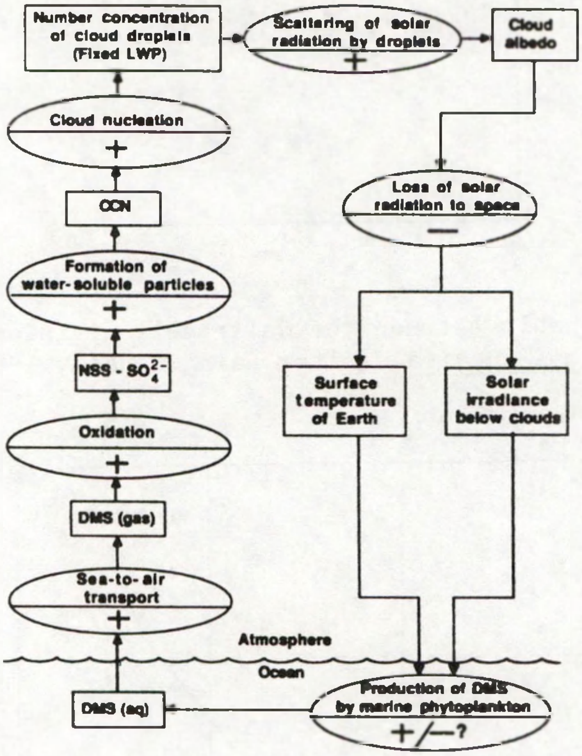


Fig 14. Conceptual diagram of a possible climatic feedback loop. (after Bates et al., 1987).

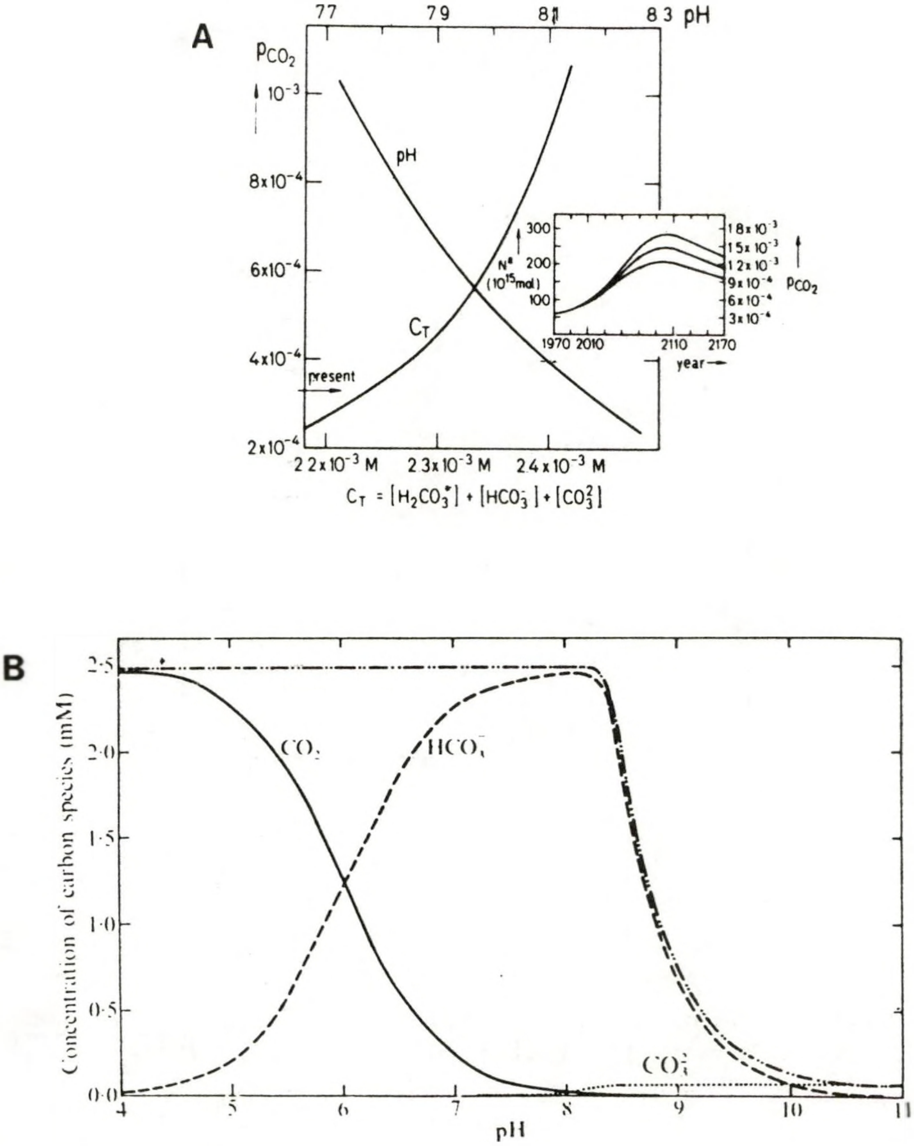


Fig 15. A. Effect of increasing pCO_2 upon total carbon (C_T) and pH of surface ocean water (after Stumm & Morgan, 1981). B&C. The effect upon the relative proportions of oceanic inorganic carbon species (B. after Borowitzka & Larkum, 1976; C. after Beer et al., 1977).

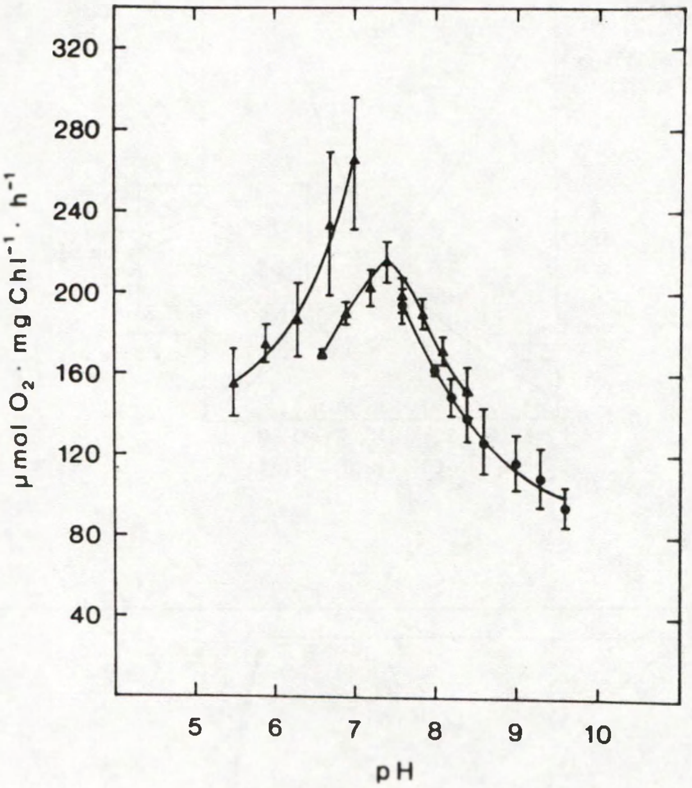


Fig 16. Rates of photosynthetic O_2 evolution of Rhodymenia palmata in response to variations in pH. (after Colman & Cook, 1985).

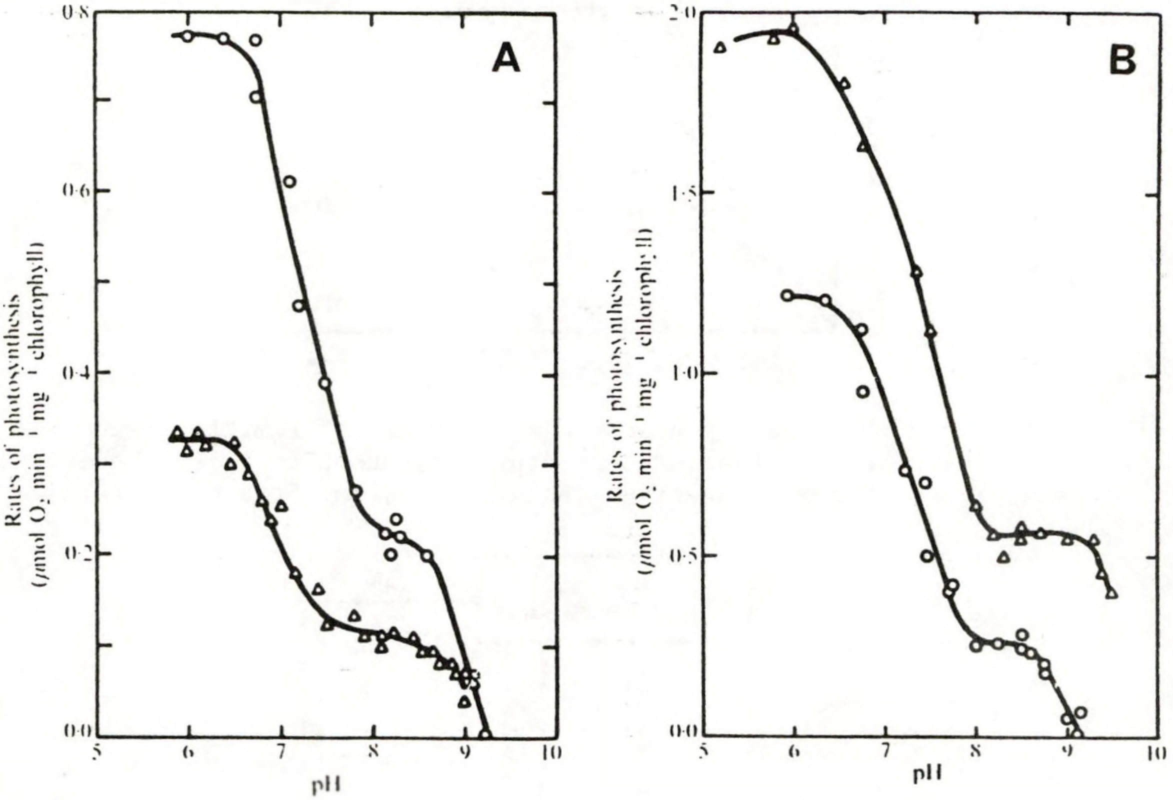


Fig 17. Rates of photosynthesis as a function of pH for A. *Syringodium isoetifolium* (△) and *Halodule uninervis* (o) and B. *Halophila stipulacea* (△) and *Thalassodendron ciliatum* (o). (after Beer *et al.*, 1977).

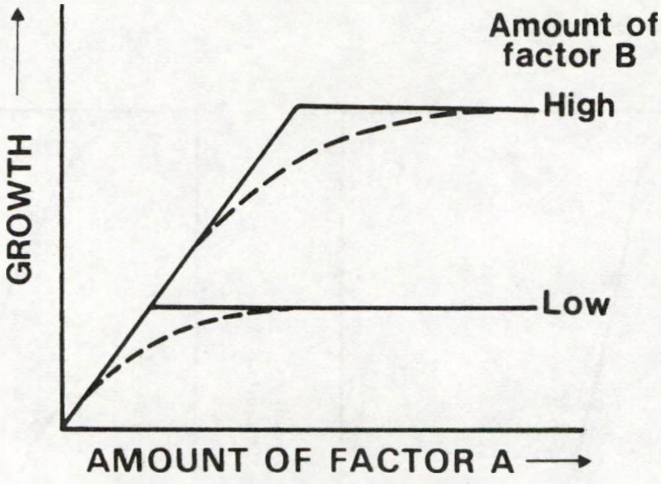


Fig 18. Diagram illustrating Blackman's principle of limiting factors. The solid lines show the responses predicted by the principle, whereas the dashed lines represent observed responses. (after Strain & Cure, 1985).

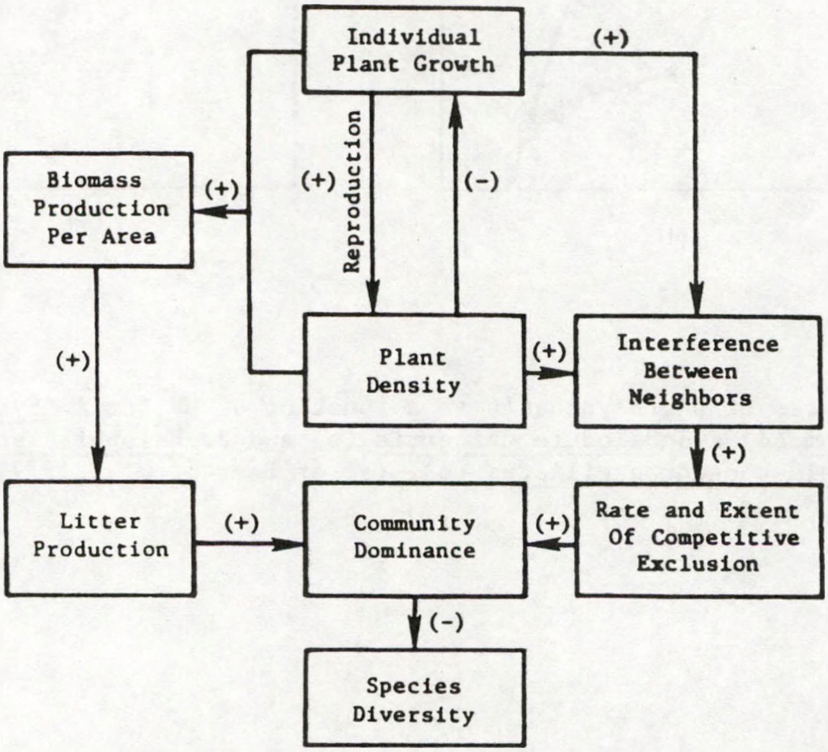


Fig 19. Some population and community responses to increased plant productivity. (after Wetzel & Grace, 1983).

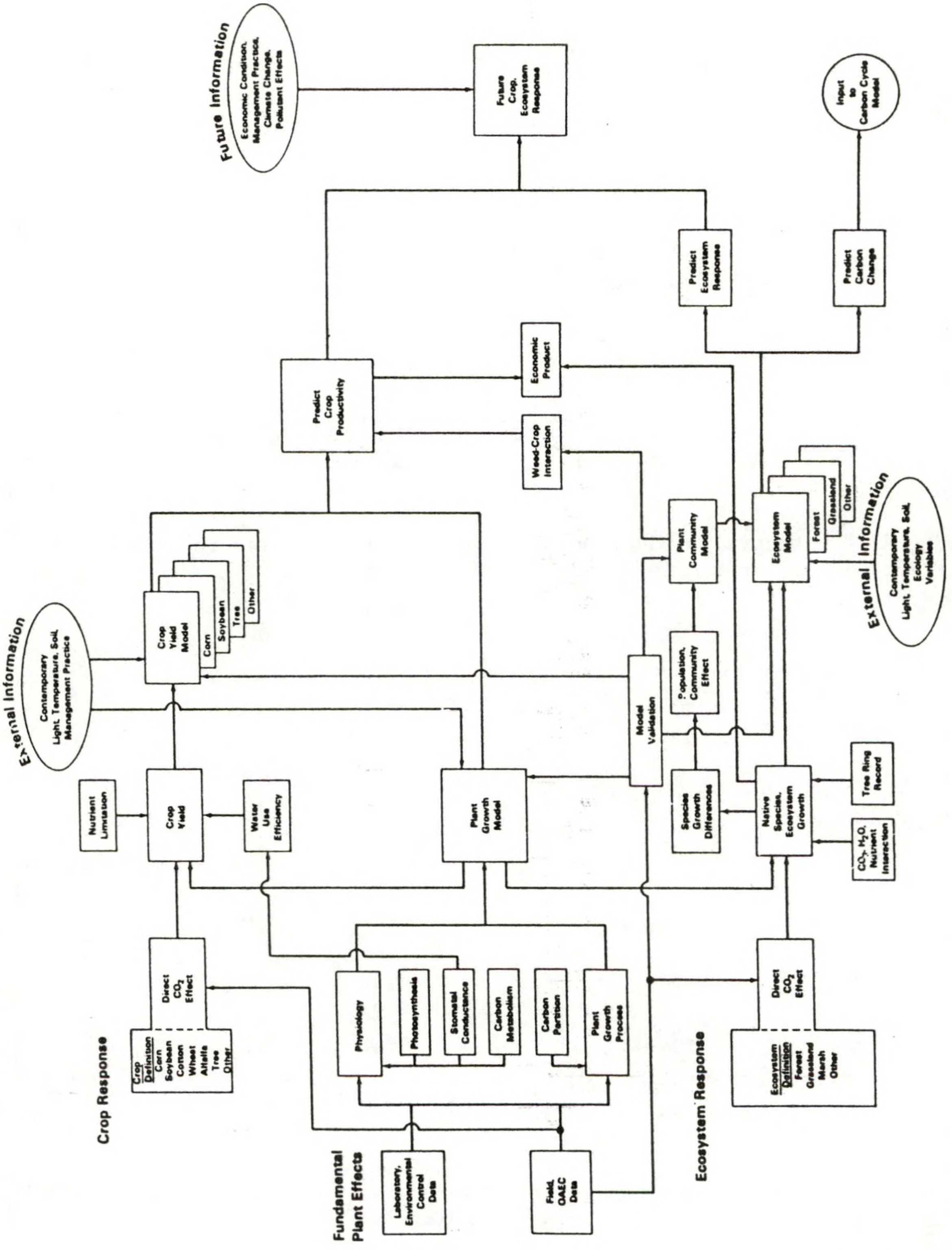


Fig 20. Interactions of responses of plants to CO_2. (after Dahlman, 1984 and Dahlman <u>et al</u>., 1985).

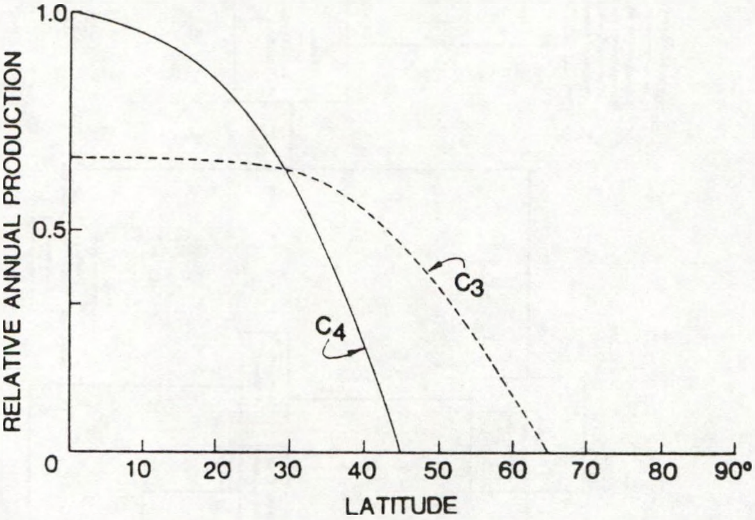
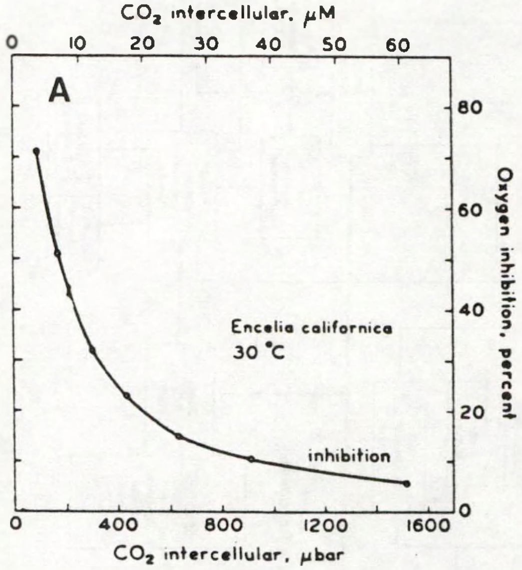


Fig 21. Potential production of C_3 and C_4 crop species in relation to latitude (after Loomis & Gerakis, 1975).



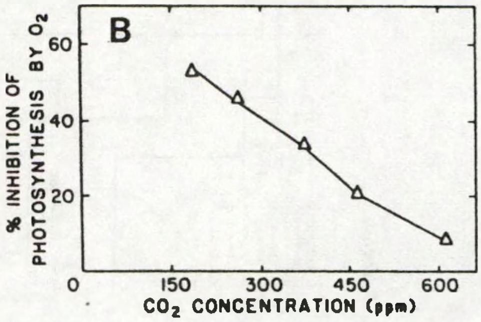


Fig 22a. Oxygen inhibition of photosynthesis in relation to C_i in Encelia californica (after Ehleringer & Björkman, 1977)

Fig 22b. Oxygen inhibition of photosynthesis in relation to C_a in Solanum tuberosum (after Ku et al, 1977).

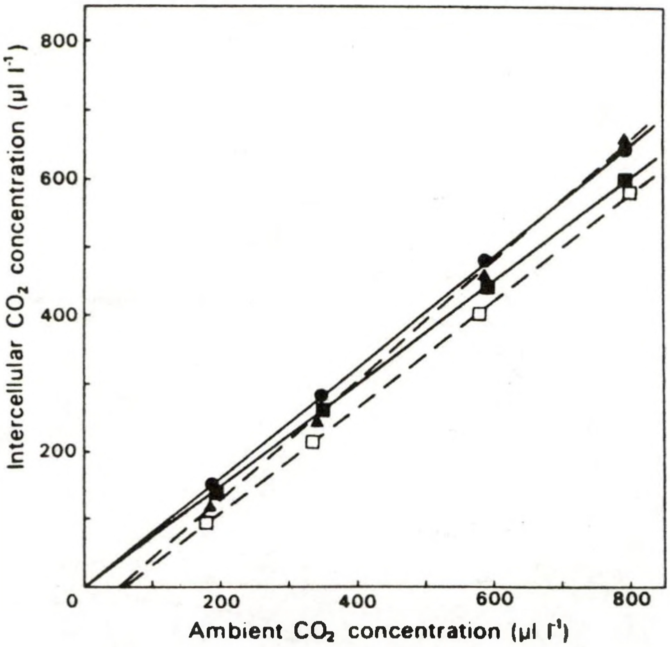


Fig 23. The relationship between intercellular CO_2 concentration (C_i) and ambient CO_2 concentration (C_a) in C_3 and C_4 grasses. (after Morison & Gifford, 1983).

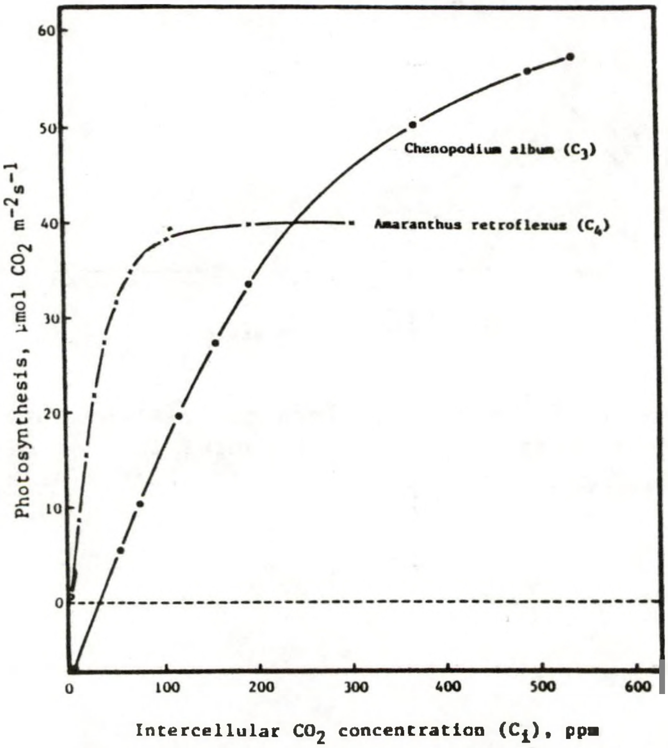


Fig 24. Response of photosynthesis to intercellular CO_2 (C_i) in a C_3 and a C_4 plant. (after Pearcy et al, 1981).

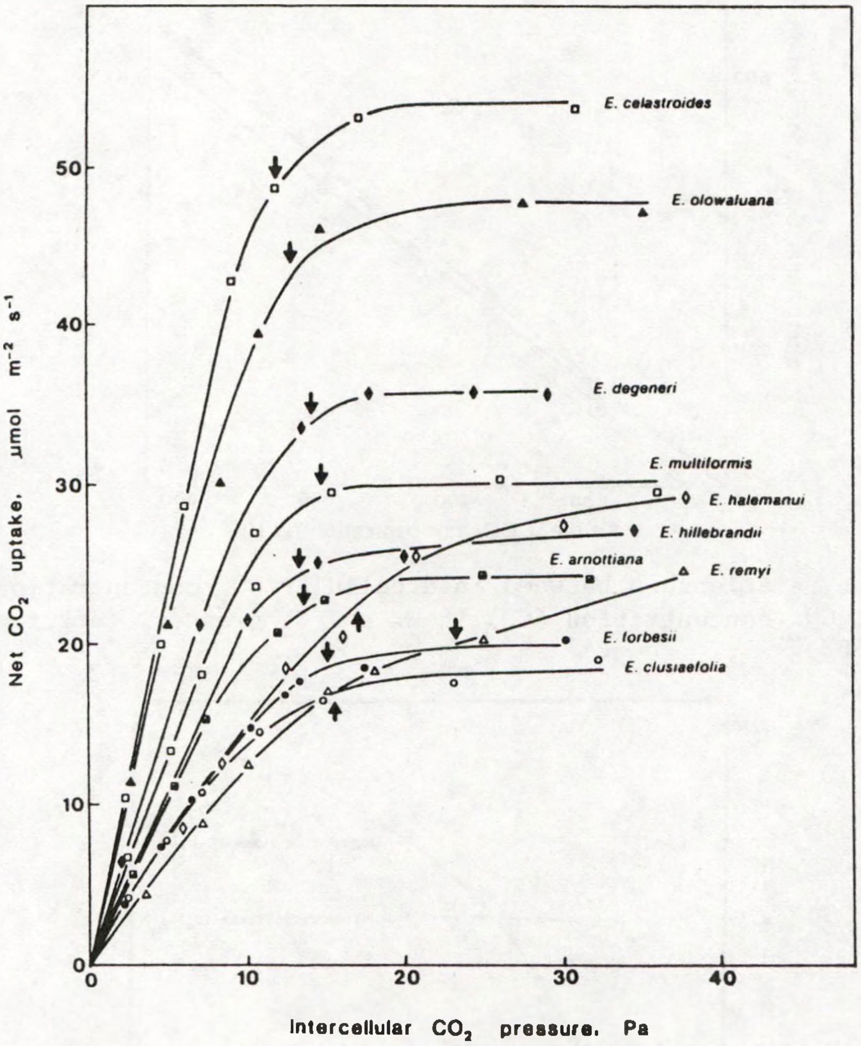


Fig 25. Responses of CO_2 uptake to intercellular CO_2 pressure for 10 Euphorbia species illustrating the differences in response to elevated CO_2 within species of the same genus. (after Pearcy et al., 1982).

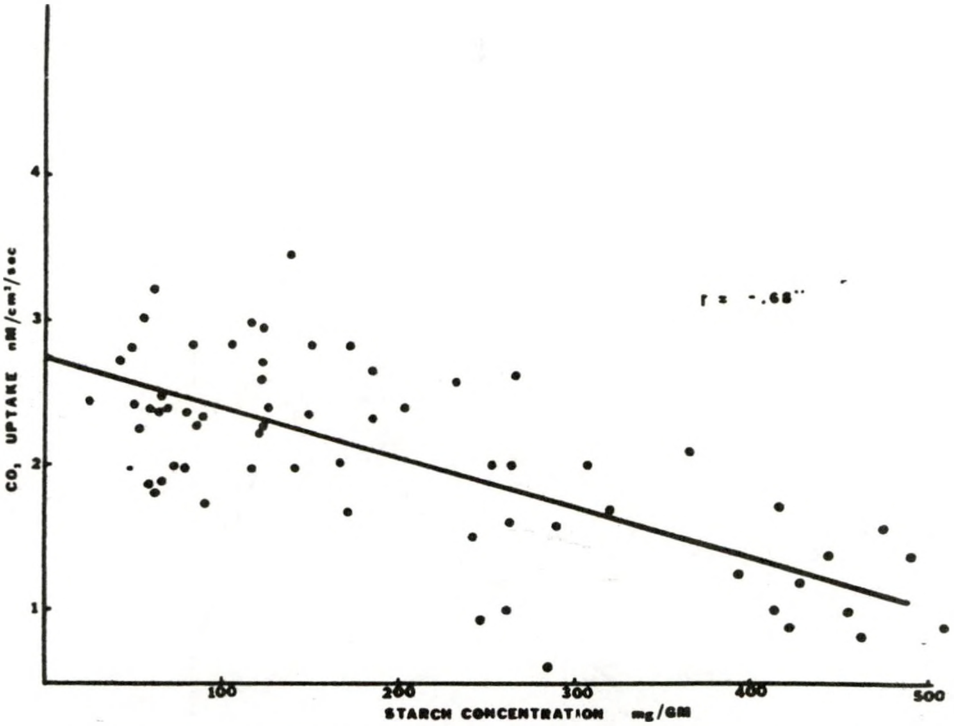


Fig 26. Correlation of leaf starch concentration and CO_2 uptake in cotton. (after Mauney et al, 1979).

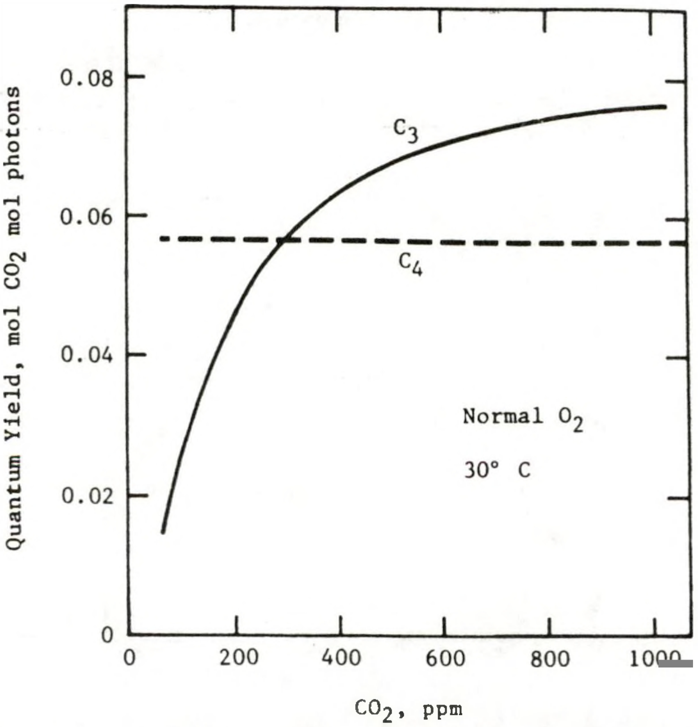


Fig. 27. CO_2 dependence on quantum yield in C_3 and C_4 plants. (from Pearcy & Björkman, 1983, after Osmond et al., 1980)

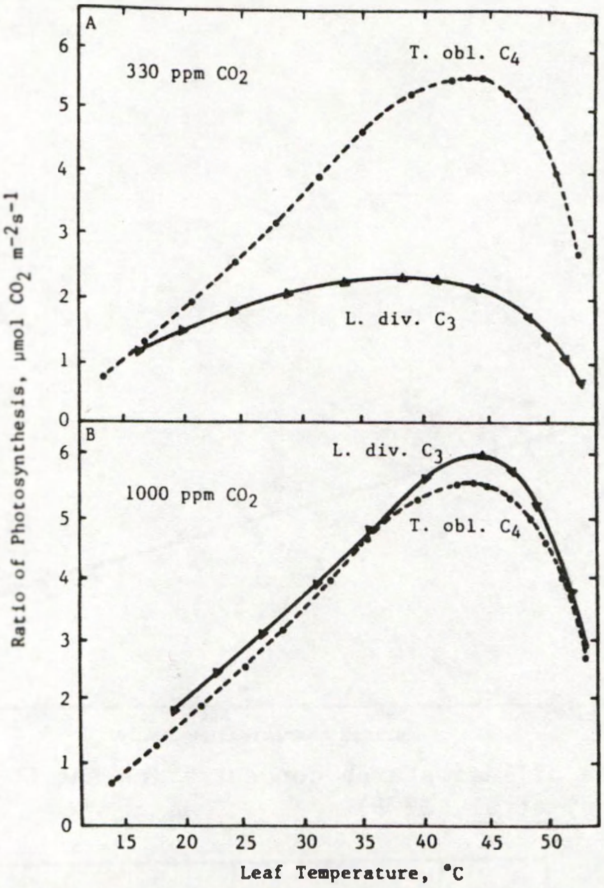


Fig 28. Temperature dependence of CO$_2$ uptake at 330 ppm CO$_2$ (A) and 1000 ppm (B) for a C$_3$ plant (*Larrea divaricata*) and a C$_4$ plant (*Tidestromia oblongifolia*). (from Pearcy & Björkman, 1983, after Osmond *et al*., 1980).

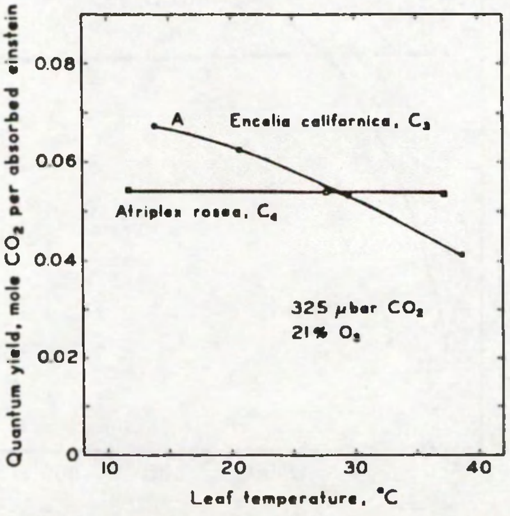


Fig 29. Quantum yield for CO$_2$ uptake in *Encelia californica* (C$_3$) and *Atriplex rosea* (C$_4$) as a function of leaf temperature. (after Ehleringer & Björkman, 1977).

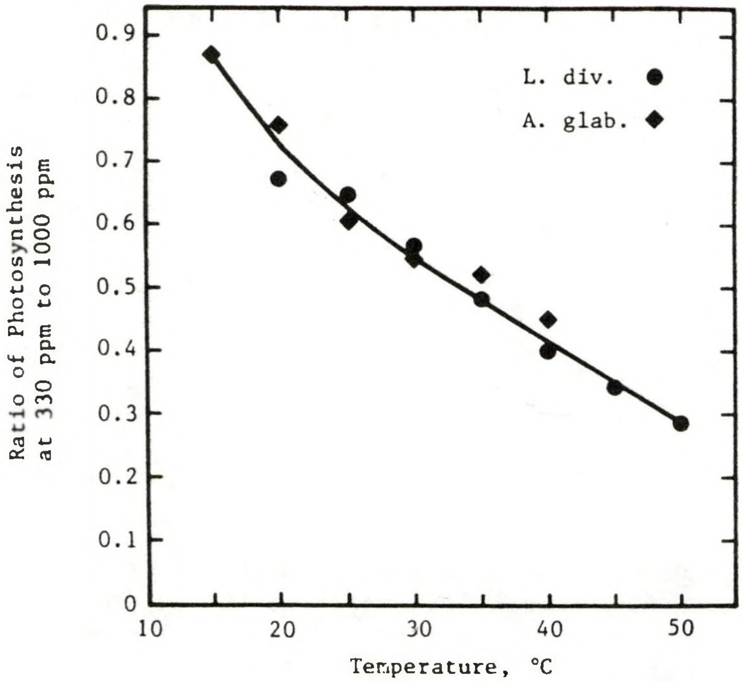


Fig 30. The effect of temperature on the ratio of CO_2 uptake at 300 ppm to that at 1000 ppm in a C_3 plants (*Larrea divaricata* and *Atriplex glabriscula*) (from Pearcy & Björkman, 1983).

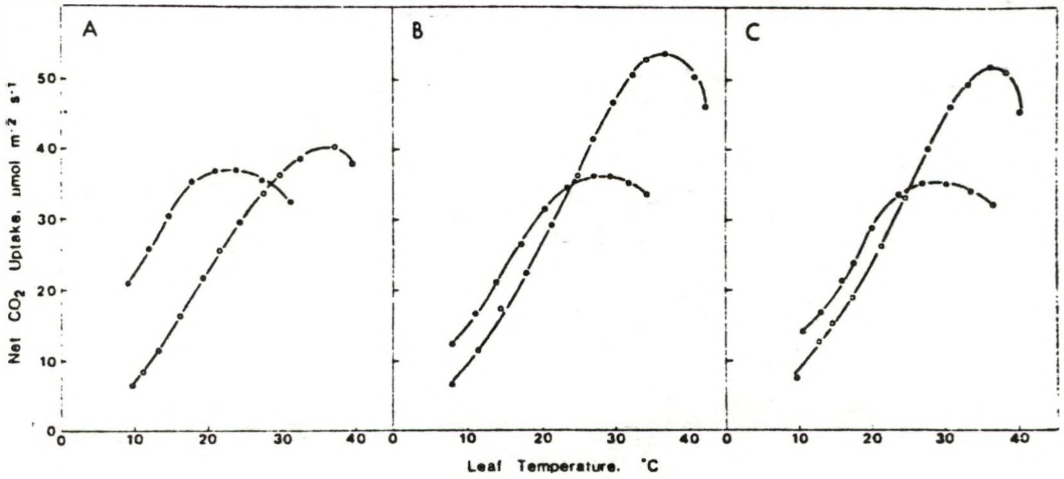


Fig 31. The temperature dependence of photosynthesis for *Chenopodium album* (•) and *Amaranthus retroflexus* (o) and the influence of the acclimation temperature. Growth temperatures (day/night) were; a. 17/14 °C; b. 25/18 °C; c. 34/28 °C. (after Pearcy *et al.*, 1981)

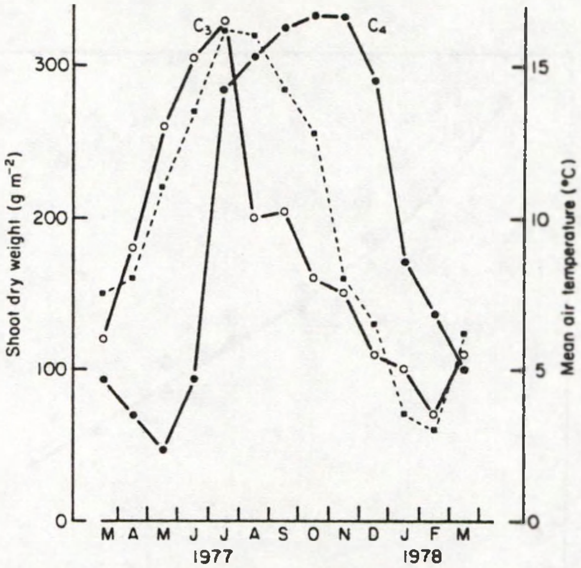


Fig 32. The dry weights of the living shoot material in monotypic stands of two salt marsh grasses, Puccinellia maritima (C_3 o) and Spartina anglica (C_4 ●), in north-east Essex, coplotted with mean air temperatures (■). (after Long, 1983).

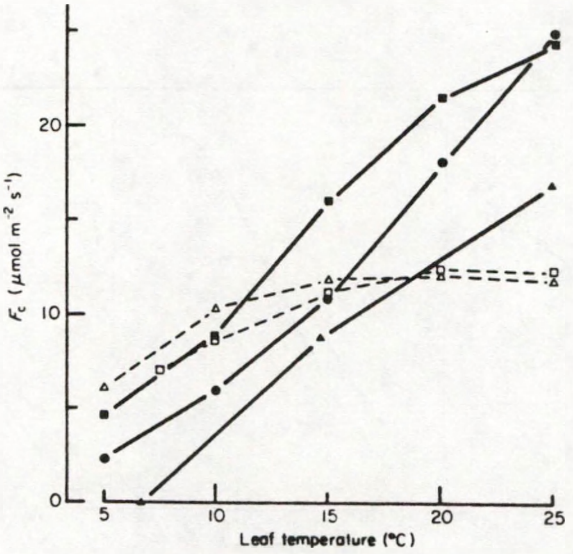


Fig 33. Net photosynthetic rates of CO_2 assimilation per unit of leaf area (F_c) at different leaf temperatures, for the temperate C_3 grasses Sesleria albicans (□) and Puccinellia maritima (Δ), the temperate C_4 species Spartina anglica (■), a cultivar of Zea mays (●), and the tropical grass Pennisetum purpureum (▲). (after Long, 1983).

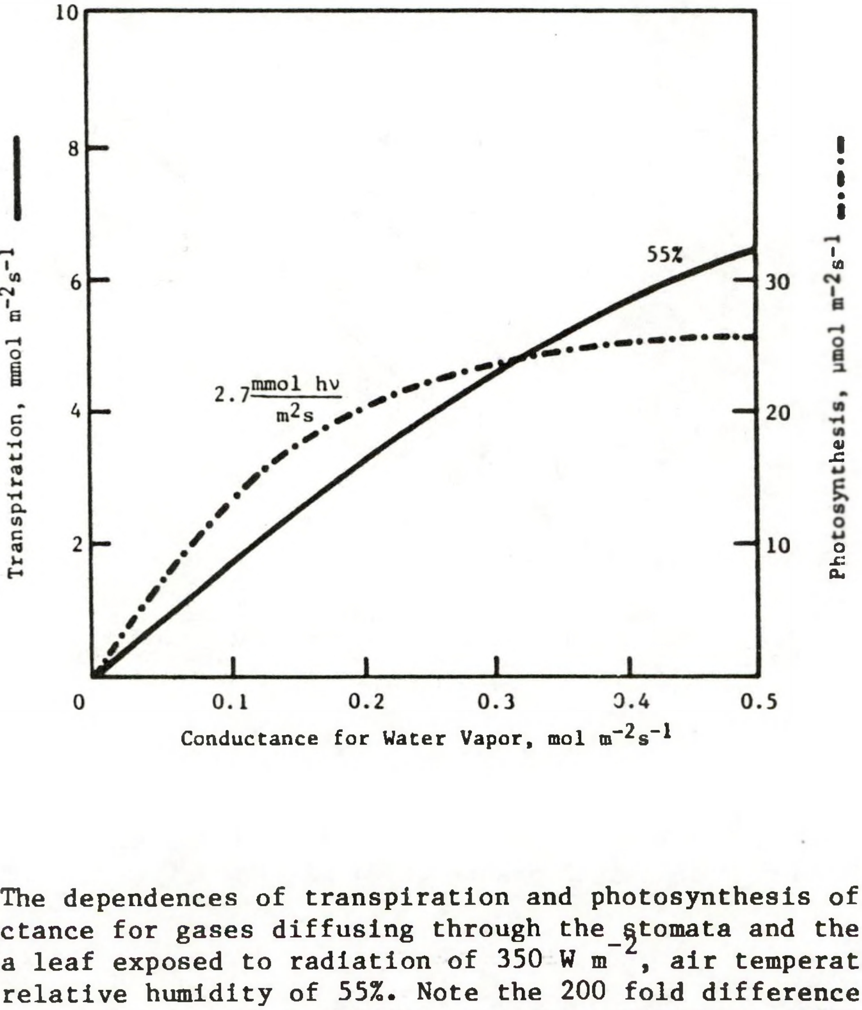


Fig 34. The dependences of transpiration and photosynthesis of CO_2 on the conductance for gases diffusing through the stomata and the boundary layer of a leaf exposed to radiation of 350 W m^{-2}, air temperature of 25 °C and a relative humidity of 55%. Note the 200 fold difference in scale between transpiration and photosynthesis. (after Raschke, 1975).

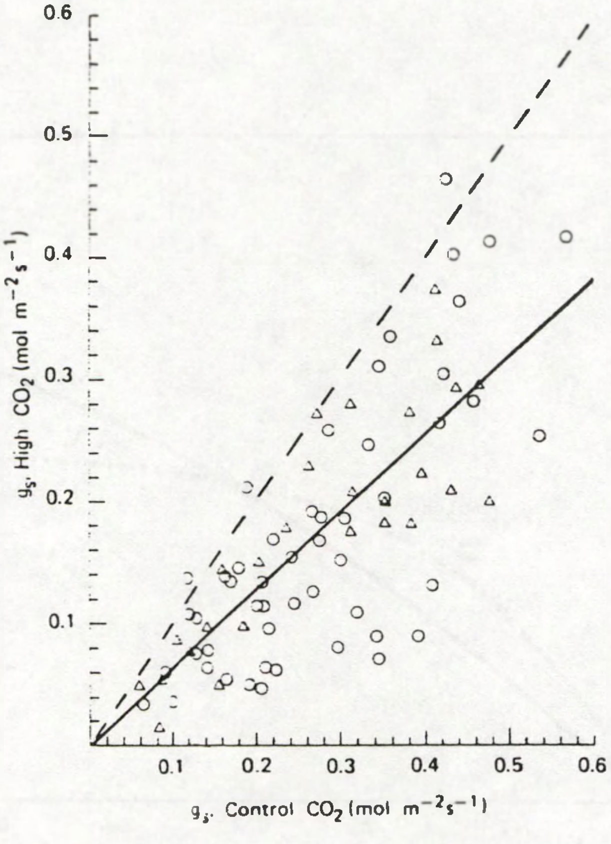


Fig 35. Relationship between stomatal conductance g_s, of plants grown in high CO_2 concentration and of plants grown in normal CO_2. (after Morison & Gifford, 1983).

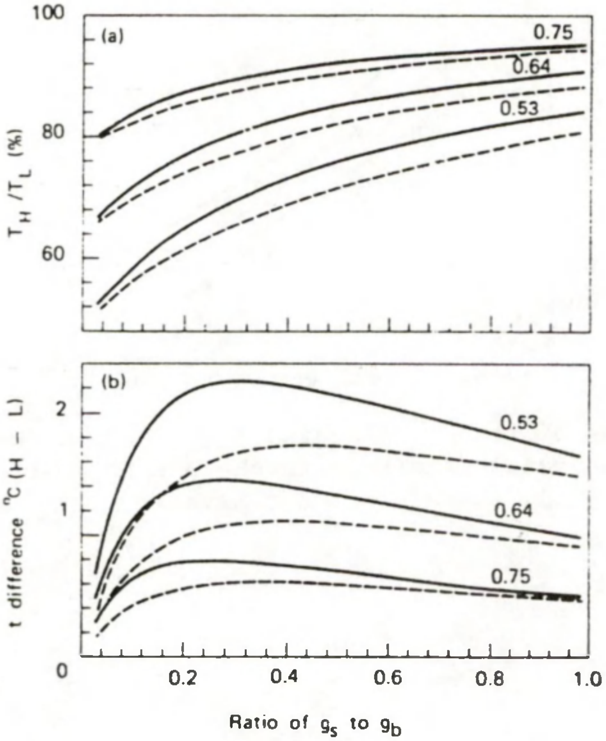


Fig 36. Effect of doubling present atmospheric CO_2 concentrations on transpiration rate (T) and leaf temperature (t), calculated from heat-balance equations. Results are plotted as a function of the ratio of stomatal (g_s) to boundary layer (g_b) conductance, given three estimates of the reduction of stomatal conductance at high CO_2; 0.75, 0.64 and 0.53. (a) The ratio of transpiration at high CO_2 (T_h) to that in normal CO_2 (T_1). (b) The differnce in leaf temperature between high CO_2 and normal CO_2. (after Morison & Gifford, 1984).

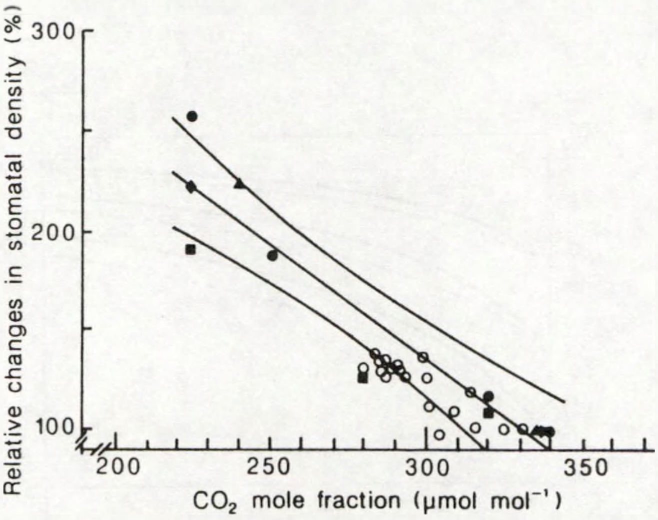


Fig 37. Comparison of the experimental effects of a change in the CO_2 mole fraction on stomatal density with the putative effects shown in herbarium material (o). (after Woodward, 1987).

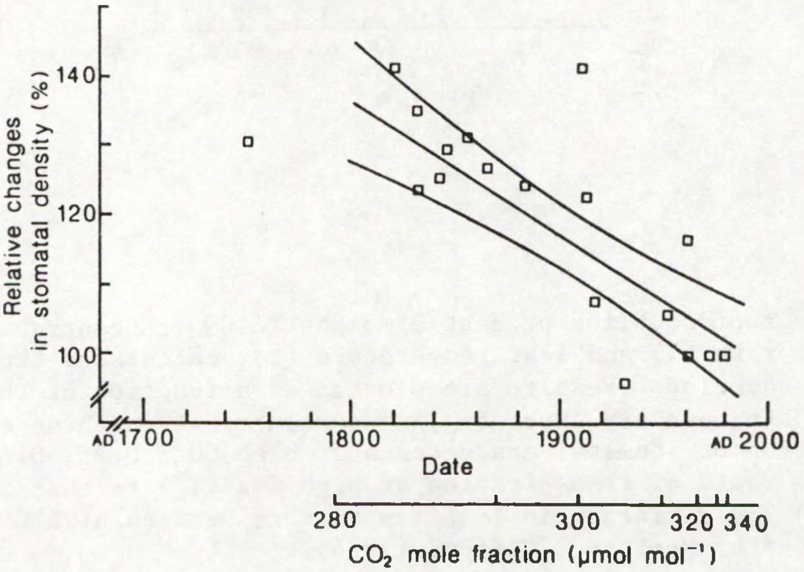


Fig 38. Abaxial stomatal densities of herbarium stored leaves, dating back to 1750 AD. The linear regression line, with 95% confidence slimits, shows a 40% reduction in the ratio of stomatal densities over a period of 200 years. (after Woodward, 1987).

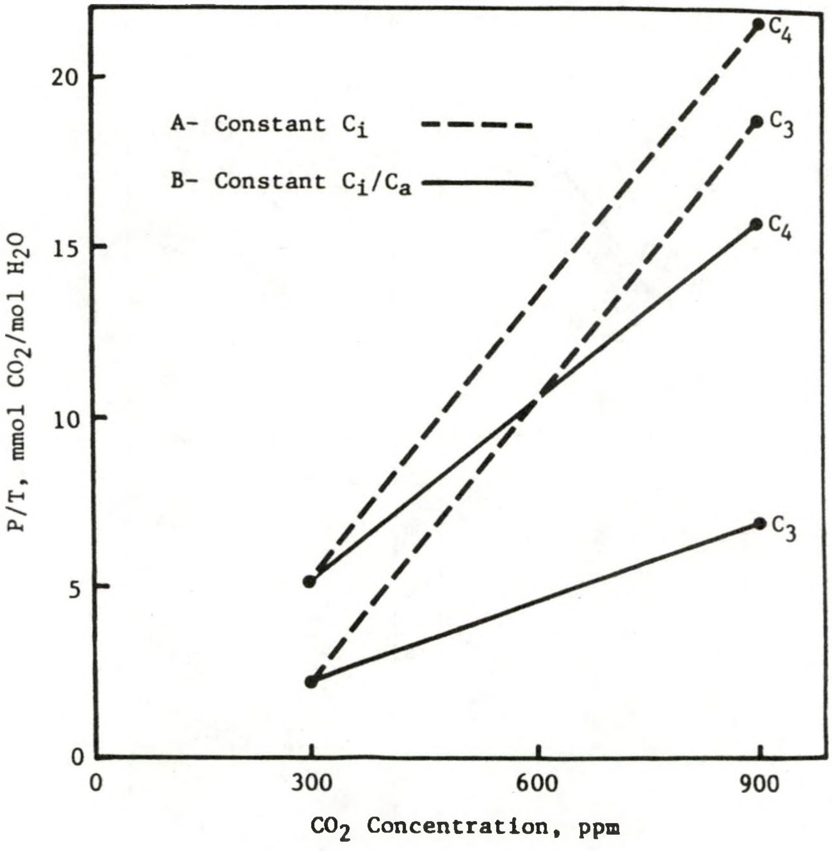


Fig 39. Response of photosynthetic water use efficiency (P/T) in C_3 and C_4 plants assuming (A), a constant C_i of 240 ppm in C_3 plants and 120 ppm in C_4 plants, or (B) a constant C_i/C_a of 0.72 in C_3 plants and 0.36 inb C_4 plants. (after Pearcy & Björkman, 1983).

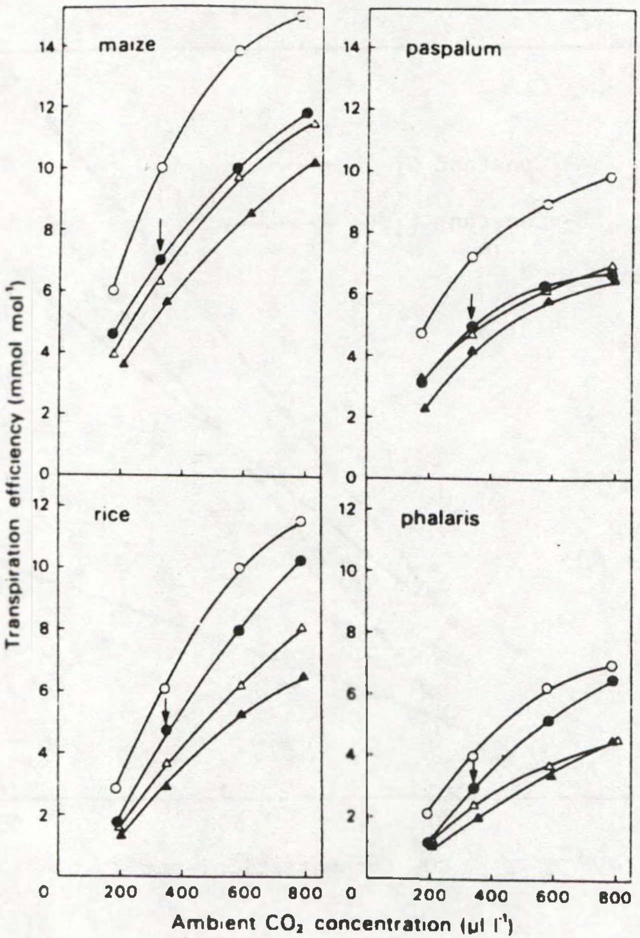


Fig 40. Relationship between transpiration efficiency and C_a at four levels of vapour pressure deficit. (after Wong, 1980).

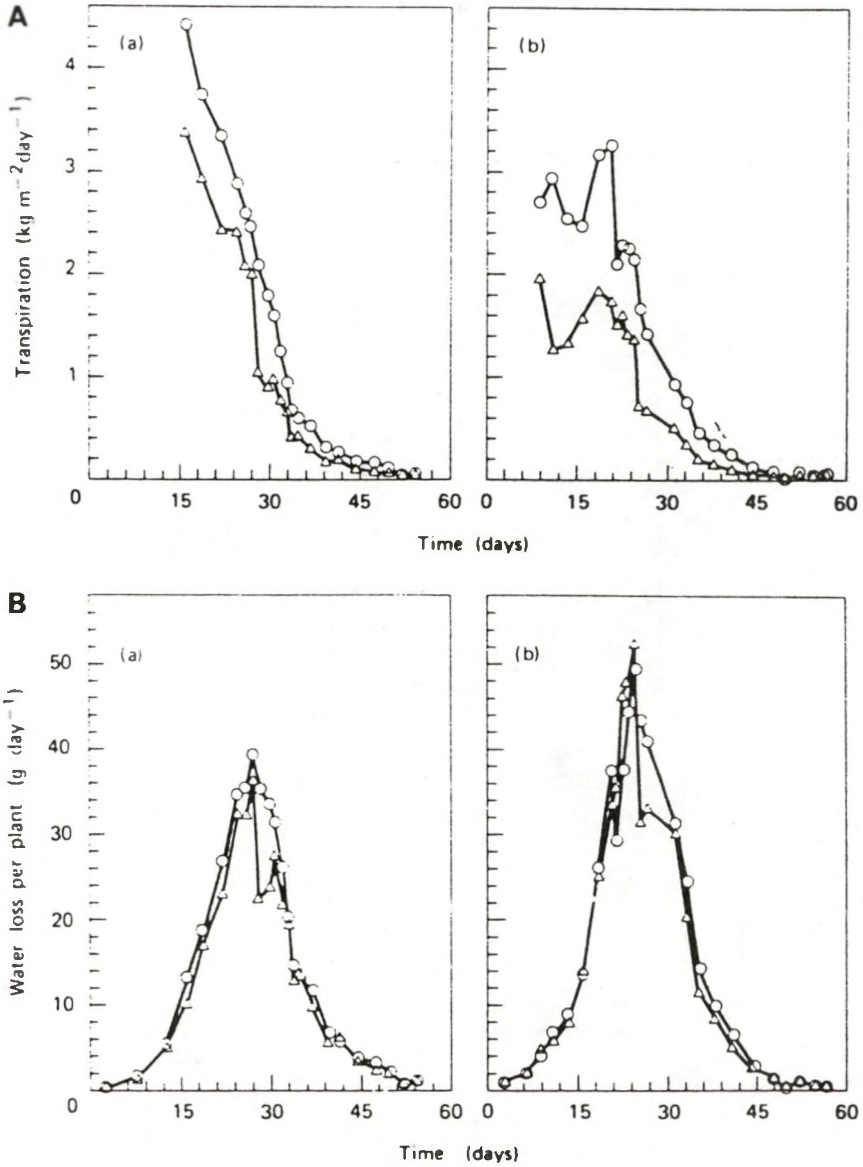


Fig 41. Time course of daily transpiration rate per (A) unit leaf area or (B) whole plant of Siratro (a) and wheat plants (b) in control (0) or high CO_2 concentration. (after Morison & Gifford, 1984).

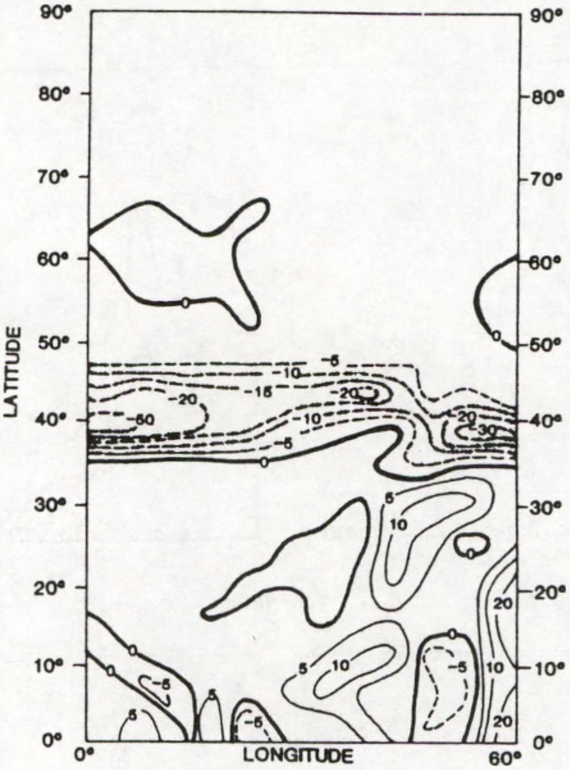


Fig 42. Horizontal distribution of the change of soil moisture (mm) over the continent in response to a doubling of CO_2 content. (after Manabe & Wetherald, 1980).

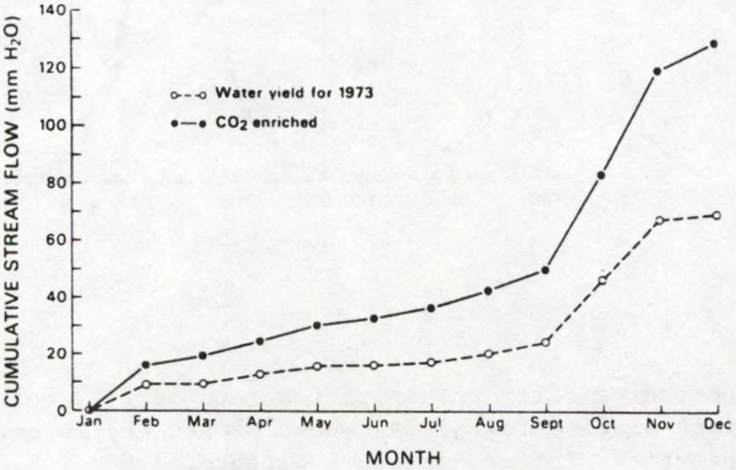


Fig 43. The computed cumulative monthly water yield of a 5 ha experimental catchment and the effect of doubling of atmospheric CO_2. (after Aston 1984)

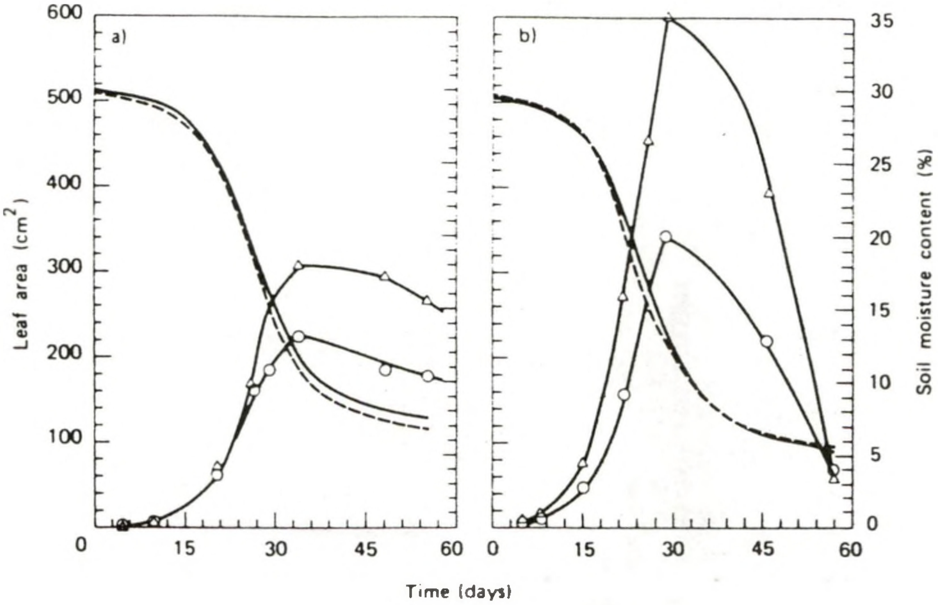


Fig 44. Time course of projected leaf area per plant and average soil moisture content for Siratro (a) and wheat (b) grown in control (o) or high (△) CO_2 concentration. (after Morison & Gifford, 1984).

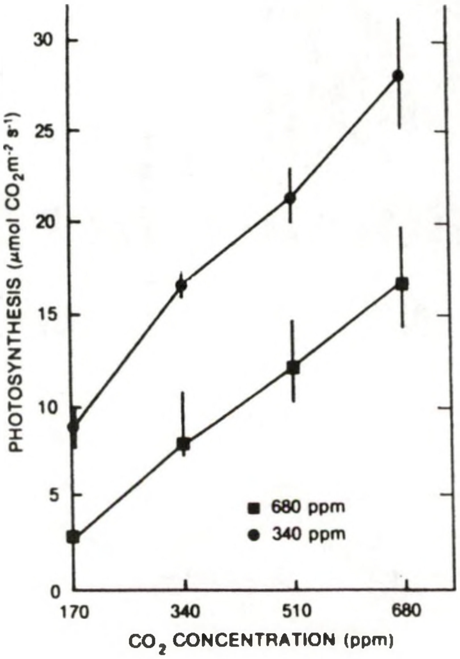


Fig 45. Net photosynthetic response of <u>Eriophorum</u> <u>vaginatum</u> grown at 340 and 680 ppm CO_2 when exposed to a range of CO_2 concentrations (after Tissue & Oechel, 1987).

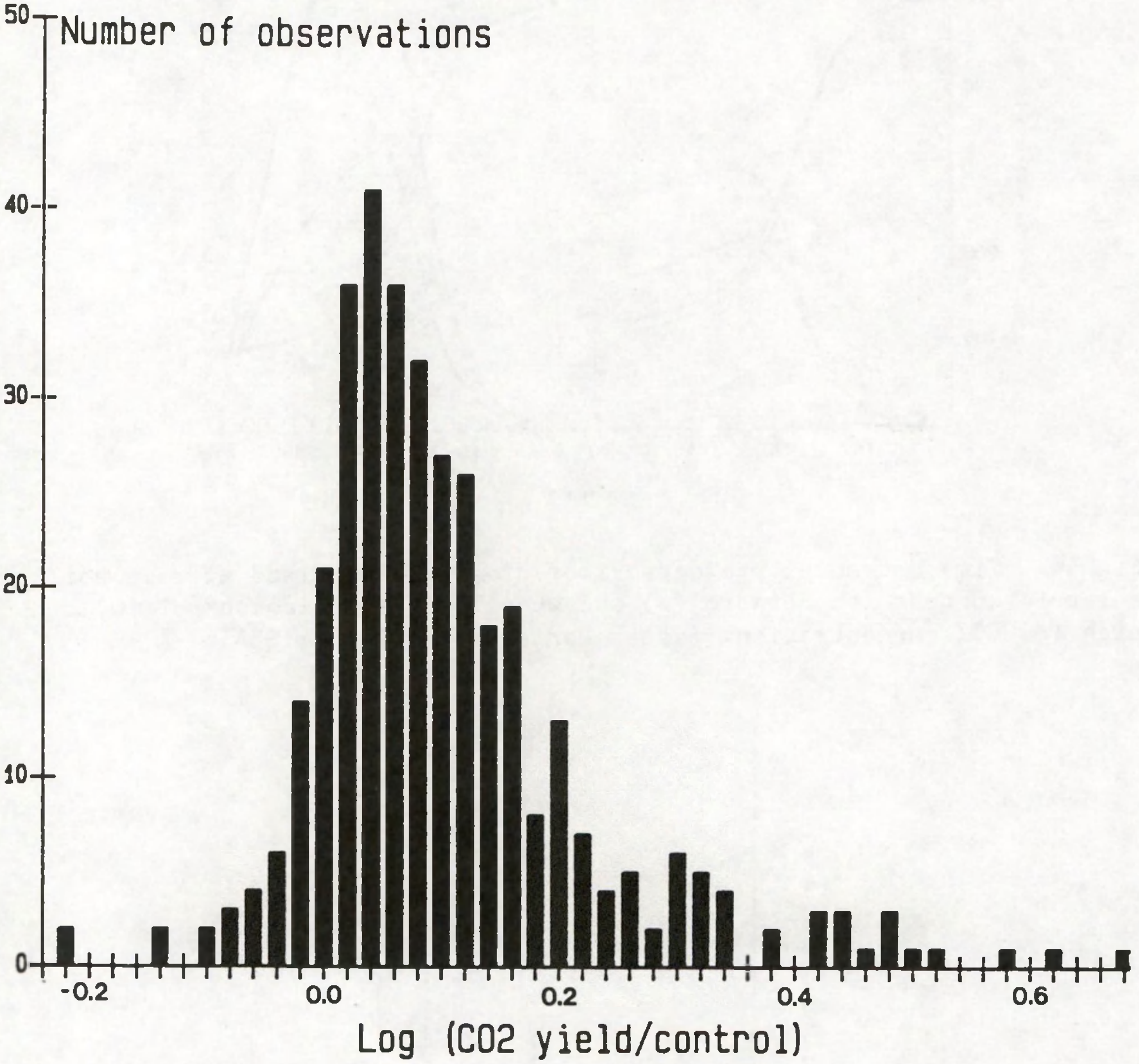


Fig 46. Frequency distribution of the logarithms of the relative yield increases (ratios) of CO_2 enriched plants to their controls (after Kimball, 1983).

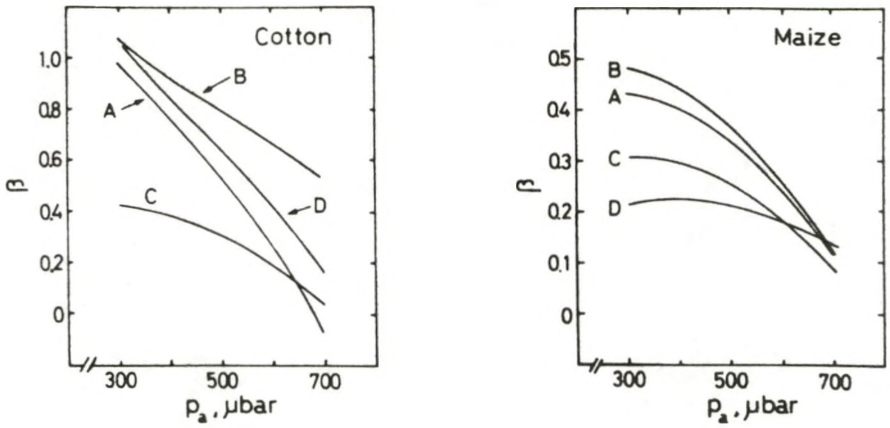


Fig 47. The magnitude of (b), versus ambient partial pressure of CO_2 in cotton and maize grown in 330 ppm and 660 ppm CO_2 and two levels of nitrogen nutrition. A. grown in 330 ppm CO_2 and high NO_3. B. grown in 660 ppm CO_2 and high NO_3. C. grown in 330 ppm CO_2 and low NO_3. D. grown in 660 ppm CO_2 and low NO_3. (after Wong, 1980).

NIOZ - RAPPORT 1988 - 7
RIN - RAPPORT 88 - 58

CONTENTS