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Effects on Ecosystems

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EXECUTIVE SUMMARY

Ecosystem Metabolism and Climate Change

Photosynthesis, plant and microbial respiration tend to increase with increasing temperatures, but at higher temperatures respiration is often the more sensitive process. As a consequence, global warming may result in a period of net release of carbon from the land to the atmosphere. The magnitude of this release is uncertain. Factors that will influence the amount of carbon released include local patterns of climate change and the responses of the biota to simultaneous changes in soil moisture and atmospheric CO_2 concentration.

Increased soil water availability will tend to stimulate plant growth in dry ecosystems and increase carbon storage in cold and wet ecosystems like lowland tundra. A number of recent modelling studies have predicted that water stress will be a primary cause of tree death in the southern temperate forests of the Northern Hemisphere as climate changes. Forest death and replacement by grasslands would result in a net flux of carbon from the terrestrial biosphere to the atmosphere.

Increased atmospheric CO_2 has the potential to increase plant growth in a variety of ways: stimulation of photosynthesis, depression of respiration, relief of water and low light stresses, relief of nutrient stress by several mechanisms (greater nutrient use efficiency, increased nutrient uptake through root-microbial associations, increased symbiotic nitrogen fixation), and delay of senescence that prolongs the growing season. Some of the mechanisms that promote increased growth could be particularly important in arid/semi arid and infertile areas. However, there is great uncertainty about whether or not these mechanisms operate for prolonged periods in natural ecosystems. For example, there are no field data from whole ecosystem studies of forests that demonstrate a 'CO_2 fertilization' effect. If elevated CO_2 does stimulate the growth of woody vegetation, this could lead to long term net carbon storage in terrestrial ecosystems.

Ecosystem Structure and Climate Change

Because species respond differently to climatic change, some will increase in abundance while others will decrease. Ecosystems will therefore change in structure. Over time some species may be displaced to higher latitudes or altitudes. Rare species with small ranges may be prone to local or even global extinction.

Warming rates are predicted to be rapid (0.3°C per decade) and there is great uncertainty about how species will respond to these rapid changes. Ecosystems of large stature such as forests may not be able to migrate fast enough to keep pace with climate change. In past times, species migrations were largely unaffected by human land use. Barriers to migration now exist (e.g., human settlements, highways, etc.). Therefore, inferences from previous migrations cannot be applied without caution to the present and future situations.

Human Activities, Ecosystem Changes and the Climate System

Human activities such as deforestation in the tropics and forest harvest and regrowth in mid latitudes of the Northern Hemisphere are influencing the climate system by affecting greenhouse gas fluxes. Deforestation in the tropics is releasing 1.6 ± 1 Pg C annually to the atmosphere.

The net exchange of carbon between the land and the atmosphere due to forest harvest and regrowth in the mid latitudes of the Northern Hemisphere is uncertain. These regrowing forests may be accumulating 1-2 Pg C annually. One analysis suggests that an equivalent amount of carbon is released back to the atmosphere through the burning and decay of previously harvested wood.

The issue of carbon storage in the mid latitudes of the Northern Hemisphere is further complicated by the eutrophication of the region with nitrogen. Nitrogen in agricultural fertilizers and in acid rain may be promoting carbon storage at the rate of 0.5-1.0 Pg C annually, but there is considerable uncertainty in this estimate.

Reforestation as a Means of Managing Atmospheric CO_2

Reducing the atmospheric CO_2 concentration through an afforestation program would require the planting of a vast area of forest. Approximately 370 x 10^6 ha of temperate forest would have to be planted in order to accumulate 1 Pg C annually. This assumes a forest with an annual carbon accumulation rate of 2.7 t per hectare. The carbon accumulation would continue for almost a century. After that time the forest would be mature and would not sequester more carbon.

Methane and Nitrous Oxide Fluxes

Microbial activity is the dominant source to the atmosphere of methane and nitrous oxide. Warmer and wetter soil conditions may lead to increased fluxes of these gases to the atmosphere. Changes in land use and fertilizer and atmospheric inputs of nitrogen, also have the potential to affect methane and nitrous oxide fluxes.

Deforestation and Regional Hydrology

The conversion of large areas of tropical forest to grassland will likely change the hydrological regime of the region. Rainfall will be reduced and surface water flow will be affected.

Marine Ecosystems

Climate change will probably affect ocean circulation and mixing patterns. Circulation and mixing control nutrient availability to the oceans' microscopic plants (phytoplankton) and their access to solar radiation required for photosynthesis. Since nutrients are an important controller of net primary production in marine environments, production will be changed to the degree that upper ocean physical processes change in response to climate change. Different nutrient and mixing regimes are characterized by different plankton communities, which have wide ranging efficiencies of processing carbon, with important implications for long term ocean storage of organic carbon.

10.0 Introduction

On the basis of current evidence from climate modelling studies it appears that the change in globally averaged surface temperature due to doubling CO_2 probably lies in the range 1.5 to 4.5°C (Section 5). Temperature changes of this magnitude in the Earth's history have been associated with shifts in the geographic distribution of terrestrial biota. For example, the boreal forests of Canada extend well north of the current timber line during the Medieval Warm Epoch (800 to 1200 AD), a time when temperatures in that region were about 1°C warmer than today's. At the same time, farmers in Scandinavia grew cereal crops as far north as 65° latitude (Lamb, 1977). Evidence from the past suggests that the potential for ecosystem change in a warmer future is large (Warrick et al., 1986a).

A shift in the geographic distribution of terrestrial biota is a long-term (decades to centuries) response to climate change. Responses to a changing climate will also occur at other time-scales. In the short term (minutes to years), likely ecosystem responses include changes in the rates of processes such as photosynthesis and decomposition, and changes in the interactions between species such as those between plants and insect pests. In the intermediate term (years to decades), these changes in processes and interactions will lead to changes in community structure. For example, in a mixed forest type in the mid-latitude region, where both deciduous and coniferous tree species coexist, a warmer climate could lead to the loss of the conifers.

Some climate-induced changes of ecosystem structure and function are expected to feed back to the climate system. For instance, the warming of high latitude wetlands will almost certainly increase the production of CH_4 and its release to the atmosphere and this will accelerate warming.

10.1 Focus

In this section we consider two general issues: the effects of global change on ecosystems and the effects of ecosystem changes on the climate system. We center most of our discussion on process-level responses of ecosystems to global change. To understand many ecosystem responses to climate change, we consider them in the context of other components of global change such as increases in the atmospheric concentration of CO_2. We also consider the ecological consequences of tropical deforestation and the eutrophication of Northern Hemisphere areas with nitrogen in agriculture fertilizers and in acid precipitation as examples of ecosystem changes influencing climate systems. While the primary focus of this section is on terrestrial ecosystems, we end the section with a brief discussion of climate change and marine ecosystems.

10.2 Effects of Increased Atmospheric CO_2 and Climate Change on Terrestrial Ecosystems

Increases in atmospheric CO_2, warming and changes in precipitation patterns all have the potential to affect terrestrial ecosystems in a variety of ways. Here we review some of the major effects and identify some of the ways that these three factors interact to influence ecosystems.

10.2.1 Plant and Ecosystem Responses to Elevated CO_2

Current climate models estimate that even if man made emissions of CO_2 could be kept at present rates, atmospheric CO_2 would increase to about 450 ppmv by the year 2050 and to about 520 ppmv by the year 2100 (Section 1). Regardless of how the climate changes over this period, the Earth's biota will be living in a CO_2-rich environment. How will plants and ecosystems respond to elevated CO_2?

10.2.1.1 Plant responses

In this part of the report we will refer to two general groups of plants - C_3 plants and C_4 plants. These plant groups differ in a number of ways including certain aspects of the biochemical pathways they use in the photosynthesis process. Most of the Earth's plant biomass (about 95%) is accounted for by C_3 species, but a number of plants important to humans, such as maize, are C_4 species.

10.2.1.1.1 Carbon budget Atmospheric CO_2 affects various components of a plant's carbon budget including photosynthesis, respiration and biomass accumulation and allocation.

Photosynthesis - It has been shown many times that a doubling of CO_2 in the atmosphere will cause a short-term (minutes to hours) increase in photosynthesis (Kimball, 1983; Gifford, 1988). In some plants the increase is reduced after longer-term (weeks to months) exposure (Tissue and Oechel, 1987; Fetcher et al., 1988; Sage et al., 1990). This reduction may occur because other factors such as low nutrient availability eventually limit CO_2 uptake.

Respiration - Two types of respiration are recognized in plants: one, known as photorespiration, is intimately associated with photosynthesis and the other, dark respiration, includes all plant respiration except photorespiration. Photorespiration of C_3 plants is greatly reduced at high CO_2. The pattern is not so clear for dark respiration. The published data on dark respiration rate per unit of dry weight or leaf area indicate increases in some cases (Oechel and Strain, 1985) and decreases in others (Gifford et al., 1985).

Biomass accumulation - When grown at high CO_2 levels under favorable environmental conditions (e.g., favorable temperature, plentiful water and nutrients), C_3 plants almost always show increases in biomass accumulation

The C_4 plants are less responsive to high CO_2 levels in terms of biomass accumulation but nonetheless the response is generally positive. For both C_3 and C_4 plants the response is very species dependent and closely linked to environmental conditions (Mooney et al. 1990).

Allocation - Increases in CO_2 affect how plants allocate carbon among their various organs. Many studies indicate that with increasing atmospheric CO_2, plants allocate proportionally more carbon below ground than above ground, causing an increase in root to shoot ratios (Larigauderie et al. 1988, Curtis et al. 1990). High CO_2 can also increase the number of branches, tillers, flowers or fruits that a plant has (e.g., Curtis et al. 1989).

The ways in which other environmental factors interact with CO_2 to determine carbon allocation in plants is largely unknown. This is a serious gap in our knowledge and is a major stumbling block to the development of mechanistic, whole-plant models of carbon dynamics.

Tissue quality - Plant tissue quality can change with exposure to high CO_2. Changes in tissue quality include higher carbohydrate levels (Sionit et al. 1981) and, at least in one instance, higher levels of soluble phenolics and structural compounds (Melillo 1983). Nutrient concentrations are also often decreased (Curtis et al. 1990, see 10.2.1.1.3). These changes in tissue quality could have far-reaching consequences for herbivory, host-pathogen relationships, and soil processes such as decomposition and nutrient cycling. Much more work is needed in this area before we can make generalizations about the linkages between elevated CO_2, tissue chemistry and ecosystem effects.

10.2.1.1.2 Interactions between carbon dioxide and temperature Temperature and CO_2 interact to affect photosynthesis and growth. Although the reactions are species specific, the general response for C_3 plants is that the optimum temperature increases for net photosynthesis. Idso and colleagues (1987) have suggested that plant growth response to elevated CO_2 seems to be greater at higher temperatures. If, however, temperature becomes extremely high, enzyme degradation will limit both photosynthesis and growth. Likewise, plants growing at low temperatures are not as responsive to elevated CO_2 for physiological reasons that lead to a feedback inhibition of photosynthesis.

10.2.1.1.3 Carbon dioxide and environmental stress Elevated CO_2 can influence plant responses to limitations of water, light and nutrient availability and other environmental factors (Table 10.1).

Table 10.1 *Relative effects of increased CO_2 on plant growth and yield: a tentative compilation*[1] *(from Warrick et al. 1986b)*

	C_3	C_4
Under non-stressed conditions	++	0 to +
Under environmental stress:		
Water (deficiency)	++	+
Light intensity (low)	+	+
Temperature (high)	++	0 to +
Temperature (low)	+	?
Mineral nutrients	0 to +	0 to +
Nitrogen (deficiency)	+	+
Phosphorous (deficiency)	0?	0?
Potassium (deficiency)	?	?
Sodium (excess)	?	+

[1] Sign of change relative to control CO_2 under similar environmental constraints
++ strongly positive
\+ positive
0 no effect
? not known or uncertain

Water stress - Water use can be affected by high CO_2. Short-term measurements show that increased CO_2 reduces water-loss (transpiration) rates per unit leaf area and increases water use efficiency (WUE), which is the ratio of photosynthesis to transpiration (Farquhar and Sharkey 1982). Increased WUE could lead to increased biomass accumulation for plants growing in arid environments.

The net effect of high CO_2 on total water use per unit land area under field conditions is less certain. This is because the increases in leaf area and root extension observed in high-CO_2 plants tend to increase total water use and may counteract the effect of low transpiration per unit leaf area. Gifford (1988) has concluded that for both physiological and meteorological reasons, high CO_2 concentration might exert little or no effect on regional evapotranspiration, but this issue is far from resolved.

Low light - Carbon dioxide enrichment can increase plant growth at low light intensity. In fact, the relative enhancement of growth at low light can even be greater than at high light (Gifford 1979). For some plants, however, the relative enhancement of growth by high CO_2 appears equal at low and high light (Sionit et al. 1982).

Nutrient stress - High CO_2 can increase plant growth in some situations of nutrient-stress. A number of C_3 plants growing under nitrogen-deficient conditions exhibited increased growth when the CO_2 concentration was doubled (Wong 1979, Sionit et al. 1981, Goudriaan and de Ruiter 1983). In these instances there was an increase in the nitrogen use efficiency (NUE), that is, the ratio of carbon gain to nitrogen used was increased.

10.2.1.1.4 Phenology and senescence. Elevated CO_2 has been shown to influence the phenology and senescence of plants. Annual plants 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 (Paez et al. 1984). Early leaf and seed production could shift the population dynamics and competitive relationships of plants growing under field conditions.

There is also evidence of delayed senescence of some species under elevated CO_2 (Hardy and Havelka 1975, Mooney et al. 1990). Delayed leaf senescence could extend the growing season and this could lead to increased biomass accumulation (Mooney et al. 1990). In ecosystems with cold climates, however, the growing season could also expose plants to frost damage (Oechel and Strain 1985).

10.2.1.2 Community and ecosystem responses to elevated carbon dioxide

10.2.1.2.1 Plant-plant interactions. We can expect changes in the interactions of C_3 plants with elevated CO_2. As we noted earlier (see 10.2.1.1.1) the responses of C_3 plants to increased CO_2 are species dependent.

Some ecosystems such as temperate zone grasslands can contain a mixture of C_3 and C_4 plants. Elevated CO_2 could affect the competition between them. Based on what we know about the biochemistry and physiology of C_3 and C_4 species, we would expect that as the CO_2 concentration increases, the C_3 plants should do progressively better than the C_4 plants, unless there is water stress. A number of studies have shown just these results. For example Bazzaz and Carlson (1984) studied the competition between C_3 and C_4 herbaceous plants grown under two moisture regimes and three levels of CO_2 (300, 600 and 1200 ppm). The C_3 species grew progressively more rapidly (was a better competitor) than the C_4 species as the CO_2 and moisture levels increased.

10.2.1.2.2 Interactions between plants and animals. The effects of increased CO_2 on plant-animal interactions have received relatively little attention. Some work has been done on herbivory and the conclusion is that herbivory may be indirectly affected by high CO_2 concentrations. Several reports (Overdieck et al. 1984, Lincoln et al. 1984, 1986, Lincoln and Couvet 1989, Fajer et al. 1989) have indicated that rates of herbivory increase on plant tissues grown at high CO_2. These increases in herbivory appear to be related to changes in the tissue quality of plants exposed to elevated CO_2 (see 10.2.1.1.1). The increased herbivory could affect plant growth as well as feed back to ecosystem-level phenomena like nutrient cycling. Increased herbivory would be expected to accelerate nutrient cycling.

Linkages between the effects of elevated CO_2 on plant phenology and herbivory have been suggested (Oechel and Strain 1985), but to our knowledge no research has been carried out on this topic. One argument is that changes in the timing of herbivore feeding relative to plant phenology could affect productivity and competitive ability of the plants concerned.

10.2.1.2.3 Interaction between plants and microbes. Elevated atmospheric CO_2 and climate change will probably have major effects on microbial symbionts of plants such as nitrogen-fixing bacteria and mycorrhizal fungi.

Symbiotic nitrogen fixing organisms have large requirements for energy provided as plant photosynthate. These organisms are primarily responsible for giving plants access to the large reservoir of nitrogen in the atmosphere by converting that gaseous nitrogen into organic nitrogen. For many ecosystems, high rates of productivity are linked to nitrogen fixation. Numerous experiments have shown that climatic variables and CO_2 concentration are important controllers of the relationship between plants and symbiotic nitrogen fixers. For example, a field experiment by Hardy and Havelka (1975) showed that over a nine-week period, plants grown with supplemental CO_2 exhibited a five-fold increase in nitrogen fixation rate over untreated controls.

Mycorrhizae are symbiotic associations between the host-plant root and a mycorrhizal fungus. As with symbiotic nitrogen fixers, the mycorrhizal fungi depend on plants for a supply of reduced carbon. Thus climate and CO_2 changes that affect a plant's ability to fix atmospheric CO_2 have the potential to affect mycorrhizal functioning. Mycorrhizae may affect plant nutrition, especially phosphorus nutrition, and plant water relations. Luxmoore and co-workers (Luxmoore et al. 1986, Norby et al. 1986, O'Neill et al. 1987) have shown that mycorrhizal infection is enhanced by elevated CO_2, and the increased infection resulted in increased plant growth on nutrient-poor soils.

10.2.1.2.4 Decomposition. Free-living soil microorganisms are responsible for organic matter decay. Decay rate is a function of the chemical quality of the organic matter and environmental factors such as temperature and moisture (see 10.2.2.2.3). Earlier we noted that plants grown in elevated CO_2 have altered tissue chemistry such as higher carbon to nitrogen ratios. These changes in tissue chemistry could slow decomposition and possibly lead to plant nutrient stress.

10 2 1 2 5 Whole-ecosystem exposure to elevated carbon dioxide Many of the direct effects of elevated CO_2 on plant growth have been observed in short term studies in the laboratory Serious questions have been raised about whether or not these phenomena actually occur in the field and if they do, whether they are long-term or only transient Some answers to these questions may be gained from a review of two recent experiments on intact ecosystems - one a tussock tundra ecosystem in Alaska and the other a mid-latitude salt-marsh ecosystem in Maryland These are the only whole-ecosystem experiments we know of in which the entire system has been subjected to doubled CO_2 concentrations for more than one growing season Both experiments have been run for three years

At the tundra site, CO_2 and temperature were controlled in greenhouses placed over intact field plots (Oechel and Riechers 1987, Tissue and Oechel 1987) Experimental treatments included ambient CO_2 and temperature conditions, elevated CO_2 (510 and 680 ppmv) and ambient temperature, and elevated CO_2 and temperature (680 ppmv CO_2, +4°C temperature above ambient)

At the salt-marsh site CO_2 was controlled through the use of open top chambers set over intact field plots (Drake et al 1989) The experimental treatments included ambient CO_2 and temperature, and elevated CO_2 (ambient plus 340 ppm) and ambient temperature

The tundra ecosystem is floristically diverse but is dominated by a sedge, while the marsh system is comprised largely of pure patches of two higher plants, a sedge and a grass The tundra and salt marsh sedges are C_3 plants and the salt marsh grass is a C_4 plant The plant and ecosystem responses of these two systems (Table 10 2) generally follow predictions based on the interactions of CO_2 and the other environmental factors discussed earlier

Significant ecosystem-level effects were noted in both the tundra and the salt marsh For the tundra plots exposed to elevated CO_2, there was a complete homeostatic adjustment of whole ecosystem carbon flux within three years, with the result being no change in net carbon storage in CO_2-treated plots relative to controls However, the combination of elevated CO_2 and temperature rise resulted in an increase in net carbon storage that lasted for the three years of observations (Oechel and Riechers 1986, 1987)

The CO_2 treatment in pure stands of the C_3 marsh plant resulted in increased net carbon storage for the whole system In the pure stands of C_4 grass, net carbon storage for the whole system was not increased

One of the most important points that can be made about the comparison of the responses of the two ecosystems to elevated CO_2 is that the interactions among temperature, CO_2 and nutrient availability are key controlling factors Temperature affects both plant photosynthetic response to elevated CO_2 and nutrient availability through organic matter decomposition (see 10 2 2 2 3) Both temperature and nutrient availability exert control on the growth of plant organs where fixed carbon can be stored In cold, low nutrient environments, the growth of storage organs is slow and this can lead to an 'end product' inhibition of photosynthesis If temperature is not limiting, but nutrients are, the increased allocation of fixed carbon to roots could result in more of the soil volume being "mined" to meet plant nutrient demand, thereby allowing the plant to utilize the CO_2

Have we correctly interpreted the interactions and do they operate in other terrestrial ecosystems? We do not know the answers to these questions There have been no long-term studies of the responses of most of the world's ecosystems to elevated CO_2 or climate change For example, we currently have no information about many of the responses of forests and other woody ecosystems to elevated CO_2 Some scientists have argued that limitations of water, nutrients and light, will prevent these ecosystems, especially unmanaged foresets, from showing significant responses to elevated levels of atmospheric CO_2 (e g , Kramer, 1981) The responses of forests to increased CO_2 are very uncertain A high research priority for the near future has to be a series of whole ecosystem manipulations, including forest manipulations, in which key controlling factors such as CO_2, temperature, moisture and nutrient availability are varied

10 2 1 3 Summary

Increased atmospheric CO_2 has the potential to alter ecosystem metabolism Net primary production could be enhanced by increased CO_2 in a variety of ways including the following stimulation of photosynthesis, depression of respiration, relief of water and low light stresses, relief of nutrient stress by several mechanisms (greater nutrient use efficiency, increased nutrient uptake through root-microbial associations increased symbiotic nitrogen fixation), and delay of senescence that prolongs the growing season

Elevated CO_2 could also lead to net carbon storage, especially if the growth of woody vegetation is stimulated and there is not an equal stimulation of decomposition by some other factor such as warming At this time we have no evidence that elevated CO_2 has increased net carbon storage in natural ecosystems dominated by woody vegetation

Increased CO_2 could also change species composition by affecting plant reproductive processes, competition, plant-animal interactions, and plant-microbe interactions

Table 10.2 *Effects of doubling CO_2 on several plant and ecosystem properties and processes. In the arctic all species are C_3. Saltmarsh communities are mono-specific stands of the sedge Scirpus olneyi (C_3) and the grass Spartina patens (C_4). The symbols indicate the response to elevated compared to normal ambient CO_2 as an increase (+), decrease (-), no change (0), or no data as a blank.*

		ARCTIC	SALTMARSH	
			C_3	C_4
I	PLANT EFFECTS			
A	Carbon exchange			
	Photosynthesis	0	+	0
	Acclimation of photosynthesis	+	0	0
	Plant respiration	0	-	-
	Decomposition of dead shoots		-	-
B	Growth			
	Shoot expansive growth	0	0	0
	Root biomass	-/0	+	0
	Number of shoots	+	+	0
	Size of shoots	0	0	0
	Root/shoot ratio	-/0	+	0
C	Tissue Composition			
	N tissue concentration	-	-	0
	Carbon/nitrogen	+	+	0
	Starch content	+		
	Tissue density/specific wt.	+	0	0
	Salt content		-	
D	Development/reproduction			
	Senescence	-	-	0
	Tillering	+	+	0
	Number of flowers	-	0	0
	Number of seeds/stem		0	0
	Sexual/asexual reproduction	-		
E	Water Use			
	Transpiration	0	-	-
	Water use efficiency	0	+	+
	Leaf tempertaure	0	+	+
	Leaf water potential		+	+
II	ECOSYSTEM EFFECTS			
	Evapotranspiration	0	-	-
	Net carbon storage	+/0	+	0
	Acclimation of NCE to CO_2	+	0	0
	Net ecosystem respiration Species		-	-
	composition	+	+	0
	Water use	0	-	-
	Nitrogen content of canopy	-	0	0
	Soil enzyme activity	+/-		
	Soil solution nitrogen	-/0		

NCE = Net Carbon Exchange. (Moung et al., 1990)

10.2.2 Plant and Ecosystem Responses to Changes in Temperature and Moisture

Temperature and moisture are considered major controllers of plant and ecosystem processes. They exert a strong influence on birth, growth and death rates of plants. They also act as primary controllers of the biogeochemistry of ecosystems. In this section we review some of the aspects of these controls.

10.2.2.1 Plant responses to changes in temperature and moisture

10.2.2.1.1 Carbon budget: Temperature and moisture are important controllers of the carbon budgets of plants. These environmental factors directly influence basic processes such as photosynthesis and respiration.

Temperature - Photosynthesis and plant respiration respond differently to temperature. For example, gross photosynthesis of many mid-latitude plants ceases at temperatures just below 0°C (minimum) and well above 40°C (maximum), with optimum rates in the range of 20-35°C (Figure 10.1.b). Above 0°C the response of photosynthesis to temperature is initially rapid, but slows in the optimum range. In contrast, plant respiration rate tends to be slow below 20°C, but at higher temperatures it accelerates rapidly up to the temperature where the rate of respiration equals the rate of gross photosynthesis, and there can be no net assimilation of carbon (Figure 10.1.b). The response of net photosynthesis is broadly similar to that of overall growth (Figures 10.1.a and 10.1.b). These differences in the responses of photosynthesis and respiration to temperature increases have been used to support the argument that global warming may result in a reduction in net carbon uptake by plants (Woodwell, 1987).

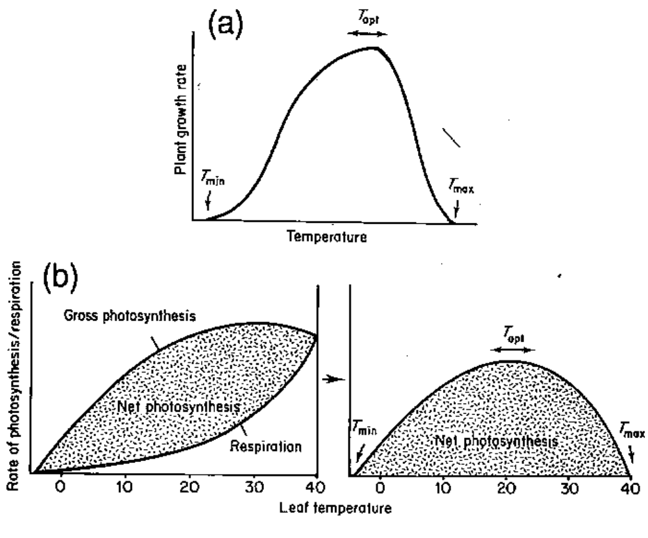

Figure 10.1: Schematic representation of plant responses to temperature. Panel (a) is the general response of plant growth, and panel (b) is the general response of photosythesis and respiration. T_{min} = a minimum temperature, T_{opt} = optimum temperature range, and T_{max} = a maximum temperature. (From Fitter and Hay, 1981).

It must be noted that some plants do appear to have the ability to adjust to temperature changes. Cases have been documented where respiratory response to temperature is adjusted to stay within a limited range of rates in spite of the prevailing temperature (e.g., McNulty and Cummins, 1987).

Moisture - Water stress can decrease photosynthesis in a wide range of plants (e.g., Hsaio, 1973). As we discussed earlier (10.2.1.4), water stress can be alleviated, at least in the short term, when plants are exposed to increased atmospheric CO_2.

The effects of water stress on respiration are complex. A reduction in moisture supply will, in many cases, reduce plant growth and so reduce respiration associated with growth (Hanson and Hitz, 1982). If water stress is severe it will cause cellular damage and this may lead to increased rates of protein turnover with an associated increase in respiration.

10.2.2.1.2 Phenology and senescence: As well as influencing the rate of plant growth and metabolism, temperature and moisture can influence the timing of development and senescence. For example, the annual leaf canopy development and abscission in autumn-deciduous trees and shrubs are partially under temperature control. In the drier tropical ecosystems, moisture often functions as the primary controller of canopy development and leaf senescence (Long, 1990). Thus, depending on the ecosystem, either temperature or moisture can function as a primary determinant of the length of the growing season.

Canopy development in northern ecosystems often depends on winter temperatures. In the well documented case of the spruce *Picea sitchensis* (Cannell and Smith, 1986), bud-burst is only triggered after a winter period providing 140 days with a temperature of less than 5°C, followed by a spring period of warmer weather. If the winter temperatures increase, as predicted, so that there is a period shorter than 140 days when temperatures are less than 5°C, then bud-burst may be delayed or even fail to occur. This is the type of climate effect that will result in the migration of plant species to higher latitudes or higher elevations (see 10.2.2.3).

Not all species will respond to climate changes by migrating to higher latitudes or higher elevations. Field experiments have shown that species are able to evolve new phenological characteristics in a new climate. This has been observed to occur within 8 years of transplanting populations to a new climate (Woodward, 1990). The rapidity of this response was observed in an herbaceous perennial, which showed marked temporal changes in seed germination and dormancy in the new environment. The universality of this response is unknown but it could prove to be a powerful agent for disrupting community synchrony, for initiating structural change and for enhancing the capacity of species to migrate

10 2 2 2 Community and ecosystem responses

10 2 2 2 1 Plant community composition Changes in climate will likely alter differentially the regeneration success, growth and mortality rates of plants The resulting changes in competitiveness of species or species groups will affect community composition Where species occur at their distributional limits, in transition zones, small changes in climate are likely to promote disproportionately large responses in the plant species Changes in community structure will, therefore be identified sooner in transitional zones between vegetation types than elsewhere

10 2 2 2 2 Interactions between plants and animals Of crucial importance in plant community functioning is the synchronous operation of the life cycles of interacting plants, animals and soil organisms Complex synchronies are found in communities in which the life cycles of plants and pollinating and seed-dispersing animals must be closely linked Changes in climate could disrupt these synchronies

Climate-related stresses such as drought stress, can make plants susceptible to insect attack As an example, oak wilt disease in the USSR appears to be dependent on the decreased ability of the trees to resist leaf-eating insects during drought (Israel et al , 1983)

Warming may expand the overwintering ranges of some plant pests and this could prove a serious problem for agroecosystems For example, in the United States the potato leafhopper, a serious pest on soybeans and other crops, currently overwinters only in a narrow band along the coast of the Gulf of Mexico Warmer winter temperatures could cause a doubling or a tripling of its overwintering range This would increase invasion populations and lead to greater insect density and increased plant damage (Smith and Tirpak, 1989)

10 2 2 2 3 Decomposition Climate is an important controller of the decomposition of both surface litter and organic matter dispersed through the soil profile The chemical composition of the decomposing material also influences decay rate

Surface litter - The decomposition of surface litter is very clearly related to climatic factors, with rates generally increasing with increasing temperature and precipitation in well-drained sites In poorly drained sites, excessive moisture (waterlogging) can slow decay rates Climatic control is most often quantified by a relationship with actual evapotranspiration (AET)

It has been known for some time that litters from different plant species decay at different rates under similar conditions (Minderman, 1968) This has been linked to differences in the quality of carbon Litters with high lignin concentrations will decay more slowly than those with lower concentrations The ratio of lignin to nitrogen has proven a good predictor of litter decay rate in temperate and boreal ecosystems (Melillo et al , 1982)

A number of attempts have been made to integrate the climate and chemical quality controls of litter decay These models generally indicate that when AET is low the decomposition rates do not vary much with lignin concentrations, but as AET increases resource quality accounts for more of the variation in decomposition rates (Meentemeyer, 1978, 1984, Pastor and Post, 1986)

Soil organic matter - Temperature, moisture and soil texture are important controllers of soil organic matter decomposition These factors assume more or less importance depending on the ecosystem In tundra ecosystems soil respiration can be limited by an excess of moisture (waterlogging) as well as by low temperatures

Soil respiration in the well drained forests of the boreal and temperate zones are most often temperature limited (Van Cleve and Sprague 1971, Bunnell et al 1977) Soil respiration in these systems is rarely limited by moisture deficit (Anderson, 1973 Schlesinger, 1977, Moore 1984) In very dry sub tropical forests, lack of moisture can limit decay (Carlyle and U Ba, 1988)

Overall, litter decomposition and SOM accumulation in climax grasslands follow predictable climate and soil texture-related patterns (Brady 1974) which are amenable to the development of simulation models of carbon dynamics (Hunt, 1977, McGill et al , 1981 Van Veen and Paul, 1981 Parton et al 1987) In dry grassland sites soil respiration is primarily a function of soil moisture (Hunt 1977, Warembourg and Paul 1977 Orchard and Cook 1983) although computer model simulations of the response of semi-arid soils of North America to warming suggest that higher soil temperatures will result in increased carbon losses (Schimel private communication) In mesic grasslands as in forests temperature is the main determinant of carbon mineralization rates for the soil system Fine textured soils, those rich in clays are thought to render soil organic matter more stable through the mechanism of physical protection than are the coarse textured sandy soils

There is concern that global warming will accelerate the decomposition of surface litter and soil organic matter especially at high latitudes of the Northern Hemisphere In the Arctic tundra, there are about 160 Pg carbon stored in the soil (Schlesinger, 1984) Most of it is frozen in permafrost with only 20-40cm thawing in the summer Even for the thawed material the cold and in some cases wet conditions preclude rapid decomposition But what will happen if a CO_2 doubling is accompanied by a 4.8°C temperature increase?

The experiments of Billings and his colleagues (1982, 1983, 1984) suggest that wet sedge tundra will become a net source of carbon to the atmosphere, at least for a short time, if climate changes such that air temperature is increased and there is greater soil drainage. Billings argued that warmer temperatures and a lowered water table would result in greatly increased rates of soil respiration. Using Billing's data, Lashof (1989) calculated that a 4°C temperature rise would increase the net annual flux of carbon from the tundra to the atmosphere by 1 Pg.

The consequences of soil warming in northern forests are clear from an experiment conducted on a boreal forest in Alaska. Experimental heating of the surface soil, to 9°C above ambient temperature for three summers was carried out in black spruce forest (Van Cleve et al. 1983). For the entire period there was a 20% reduction in the amount of organic carbon in the surface soil of the heated site as compared to no reduction in an adjacent control site. The increased decay of the soil organic matter resulted in an increase in nutrients available to plants. As a result of the more favourable temperature and nutrient regimes, foliage showed increased photosynthetic rates and significantly higher concentrations of nitrogen, phosphorus and other nutrients important to plant growth.

10.2.2.2.4 Models of ecosystem response to climate change. A family of population based forest growth models (e.g., JABOWA, FORET LINKAGES) has been used to consider the effects of climate change on forest composition, carbon storage capacity and geographic distribution. For example Pastor and Post (1988) ran a population-based forest growth model (LINKAGES) for several sites including a spruce-northern hardwood site in northeastern Minnesota. Forest growth was simulated on two soil types found in this region: one with low water-holding capacity and the other with high water-holding capacity. The simulations were initiated from bare plots with the seeds of trees commonly found in the area. For 200 years the sites were allowed to follow the forest dynamics appropriate to the current climate. The climate conditions were then changed linearly to reach a $2xCO_2$ climate over the next 100 years and then remained constant the final 200 years of the simulation.

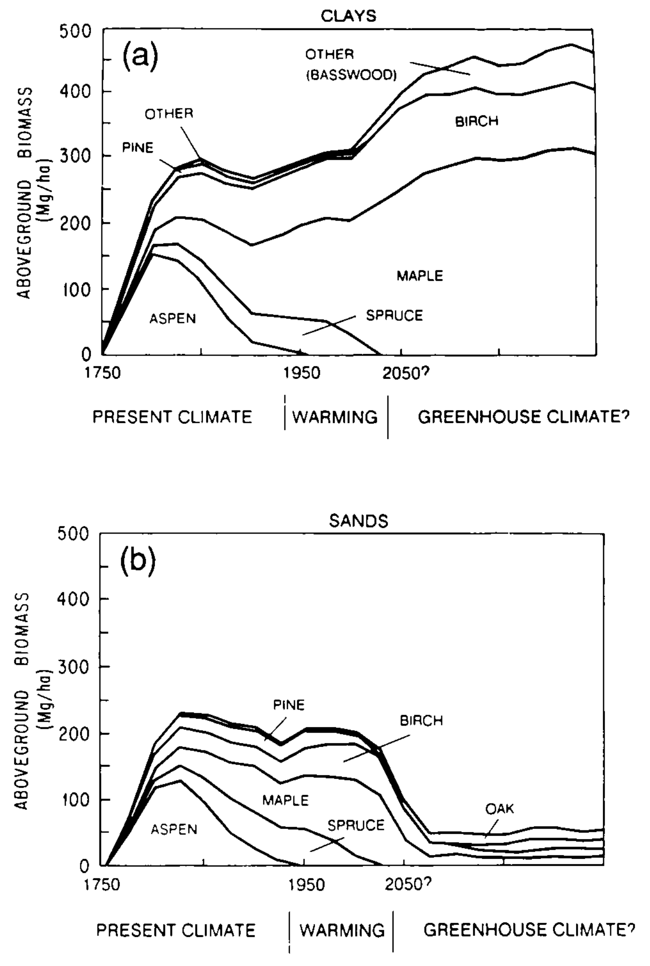

Figure 10.2: Predictions of biomass and species composition of Minnesota forests under climatic conditions predicted with CO_2 doubling. The predictions are based on a forest growth model (LINKAGES). Climate inputs were the same for the two runs but panel (a) shows simulated forest growth on a soil with high water holding capacity, and panel (b) shows simulated forest growth on a soil with low water holding capacity (After Pastor and Post 1988).

On the soil with high water-holding capacity the spruce-northern hardwood forest was replaced by a more productive northern hardwood forest (Figure 10.2). The aboveground carbon mass in the mature post-climate-change forest was about 50% greater than in the pre-climate-change forest. The northern hardwood forest was more productive for two reasons. First, in the model northern hardwoods have a faster growth rate and can attain a greater biomass than the spruce. Second, the warmer climate, as well as the relatively easy-to-decompose litter of the hardwoods, increases nitrogen availability and this enhancement amplifies the effect of warming on productivity.

On the soil with the low water-holding capacity, the spruce-northern hardwood forest was replaced by a stunted pine-oak forest of much lower carbon storage capacity. At maturity, the oak-pine forest contained only 25% of carbon contained in the original spruce-northern hardwood forest.

In this example, temperature, plant-soil water relations, and nitrogen cycling all interacted to affect ecosystem structure and function. Changes in climate resulted in changes in forest composition and depending on soil water relations either an increase or a decrease in ecosystem carbon storage capacity.

Solomon (1986) used another population-based forest growth model (FORENA) for 21 locations in eastern North America with 72 species of trees available as seeds at all times. Initial soil conditions were the same at all sites. The simulations were all initiated from a bare plot and were allowed to follow the forest dynamics appropriate to the modern climate with undisturbed conditions for 400 years. After year 400 the climatic conditions were changed linearly to reach the 2xCO_2 climate in year 500 (see Solomon, 1986 for details).

At the end of 400 years the forests on the 21 sites had reached structural maturity and most contained the appropriate species mixes as judged by comparing them to what actually grows at the sites. The major effects of the changes in climate that resulted from a doubling of atmospheric CO_2 were as follows:

- A slower growth of most deciduous tree species throughout much of their geographical range,
- A dieback of the dominant trees, particularly in the transition between boreal/deciduous forests,
- A reduction of carbon storage in the vegetaion in the southern two-thirds of the region and a gain in the far north,
- An invasion of the southern boreal forest by temperate deciduous trees that was delayed by the presence of the boreal species.
- A shift in the general pattern of forest vegetation similar to the pattern obtained from the Holdridge map experiments (see 10.2.2.3.1)

The overall reduction in carbon stocks in the vegetation of forests of the eastern North America was estimated to be 10% (Figure 10.3). If the results are generalized to all temperate forests the annual flux from these systems to the atmosphere would be between 0.1 and 0.2 Pg C (Lashof, 1989).

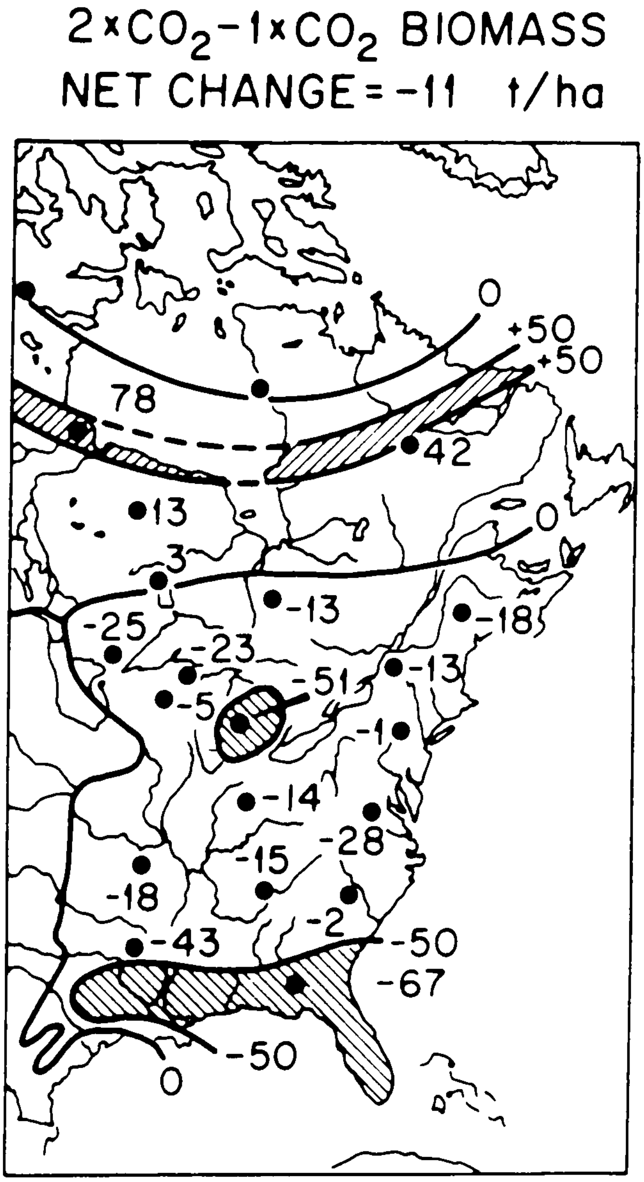

Figure 10.3: Carbon storage dynamics (in megagrams per hectare) simulated at 21 sites in eastern North America. Map shows differences above contemporary climate and 2xCO_2 climate. Only carbon in above ground biomass is represented. (From Solomon, 1986)

Solomon (1986) discussed the possible effects of several important ecological processes that were not included in the model. For example, insects and other pathogens as well as air pollutants could enhance the mortality simulated by the models. Also, plant migration (and associated lag effects) could have a negative influence on forest productivity.

These forest growth models are useful tools for making preliminary evaluations of forest ecosystem responses to climate change. They do have a number of limitations and these have been reviewed recently (Smith and Tirpak, 1989). For example, major uncertainties exist regarding the kinds and rates of response of individual tree species to changes in the environment including the CO_2 increases. Efforts are currently under way to improve the physiological and soil process components of these models.

Climate change may lead to an increase in the frequency of extreme weather events such as tropical storms. Drier conditions in some regions may lead to increased fire frequency. Large disturbances such as severe storms and large fires can destroy vegetation, increase susceptibility of sites to erosion, change nutrient cycling rates and dramatically alter animal habitat. The effects of these large-scale disturbances are currently not considered by these forest growth models.

10 2 2 3 Large scale migration of biota

One of the major consequences of climate change could be the migration of biota across the landscape The migrations could have many effects including the release of large amounts of carbon to the atmosphere from dying and decaying forests The releases could be large enough to further increase warming (Woodwell, 1987, Lashof, 1989) Both modelling studies and palaeoecological studies have been used to examine the relationships between climate change and forest migration

10 2 2 3 1 Simulation of global scale response using vegetation-climate relationships A very general approach to examining the possible responses of the world's ecosystem types to climate change is to use hypothetical relationships between climate and vegetation derived in present-day conditions, and to apply these to scenarios of changed climate Emanuel et al (1985a,b) employed a lifezone classification of Holdridge (1947, 1964) This system hypothesizes zonation of vegetation across gradients of average total annual precipitation, the ratio of potential evapotranspiration to precipitation and mean annual biotemperature (average annual temperature computed by setting all values below 0°C to zero) Using the Holdridge system, Emanuel and his co-workers (1985a,b) predicted a large shrinkage of the boreal forest (by 37%) and tundra (by 32%) and expansion of grassland lifezones under warmer climates due to a CO_2 doubling Because the temperature changes in the climate-change scenario used by Emanuel and his colleagues were small toward the equator, there were smaller changes in the tropical life zones In this modelling exercise, precipitation was maintained at current levels for all areas

There are several uncertainties attached to this type of assessment (Emanuel et al , 1985a), notably the selection of climate scenarios and low resolution of the data grid (0 5° x 0 5°) In addition, the response of ecosystems to factors such as CO_2 and the rate of climate change is not considered

10 2 2 3 2 Palaeo ecological evidence The IPCC projections of climate change indicate a rapid rise in global temperature with an increase of about 0 3°C per decade over the next century (Section 5) Rapid increase in temperature may create problems for large stature ecosystems such as forests

The significance of projected rates of temperature change becomes clear when the consequent geographic shifts in isotherms are considered For example, in mid-continental North America, each degree (°C) change in temperature corresponds to a distance of 100-125 km If similar temperature-distance relationships are assumed in

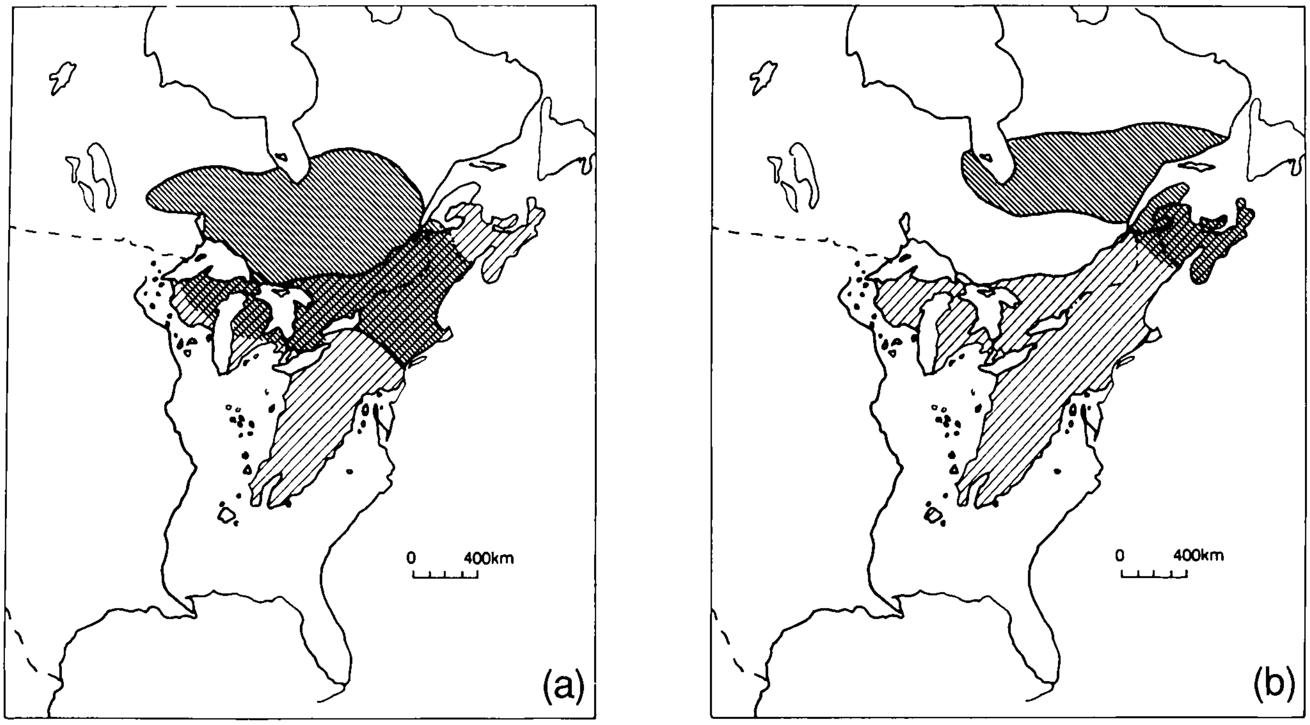

Figure 10.4: Present and future range of eastern hemlock (*Tsuga canadensis*) under two climate scenarios predicted by (a) Hansen et al 1983 and (b) Manabe and Wetherald, 1987 Light diagonal shading is the present range, and dark diagonal shading the potential range with CO_2 doubling Cross hatched area of overlap is where the trees are likely to be found 100 years from now (Davis, 1988)

the future, a 3°C rise in temperature would lead to a 300 to 375 km northward displacement in isotherms during the next century.

Based on the fossil pollen record, we know that the rate of movement of forest trees during the Holocene was generally 25 and 40 km per century (Davis, 1981, Huntley and Birks, 1983), with the fastest rate 200 km per century (Ritchie and MacDonald, 1986). With these rates of movement, most tree species would not be able to change their geographical distribution as fast as the projected shifts in suitable climate. Zaluski and Davis (unpublished data cited in Davis, 1988) provide an example based on the past rates of spread of eastern hemlock (*Tsuga canadensis*). Under two scenarios for future climate, this species would not be able to migrate fast enough to occupy much of its potential range 100 years from now (Figure 10.4).

Prehistorical species migrations were largely unaffected by human land use. In contrast, modern species migrations may be severely restricted by land use, for example the progression of the altitudinal treeline with global warming may be prevented by stock grazing. Also, because suitable habitats for many rare species characteristic of areas of low productivity are infrequent and fragmentary, being surrounded by very productive agricultural land, it is unlikely that these species will spread naturally even though climate change will increase their vigour and reproductive capacity. On the other hand, the migration of weedy species may be enhanced by land-use change, for example along corridors of dispersal formed by roads, railways, etc. and in open ground created by various forms of human disturbance.

Very little is known about migration rates under present or likely future climates. Models of migrations of invasive species based on diffusion (Williamson, 1989) or epidemic theory (Carter and Prince, 1981) suggest that the outcome of invasions is often unexpected and accurate prediction has rarely ever been achieved. The relationship between species migrations and climate is not simple and geographical barriers to dispersal may be locally important.

Quaternary pollen records also show that plant communities continuously change over time. Communities disassemble and new ones arise presumably because species respond to climatic variations according to unique sets of physiological and ecological requirements (Graham, 1986). The resulting new combinations of vegetation, climate and soils can change the spatial patterns of such fundamental processes as primary production (Pastor and Post, 1988). More subtle but still important relationships such as those evolved between host and pathogen may be disrupted by the stress of new conditions, resulting in increased frequency of epidemics (Leonard and Fry, 1986).

Past changes in plant associations and abundances have been so marked that some types of ecosystems have also been transient. For example, 20,000-30,000 years ago when the Earth's climate was about 5°C colder than present large parts of North America, Europe and Asia were covered by herbaceous vegetation that did not resemble modern tundra, grassland or steppe. Thus a plant community that was dominant in the Northern Hemisphere for 10,000 years does not exist today. Some well known modern ecosystems have had much shorter existences. As an example, old-growth Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest, renowned for their long-lived, massive trees and huge ecosystem carbon storage, are first recognized in the fossil record about 6000 years ago - representing only 5 to 10 generations of the dominant tree species (Brubaker, personal communication).

Thus the dynamic record of the Earth's vegetation clearly demonstrates that ecosystems as well as communities may be short lived in the face of changing climate. Ecosystems represent a set of processes linking biota and their geochemical environment in a particular climate. Because natural variations in the Earth's climate have followed a relatively unique path dictated by changes in large-scale climatic controls, a variety of ecosystems come and go over time. To the extent that human influences will cause unique future climates, we should expect fundamental changes in current ecosystems.

10.2.2.4 Summary

Both photosynthesis and plant and microbial respiration tend to increase with increasing temperatures, but at higher temperatures respiration is often the more sensitive process (see 10.2.2.1.1). As a consequence, global warming may result in a period of net release of carbon from the land to the atmosphere (Woodwell, 1987). The magnitude of the release would depend on the magnitude and the seasonality of the temperature change and the responses of the various processes to that change. One estimate is that the annual carbon flux from the boreal zone associated with a 4°C global temperature change would be in the range of 0.5-2.0 Pg C (Lashof, 1989).

Besides being dependent on temperature, photosynthesis and plant and soil respiration can be influenced by soil water. Increased water availability will tend to stimulate plant growth in dry ecosystems and to increase carbon storage in cold and wet ecosystems like lowland tundra. A number of recent modelling studies have predicted that water stress will be a primary cause of forest death in the southern and central regions of North America as climate changes (e.g. Solomon, 1986, Smith and Tirpak, 1989). Forest death has the potential for releasing large stores of carbon to the atmosphere.

A major consequence of climate change could be the migration of biota across the landscape. Communities will not migrate as units. Individual species will migrate at different rates depending upon a variety of species specific

***Table 10.3** Area coverage, plant carbon and net primary production for major terrestrial ecosystems according to Whittaker and Likens (1975), (2) Ajtay et al. (1979), (3) Olson et al. (1983). The amount of carbon in soil is also shown following the classifications by (2) Ajtay et al. (1979) and according to (4) Schlesinger (1977) based on the classification by Whittaker and Likens (1975). From Bolin 1986.*

	Area 10^{12} m^2			Plant carbon Pg C			Primary Production Pg C yr^{-1}			Detritus, soil Pg C	
	(1/4)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(2)	(4)
(1) Tropical rain forest	17.0	10.3	12.0	344	193	164	16.8	10.5	9.3	82	
(2) Tropical seasonal forest	7.5	4.5	6.0	117	51	38	5.4	3.2	3.3	41	288
(3) Temperate forest	12.0	7.0	8.2	174	88	65	6.7	4.6	4.9	72	161
(4) Boreal forest	12.0	9.5	11.7	108	96	127	4.3	3.6	5.7	135	247
(5) Woodland, shrubland interupted woods	8.5	4.5	12.8	23	24	57	2.7	2.2	4.6	72	59
(6) Savannah	15.0	22.5	24.6	27	66	49	6.1	17.7	10.7	264	63
(7) Temperate grassland	9.0	12.5	6.7	6	9	11	2.4	4.4	2.6	295	170
(8) Tundra, alpine	8.0	9.5	13.6	2	6	13	0.5	0.9	1.8	121	163
(9) Desert semidesert	18.0	21.0	13.0	6	7	5	0.7	1.3	0.9	168	104
(10) Extreme desert	24.0	24.5	20.4	0	1	0	0.0	0.1	0.5	23	4
(11) Cultivated land	14.0	16.0	15.9	6	3	22	4.1	6.8	12.1	128	111
(12) Swamps, marshes and coastal land	2.0	2.0	2.5	14	12	7	2.7	3.3	3.6	225	145
(13) Bogs and peatland		1.5	0.4		3	1		0.7	0.2		
(14) Lakes and streams	2.0	2.0	3.2	0	0	1	0.4	0.4	0.4	0	0
(15) Human areas		2.0			1			0.2		10	
TOTAL	149.0	149.3	151.1	827	560	560	52.8	59.9	60.6	1636	1515

characteristics as well as environmental factors such as natural and human-caused barriers to dispersal. Predictions of migration rates are very uncertain. It is possible that many tree species will not be able to change their geographical distribution as fast as the projected shifts in suitable climate and extinctions may occur.

10.3 The Effects of Terrestrial Ecosystem Changes on the Climate System

In this part of the report we consider how a variety of changes in terrestrial ecosystems can affect the climate system. We begin by considering the types of ecosystem changes that will affect net carbon storage in ecosystems.

10.3.1 Carbon Cycling in Terrestrial Ecosystems

Terrestrial ecosystems contain about 2000 Pg of carbon (Table 10.3), almost three times the amount held in the atmosphere. Each year about 5% of the terrestrial carbon stock is exchanged with the atmosphere. Plants take up about 100 Pg C from the atmosphere through the process of photosynthesis and release 40 Pg C through respiration. The difference between total photosynthesis and plant respiration, 60 Pg C, is called net primary production (NPP). At the global scale tropical rain forest ecosystems are the most productive and desert ecosystems are the least productive (Table 10.3).

In an unperturbed world, NPP is approximately balanced by the release of carbon from soils to the atmosphere through microbial respiration. This carbon balance can be changed considerably by direct human impact (landuse changes, particularly deforestation) and by other changes in the environment such as the composition of the atmosphere as well as by changes in climate as discussed earlier (10.2.2.4).

10.3.1.1 Deforestation in the Tropics

The current IPCC estimate for the annual net release of carbon from the land to the atmosphere due to deforestation and related land use in the tropics is 1.6 ± 1.0 Pg (Section 1). The large uncertainty associated with this number is related to the fact that we have poor knowledge of the rate of deforestation, of the carbon stocks of the forests being cleared, and of the dynamics of carbon loss through soil decay processes following clearing (Houghton, 1990).

10.3.1.2 Forest regrowth in the mid latitudes of the Northern Hemisphere

Several analyses suggest that the forest harvest and regrowth cycle is such that at this time the regrowing forests in the mid-latitudes of the Northern Hemisphere are accumulating carbon at the rate of 1-2 Pg annually (Armentano and Ralston, 1980, Johnson and Sharpe, 1983, Melillo et al., 1988). What is not clear at the present time is the rate of oxidation of the cut wood. One analysis (Melillo et al., 1988) suggests that the carbon in the cut wood is being returned to the atmosphere through decay and burning at about the rate that the regrowing forests are accumulating carbon. This subject deserves further attention especially in light of the recent modelling study of the global carbon cycle that suggests that mid-latitude ecosystems of the Northern Hemisphere are accumulating carbon at the rate of 2.0 to 3.4 Pg C annually (Tans et al. 1990).

10.3.1.3 Eutrophication and toxification in the mid-latitudes of the Northern Hemisphere

The issue of carbon storage in the mid-latitudes of the Northern Hemisphere is further complicated by the increased availability of nutrients such as nitrogen from agricultural fertilizers and from combustion of fossil fuel. This increased nitrogen availability may result in net carbon storage in plants and soils (Melillo and Gosz 1983 Peterson and Melillo 1985). In the mid to late 1980's between 70 and 75 Tg N per year have been applied to agricultural fields mostly in the mid-latitudes of the Northern Hemisphere (Eichner 1990). In addition about 18 Tg N have been deposited each year on the forests of this region in acid precipitation (Melillo et al. 1989). The addition of this nitrogen to agricultural plots and forests could be causing an accumulation of between 0.5 and 1.0 Pg carbon in soils and woody vegetation (Melillo private communication). However it should be noted that the greater availability of nitrogen is at least for the forests associated with increasing levels of pollutants which could reduce plant growth. We are uncertain about the net effects on the terrestrial carbon balance of eutrophication and toxification of mid-latitude ecosystems of the Northern Hemisphere.

10.3.2 Reforestation as a Means of Managing Atmospheric CO_2

It is sometimes suggested that we should reverse the long-term trend of land clearing and grow new forests to absorb the excess CO_2. Is this suggestion a reasonable one? What rates of carbon uptake and storage can we expect? How much land area would be needed to make a difference? How long would the uptake continue?

Recently Jarvis (1989) estimated that a rapidly growing forest in the temperate zone can accumulate a mean of 2.7tC/ha annually for almost 100 years. To accumulate 1 Pg C per annum, the equivalent of about 17% of current annual fossil fuel CO_2 emissions, the new growing forest would have to occupy 370 x 10^6 ha. This is an area equivalent to about one half the size of the Amazon Basin.

The accumulation will not be linear. Early on it will be rapid, but as the forest matures the accumulation will slow down until the annual respiration rate of the forest is about equal to carbon uptake. If the forest is left unmanaged the trees will eventually die at different times and be replaced naturally, over a large area net uptake of CO_2 by the vegetation from the atmosphere and return of CO_2 by organic matter decomposition to the atmosphere will be in balance and the forest will no longer act as a net carbon sink.

Houghton (1990) has made a similar set of calculations for the tropics. He first made an estimate of land available in the tropics for afforestation. Counting only lands that supported forests in the past and that are not currently used for either crops or settlement, he concluded that 500 x 10^6 ha of tropical lands could be reforested. He also reasoned that an additional 365 x 10^6 ha could be reforested if the current area occupied by the crops and fallow of shifting cultivation was reduced to the area required to produce similar yields under low-input continuous cultivation. The total area, 865 x 10^6 ha is larger (by about 25%) than the Amazon Basin.

Since much of the land that would be involved in the reforestation is probably degraded (low in plant nutrients especially phosphorus) the average rate of carbon accumulation was estimated by Houghton to be about 1.7tC/ha. Given these estimates of available land and carbon accumulation rate Houghton calculated that about 1.5 Pg C might be withdrawn from the atmosphere each year over the next century (150 Pg C total). After that time the new forest if left untouched would be in steady-state with respect to carbon exchange with the atmosphere. Houghton noted that the estimate is optimistic because it fails to consider ownership of the land the expense of reforestation or the ability of degraded lands to grow trees even at the modest rates used in his calculations.

Although simple, these calculations are important because they illustrate the enormity of the task facing us if we decide to manage atmospheric CO_2 by afforestation.

10.3.3 Methane and Nitrous Oxide Fluxes

The trace gas concentrations of the Earth's atmosphere have been increasing for more than a century (Section 1). Microbial activity is the dominant source to the atmosphere of two of these gases methane (CH_4) and nitrous oxide

(N_2O) Climatic factors play an important part in controlling the rates at which these gases are produced In addition, atmospheric inputs of nitrogen and sulphur to ecosystems may affect CH_4 production and consumption Nitrogen additions to ecosystems as well as forest clearing can stimulate N_2O production The controls on the fluxes of these two gases are discussed below

10 3 3 1 Methane

Bacteria known as "methanogens produce methane These organisms can only metabolize and live in the strict absence of oxygen Methanogenic ecosystems usually are aquatic, such as swamps, marshes, fens paddies lakes tundra, and so on, where oxygen-deficient zones develop due to O_2 consumption by respiration and limitation of O_2 diffusion from the atmosphere Other ecosystems such as wet meadows, potholes, and inundation zones, may be methane producers for at least part of the year but may support consumption of atmospheric CH_4 when they dry up Most of the aerobic soils do not support CH_4 production and emission, quite the contrary, they seem to function as CH_4 consumption sites (Seiler and Conrad 1987, Steudler et al , 1989) The guts of termites and the rumens of cattle are also anoxic methanogenic environments An overview of the relative importance of various sources and sinks for CH_4 are given in Section 1 (Table 1 2)

A number of factors besides the oxygen status of the environment control CH_4 production These factors include temperature, the availability of carbon substrate, pH and electron acceptors

Most methanogenic bacteria have temperature optima of 30-40°C Thus, if the supply of organic matter is not limiting, increasing the temperature generally will stimulate CH_4 production in most methanogenic environments It is estimated that a temperature increase of 10°C will lead to a 2 5 3 5 fold increase in CH_4 production (Conrad et al , 1987) This assumes no change in soil moisture, that is, the soils remain waterlogged

Warming in high latitude ecosystems such as wet tundra and the boreal wetlands will almost certainly lead to increased CH_4 emissions from these ecosystems which currently account for the release of about 40 Tg of CH_4 to the atmosphere annually Based on the simple relationship between temperature and methanogenic activity described above, a 4°C rise in temperature in the soils of the high latitude systems could lead to a 45% to 65% increase in methane release from these systems If warming is accompanied by drying, then there may ultimately be a reduction of CH_4 release to the atmosphere since the soils would become oxygen filled, a condition unsuitable for the methanogens Under drier conditions the carbon-rich northern soils would become net sources of CO_2 until a new equilibrium was reached between carbon inputs from plants and CO_2 loss associated with decomposition (see 10 2 2 2 3)

Sediments or anaerobic soils rich in organic matter are often active in CH_4 production The addition of organic substrates to methanogenic sites generally stimulates CH_4 production, provided that temperature and pH are not major limiting factors Most methanogenic bacteria grow optimally in a narrow range around pH 7 (Conrad and Schutz, 1988)

Bicarbonate functions as the electron acceptor during the process of methanogenesis Electron acceptors such as nitrate and sulfate in general are preferred over bicarbonate and thus inhibit CH_4 production So, any input of oxidized compounds such as sulfate or nitrate in fertilizers or acid rain will reduce CH_4 production The significance of this reduction for the global CH_4 budget is unclear at this time, but it is not likely to be large

The major sink for CH_4 is reaction with OH in the troposphere Soils also function as a sink for CH_4, with the magnitude of the sink being in the range of 30 ± 15 Tg CH_4 per year Recent evidence indicates that the magnitude of the soil sink for CH_4 is controlled by temperature moisture and some aspects of the nitrogen cycle in the soil (Steudler et al , 1989) Warmer temperatures increase CH_4 uptake by aerobic soils, while high soil moisture and high rates of nitrogen turnover in soils reduce CH_4 uptake The argument has been made that the eutrophication of the soils of the mid latitudes of the temperate region, with 18 Tg N per year associated with acid rain, may have reduced CH_4 uptake by soils enough to have contributed to the atmospheric increase of CH_4 (Melillo et al , 1989) The logic here is that either a reduction in a CH_4 sink or an increase in a CH_4 source will lead to an increase in atmospheric CH_4 content since the gas has such a long lifetime in the atmosphere While this nitrogen-methane interaction is an interesting example of a subtle impact of industrialisation on the global environment, the importance of this mechanism is not yet established

10 3 3 2 Nitrous oxide

Our current understanding of the global budget of N_2O is reviewed in Section 1 (Table 1 4) The budget is largely controlled by microbial processes

Nitrous oxide can be produced by four processes denitrification, nitrification, assimilatory nitrate reduction and chemodenitrification Of these processes, denitrification in aerobic soils is probably the most important source of N_2O (Matson and Vitousek, 1990) Denitrification is defined as the dissimilatory reduction of oxides of nitrogen to produce N_2O and N_2 by a diverse group of bacteria

The cellular controllers of denitrification are O_2 nitrate (NO_3) and carbon Moisture has an indirect effect on denitrification by influencing the O_2 content of soil If other conditions are appropriate, then temperature becomes an important controller of denitrification rate

Tiedje (1988) has suggested that the controllers of denitrification vary among habitats He indicated that oxygen availability is the dominant factor limiting denitrification in habitats that are exposed to the atmosphere, such as soil, while in dominantly anaerobic habitats, such as sediments, NO_3 is the most important cellular controller When anaerobic zones occur in soils, then NO_3 availability, or carbon availability, as controlled by wetting and drying or freezing and thawing cycles, can become a critical factor in controlling denitrification In fertilized soils, carbon is commonly second in importance after O_2, whereas in unfertilized soils, is often second in importance

Denitrifiers in the natural environment are capable of producing either N_2O or N_2 as end products Numerous factors have been reported to affect the proportion of N_2O produced relative to N_2 in denitrifying cells and soils If the availability of oxidant (N-oxide) greatly exceeds the availability of reductant (most commonly carbon), then the oxidant may be incompletely utilized, that is, N oxides will not be completely reduced to N_2 In other words, the dominant product of denitrification may be N_2O in systems where, at least for a time, nitrate supply is high and carbon supply is low, but not excessively so (Firestone and Davidson, 1989)

A wetter climate may lead to increased N_2O production since soil moisture influences O_2 availability to microbes and low oxygen tension is a precondition of denitrification Warming will accelerate N_2O production by accelerating the nitrogen cycle in the soil and making more nitrate available to the denitrifiers

In the tropics, conversion of forest to pasture has been shown to increase N_2O flux (Luizao et al , 1990) Nitrous oxide emissions also increase immediately after forest harvest in the temperate zone (Bowden and Bormann, 1986) In both of these cases, ecosystem disturbance has resulted in warmer and wetter soils that are cycling nitrogen more rapidly than pre-disturbance soils

10.3.4 Ecosystem Change and Regional Hydrologic Cycles

Vegetation affects continental and regional hydrology by influencing the processes of evapotranspiration and surface runoff Inclusion of vegetation in general circulation model simulations influences continental rainfall and other climate paramaters (e g , Sellers, 1987, Sato et al , 1989) At the regional scale, Pielke and co-workers have shown that vegetation influences boundary layer growth and dynamics, and that vegetation mosaics affect small-scale and meso scale circulations, convective activity and rainfall (Avissar and Pielke, 1989)

At the continental scale, several simulations have been done on the climatic impact of complete deforestation of the Amazon Basin (Henderson-Sellers and Gornitz, 1984, Wilson, 1984, Dickinson and Henderson Sellers, 1988, Lean and Warrilow, 1989, Nobre et al 1990) The Amazon Basin contains about half of the world s tropical rainforests and plays a significant role in the climate of that region It is estimated that approximately half of the local rainfall is derived from local evapotranspiration (Salati et al , 1978) The remainder is derived from moisture advected from the surrounding oceans A major modification of the forest cover could therefore have a significant climatic impact Reduced evapotranspiration and a general reduction in rainfall, although by variable amounts, was found in most simulations

The studies by Lean and Warrilow (1989) and Nobre et al (1990) show reductions of about 20% in rainfall in simulations in which forest was replaced by grassland Lean and Warrilow showed that albedo and roughness changes contributed almost equally to the rainfall reduction Nobre et al suggest that the switch to a more seasonal rainfall regime, which they obtained, would prevent forest recovery

Recall that these simulations were ' all or nothing , forest or grassland The consequences of intermediate changes (partial land conversion) have not yet been studied but, given the nonlinearity of the coupled vegetation-climate system, may not be intermediate The consequences of fragmentation of continental ecosystems and partial conversion will need to be studied using mesoscale simulations as well as by using general circulation models, and both must be pursued

Consequences of altered ecosystem-atmosphere exchange on runoff, resulting from changing vegetation have not been much studied but are of major importance Appropriate regional scale simulations for runoff routing and river flow are just now being developed (e g Vorosmarty et al 1989) and will be crucial tools in evaluating the surface hydrology component of the hydrologic cycle, and its interactions with ecosystems and climate

The central issue for upcoming research in this area is to analyze the feedbacks between vegetation and climate to understand how the effects of climate forcing will be modulated by vegetation response This question has two components First, the biophysical coupling between vegetation and the atmosphere must be understood and quantified to allow simulation of evapotranspiration, albedo and roughness as a function of vegetation attributes Second, the response of vegetation to climate forcing must be understood and quantified so that in our models vegetation structure and physiology can change as climate changes Coupling these two allows for feedback this must then be analyzed on a regional basis to determine the potential for positive and negative feedbacks between ecosystems and the atmosphere This effort must include global and regional simulations and large-scale field studies for parameterization and validation

10.3.5 Summary

The effects of ecosystem change on the net carbon balance of terrestrial ecosystems is potentially large but it is uncertain Deforestation is clearly a source of carbon to the atmosphere of 1 6 ± 1 0 Pg annually The net carbon balance of mid-latitude ecosystems of the temperate zone is uncertain The combination of forest regrowth and eutrophication of these systems with nitrogen appears to be causing them to function as carbon sinks in the range of 1 5 to 3 0 Pg annually The combined effects of wood burning and decay of cut wood and the toxification of mid-latitude ecosystems with a variety of pollutants may be offsetting the carbon uptake in these systems The magnitude of net carbon storage in mid latitude terrestrial ecosystems of the Northern Hemisphere is very uncertain

The management of atmospheric CO_2 by global-scale reforestation will be an enormous task To remove just 1 Pg C annually by this mechanism would require a very large area

Warmer and wetter soil conditions have the potential for increasing the fluxes of CH_4 and N_2O from terrestrial ecosystems to the atmosphere If the northern wetland soils are warmed by 4°C, the CH_4 flux to the atmosphere could increase by as much as 36 Tg annually If the soil moisture decreases in northern ecosystems, CH_4 production would be decreased while CO_2 flux would increase

At the regional scale, changes in vegetation structure such as deforestation, have the potential to alter the hydrological cycle Both precipitation and surface runoff can be affected We do not yet have models to predict the affects of complex changes in land use patterns on regional hydrology

10.4 Marine Ecosytems and Climate Change

10.4.1 Climate Change and Community Response

Based on the record of the past there is little doubt that global warming will result in different distributions of marine planktonic organisms than those of today (CLIMAP Project 1976) If the ocean warming were to be simply and positively correlated with latitude the expansion of habitat in a poleward direction which has occurred during the Holocene, would continue But since the rate of change is expected to be very rapid (see Section 5), questions immediately arise regarding the potential of the biota to accommodate to these rates of change

Changes in temperature and precipitation will have an influence on the circulation of surface waters and on the mixing of deep water with surface water This mixing exchanges water to great depth in a few places in the ocean such as the North Atlantic Changes in circulation and/or a restriction of the mixing could reduce ocean productivity

The palaeo record for global temperature patterns during recent ice age cycles and the output of general circulation models that simulate increases in global temperatures resulting from higher concentrations of radiatively active gases in the troposphere both indicate that the warmer the planet the less the meridional gradient in temperature Temperatures in polar regions could warm 2-3 times the global mean warming associated with a doubling of the equivalent of preindustrial atmospheric CO_2 concentrations

At high latitudes warming would result in diminished temporal and spatial extent of sea-ice some models even predict an ice-free Arctic A significant reduction in the extent and persistence of sea-ice in either polar region would have profound consequences for marine ecosystems Sea-ice itself is a critical habitat for Arctic marine plankton (Clarke 1988) The underneath of the ice and interstices in the ice are highly productive habitats for plankton The low light in winter limits primary production in the water column, and the relatively high concentrations of algae living on and actually in the ice, are an important source of food for herbivores both while sea-ice is in place and when it breaks up in the spring The quantitative importance of sea-ice in the high latitude marine ecosystem is now well established with important food web implications for fish seabirds and marine mammals (Gulliksen and Lonne, 1989) During the spring melting the resultant freshwater lens is also believed to be critical in the life cycle of many pelagic polar species The most intense aggregations or blooms of plankton occur at the ice margin, evidently in response to the density stratification resulting from the overlying lens of fresh water, and perhaps also in response to the release of nutrient materials that had accumulated in the ice Although total global primary production for a polar region might not be very different with or without the ice edge blooms such transient peaks in plankton abundance can be critical in the life cycle of certain higher trophic level organisms, and are most definitely of importance in terms of the flux of carbon to deep water and the ocean floor

Certain marine animals, mammals and birds in particular have life history strategies that reflect adaptation to sea ice An extreme case may be the polar bear, which shares ancestors with the grizzly bear, and would not exist today had it not been for the reliability of the ice habitat for hunting its primary prey, the seal

In sub-polar and temperate waters the effects of global warming on the plankton habitat in near surface waters are at present unpredictable Physical, chemical and biological conditions in these regions are inherently variable on both seasonal and annual bases This results primarily from the variability in atmospheric forcing including surface heat exchange with the atmosphere and associated thermal stratification and destratification in the upper ocean, seasonal storm events and associated mixing, and cloud cover. These processes and properties determine the mass upward flux of nutrients from the deep ocean, the residence time of plankton in the upper sunlit region of the water column, and the availability of light at the surface of the sea. These seasonal variations in conditions give rise to seasonality in primary production with attendant "blooms" and corresponding high rates of organic carbon flux to the deep-sea (Honjo, 1984).

Long-term oceanographic studies in several regions demonstrate high correlations between the abundance and productivity of marine ecosystems and atmospheric conditions. A clear example of this is the 1950-80 period in the vicinity of the United Kingdom. During this period there was a decline in the abundance of plankton that has been correlated with changes in wind strength and direction (Dickson et al., 1988). Temperature changes per se were small and poorly correlated with the plankton changes, and it is judged that changes in wind driven mixing in the upper ocean was the primary factor contributing to the decline in plankton abundance. From studies such as this it seems likely that the type of climate changes being forecast in association with increased radiative forcing in the troposphere will have significant effects on plankton abundance and productivity.

In addition, the effect of intensity and frequency of mixing events on plankton assemblages depends on the physiology and structure of the plankton. Diatoms, for example, are phytoplankton that typically dominate in cold nutrient-rich waters, such as those that are seasonally well mixed. Because they have high sinking rates, diatoms require a turbulent mixed layer in order to remain successful constituents of the plankton community (Smayda, 1970). Diatoms are the preferred food for many organisms in the marine food web, and when replaced by other types of phytoplankton, fish productivity can be dramatically reduced (Barber and Chavez, 1983). The dense cell encasement of the diatom helps to explain why these phytoplankton are an important contributor to the flux of organic carbon to the deep sea.

Along-shore winds contribute to the mixing of deep water with surface water in many coastal waters and across the equatorial Pacific. The direction, intensity, duration and frequency of these wind events determine the extent and timing of the mixing events. Because this process, which is typically highly seasonal, is very important in stimulating the primary production processes that lie at the base of the food webs for many species, it can be anticipated that the global climate change will affect higher trophic levels, including fish, in these regions.

10.4.2 Interaction Between the Land and the Ocean

Climate change has the potential to change the rate of delivery of materials from the land to the ocean and such changes could affect the biological component of ocean ecosystems. For example, climate change could lead to an increase in wind erosion and the delivery of fine particles by aeolian transport from the continents to the surface ocean. Depending on their composition, such particles could have either a biostimulatory (Martin and Fitzwater, 1987) or a biotoxic effect on oceanic productivity and other marine processes. Similarly, climate change could increase water-driven erosion and the amount of material transported to the world's coastal oceans by river systems. Again, the effects will be dependent on the nature of the terrestrial material.

10.4.3 Interactions Between the Ocean and the Atmosphere

Climate-induced changes in ocean ecology are of importance in relation both to the sustainability and management of living resources and to biogeochemical feedback on the climate system. Several atmospheric feedback processes are well-defined in General Circulation Models, but those relating to ocean productivity are not yet sufficiently well understood to be included. The three main effects of global warming that are expected to operate on ocean plankton (as mentioned above) would all tend to decrease the ocean uptake of CO_2, i.e., a positive feedback.

Ocean waters are currently a major source of dimethylsulphide (DMS) to the atmosphere. The oxidized products of this DMS, which is produced by plankton, may increase cloudiness through nucleation on sulphate aerosols in the troposphere (Charlson et al., 1987) and may increase albedo in the stratosphere from sulphate aerosols (Ryaboshapko, 1983). One group of plankton, the Coccolithophorids, are apparently a major source of DMS and their bloom processes would most likely respond, although in uncertain ways, to changes in ocean-atmosphere exchanges resulting from climate change.

While neither the direction nor magnitude of many of these effects is known with certainty, changes from present day values are expected to be greatest in mid- to high latitude ocean regions. There is evidence for major changes in the functioning of North Atlantic ecosystems in the transitions between glacial and inter-glacial periods (Broecker and Denton, 1990), supporting the view that changes in ocean plankton, once initiated, may enhance the rate of climate change ("the plankton multiplier") until a new near equilibrium is reached.

10.4.4 The Carbon System and the Biological Pump

The oceans are by far the largest active reservoir of carbon. Recent estimates of the total amount of dissolved inorganic carbon in the sea establish its range as between 34 000 and

38,000 Pg carbon Only a small fraction is CO_2 (mole fraction 0 5 percent), the bicarbonate ion with a mole fraction of 90 percent and the carbonate ion with a mole fraction of just under 10 percent are the dominant forms of dissolved inorganic carbon The dissolved organic carbon pool has been reported to be similar in size to the pool of terrestrial soil carbon, but recent data suggest that it may in fact be considerably larger

Although the oceans are the largest active reservoirs of carbon and cover 70 percent of the globe the total marine biomass is only about 3 x Pg carbon (though such estimates are uncertain at best), or just over 0 5 percent of the carbon stored in terrestrial vegetation On the other hand, the total primary production is 30 to 40 x Pg carbon/yr A portion of this production results in a sink for atmospheric CO2, primarily through the sinking of particulate carbon As a consequence of this biological pump, the concentration of dissolved inorganic carbon is not uniform with depth, the concentration in surface waters is 10 to 15 percent less than that in deeper waters There is a corresponding depletion of phosphorus and nitrogen in surface waters, even in areas of intense upwelling, as a result of biological uptake and loss of detrital material

The fate of this material depends, in part upon its chemical characteristics If it is in the form of organic tissue, then it is oxidized at intermediate depths which results in an oxygen minimum and a carbon nitrogen, and phosphorus maximum If it is carbonate it dissolves below the lysocline, raising both alkalinity and the concentration of carbon, at depths where the high pressure increases the solubility of calcium carbonate

Thus the biological pump ' lowers the partial pressure of CO_2 in surface waters and enhances the partial pressure in waters not in contact with the atmosphere The functioning of the biological pump involves the supply of nutrients to surface waters, food web dynamics, and sinking losses of particulates to the deep sea It may be expected to respond both to changes in the strength of the overall thermohaline circulation and to variations in the abundance of nutrients primarily nitrogen and phosphorus

A portion of the nutrient flux to the surface returns to the deep sea unused by the biota carried along by the return flow of waters in downwelling systems at high latitude It is important to define the physical, chemical and biological processes that regulate the concentration of organic nutrients in descending water masses, the flux of so-called preformed nutrients The concentration of preformed nutrients may be expected to reflect physical processes, and it can be influenced also by biological activity to the extent that this activity can result in packaging of carbon nitrogen and phosphate in fecal material that can fall to the deep, providing a path for transfer of nutrients from the surface to the deep independent of the physical processes such as those responsible for the formation of deep water in high latitudes

10.4.5 Summary

Climate change can affect the productivity and the storage of organic carbon in marine ecosystems The community composition of marine ecosystems will also be affected Details of these effects cannot be predicted at the present time There is also the possibility that the net exchange of trace gases (e g , organic sulphur gases) between the oceans and the atmosphere could be altered but this, too, is uncertain

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