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Modelling forest growth and carbon storage in response to increasing CO_2 and temperature

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ABSTRACT

The response of plant growth to increasing climate change remains one of the unresolved issues in understanding the future of the terrestrial biosphere. It was investigated here by using the comprehensive forest growth model CenW 1.0.5 which integrates routines for the fluxes of carbon and water, interception of radiation and the cycling of nutrients. It was run with water and/or nutrient limitations on a background of naturally observed climate at Canberra, Australia. It was parameterised for *Pinus radiata*, the commercially most important plantation species in Australia. The simulations showed that under water-limited conditions, forest growth was highly sensitive to doubling CO_2, with growth increases of over 50% on average and even greater increases in dry years. In contrast, when water supply was adequate, but nutrients were limiting, growth increases were smaller, with an initial increase of about 15% during the first year after CO_2 was doubled. This growth increase diminished further over subsequent years so that after 20 years, there was virtually no remaining effect. This diminishing response was due to developing nutrient limitations caused by extra carbon input which immobilised nutrients in the soil. When both water and nutrients were adequate, growth was increased by about 15–20% with no decrease over time. Increasing ambient temperature had a positive effect on growth under nutrient limited conditions by stimulating nitrogen mineralisation rates, but had very little effect when nutrients were non-limiting. Responses were qualitatively similar when conditions were changed gradually. In response to increasing CO_2 by 2 μmol mol^{-1} yr^{-1} over 50 years, growth was increased by only 1% under nutrient-limited condition but by 16% under water-limited conditions. When temperature and CO_2 were both changed to emulate conditions between 1950 and 2030, growth was enhanced between 5–15% over the 80-year period due to the effect of CO_2 on photosynthesis and water economy especially under water-limited conditions, and due to the effect of increasing temperature in mineralising greater amounts of nutrients. These results show that there is not one universally applicable biological growth response to increasing temperature and CO_2, but that they interact in complex ways with a number of other growth limiting factors. Any response factor of plants to CO_2 can only be quantified if the important interacting factors can be independently characterised for different situations.

1. Introduction

The atmospheric CO_2 concentration has increased from its pre-industrial concentration of about to 280 μmol mol^{-1} to over 360 μmol mol^{-1} at present, and is further increasing by about 1.5 μmol mol^{-1} yr^{-1} (Schimel et al., 1996). Unless emissions of fossil fuels can be significantly curtailed in the future, the CO_2 concentration will continue to increase for a long time, and will reach concentrations several times those that were experienced pre-industrially (Schimel et al., 1996). These increases in CO_2 concentration, together with the increase in other Greenhouse gases, are thought to have increased global average

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temperatures (Nicholls et al., 1996), and are likely to increase temperatures further in the future (Kattenberg et al., 1996).

Plant growth is intimately tied to climatic factors, such as temperature and CO_2 concentration, yet no consensus has emerged as to likely growth responses under altered climatic conditions. There is a large body of experimental evidence that showed considerable growth enhancements in response to increasing CO_2 concentration (Kimball, 1983; Cure and Acock, 1986; Wullschleger et al., 1995). However, initially enhanced growth may lead to greater subsequent nutrient limitation and curtail growth enhancements in subsequent years (Rastetter et al., 1992, 1997; Bazzaz and Fajer, 1992; Körner, 1993; Comins and McMurtrie, 1993; Kirschbaum et al., 1994, 1998).

At the same time, it is known that the response of photosynthesis to doubling CO_2 concentration alone can only lead to growth enhancements of maybe 20–30% (Kimball, 1983), yet greater relative growth enhancements would potentially be possible under water-limited conditions when increased water use efficiency under increased CO_2 concentration could become important (Gifford, 1979; Allen, 1990; Bert et al., 1997; Wang and Kellomäki, 1997).

In contrast to responses to increasing CO_2 concentration, it could be thought that plant responses to increasing temperature should be easier to predict as it is possible to study growth of plants currently growing in regions with different temperatures, and use their observed growth as a guide to plant responses with global warming. Such responses constitute important constraints on likely plant responses, but they do not represent the whole picture. Plant growth in the future represents plant responses to increasing temperature rather than to a stable higher temperature per se.

This is particularly important in relation to soil organic matter. Soils and their amounts of organic matter are likely to have been more or less in equilibrium with pre-industrial climatic conditions, with carbon loss through organic matter decomposition having been equal to carbon gain by the soil through litter fall. Plant nitrogen uptake would have been controlled by the mineralisation rate of organic nitrogen, which in turn would have depended on the prior rate of input of litter nitrogen. However, with global warming, this equilibrium may be lost as organic matter decomposition and resultant nitrogen mineralisation could be stimulated more than net primary production. This could result in a loss of soil organic carbon (Kirschbaum, 1995, 1999a), but the enhanced nitrogen mineralisation rate could thereby stimulate plant growth.

Several workers have used growth models to simulate temporal changes in total terrestrial carbon storage and net exchange of CO_2 with the atmosphere (Kindermann et al., 1996; Post et al., 1997; King et al., 1997; Cao and Woodward 1998; Xiao et al., 1998). These models generally included some of the feed-backs between the carbon, water and nutrient cycles, but in order to apply these models to simulations for the whole globe, several simplifications usually had to be made. It is not clear to what extent these simplifications may have introduced unintended spurious results that do not correspond with reality. Melillo et al. (1996) have shown how the inclusion or omission of certain factors in the plant response to climate change can lead to vastly different results for simulated carbon exchange between the atmosphere and the terrestrial biosphere. It is, therefore, important to develop a good understanding of the factors that are important in system responses under different circumstances.

Various models have attempted to simulate the extent to which these interacting factors control the response of tree growth to climate change (see reviews by Ryan et al., 1996b; Landsberg, 1996 and recent work by Kellomäki et al., 1997; King et al., 1997) The model comparison of Ryan et al. (1996a, b) was revealing as several of the leading forest growth models were tested against the same experimental data sets and were then used to predict plant responses to the same climatic changes. The model comparison resulted in widely differing predictions of changes in growth.

The approach used here was to use a detailed forest growth model which explicitly includes all the various feed-back effects that can affect tree growth. Imposed climate change caused an initial perturbation in the simulations which was then modified through the various plant and soil feedback effects to some combined ultimate effect after several years.

The purpose of these simulations was to come to a better understanding of the conditions under

which specific aspects of climate change have a large or small effect on plant growth and soil carbon storage. This will help in the interpretation of experimental results, guide the development of forest growth models in the future by highlighting the important areas that must not be excluded without losing the essence of real responses and give a better appreciation of climate change impacts that are to be expected in real stands in the future.

The model used a parameterisation developed for *Pinus radiata* (Kirschbaum, 1999b), the plantation species that is of greatest commercial importance in Australia. Different parameterisations for different C_3 species are not likely to have significant effects on the response to increasing CO_2 concentration, but temperature responses may vary. Plants already growing under temperatures that are supra-optimal may be affected negatively by further warming, whereas plants growing under conditions that are relatively cool for the species may gain some benefit from warming. The response of the same species can therefore be highly location-specific and responses for the same site may differ between species. For the simulations shown here, the climate for Canberra, Australia, was used as the base climate.

2. Modelling overview

The model, currently known as CenW 1.0.5 (**C**arbon, **E**nergy, **N**utrients and **W**ater), has been described and tested elsewhere (Kirschbaum, 1999b), and only a brief overview will be given here. The components of the model that are of particular importance in the context of assessing the response to climate change are described more fully below. CenW is a generic forest growth model that simulates the fluxes of carbon and water, the interception of solar radiation and the dynamics of nutrient cycling through plant and soil organic matter pools (Fig. 1).

For the simulations shown here, the model was run on a daily time step. Photosynthetic carbon gain was calculated in dependence on light absorption, temperature, soil water status, foliar nitrogen concentration and any foliage damage due to frost or scorching temperatures during preceding days. Some photosynthetically fixed carbon was assumed to be lost in respiration, with daily

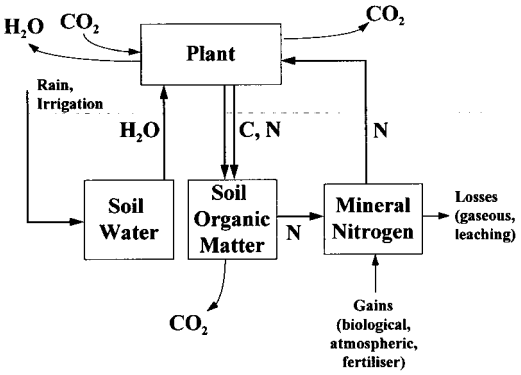

Fig. 1. The basic modelling outline showing the key pools and fluxes of carbon, nitrogen and water between these pools and the external environment.

respiration rate calculated as a constant fraction of photosynthetic carbon gain (see Amthor, 1994; Gifford, 1994, 1995; Körner, 1996; Waring et al., 1998).

The remaining photosynthate was used for growth, with allocation to different plant organs determined by plant nutrient status, tree height and species-specific allocation factors. It was assumed that the ratio of above to below-ground allocation increased with foliar nitrogen concentration. Foliar nitrogen concentrations were essentially determined through the relative rates of carbon and nitrogen uptake modified by different allocation terms. It was also assumed that 25% of foliar nitrogen would be retranslocated and retained in the plant before litter fall.

Water use was calculated using the Penman-Monteith equation, with canopy resistance given by the inverse of stomatal conductance, which, in turn, was linked to calculated photosynthetic carbon gain. Water was lost by transpiration and soil evaporation, and water was gained by rainfall or irrigation which together determined the soil water status for the following day.

Nitrogen could come from a constant rate of atmospheric deposition, fertiliser addition or mineralisation during the decomposition of soil organic matter. For the simulations with *P. radiata,* it was assumed that there was no symbiotic nitrogen fixation. Decomposition rate was determined by temperature, soil water status and soil organic matter quality in a modified formulation based on the CENTURY (Parton et al., 1987) model. Increased rates of organic matter

decomposition could lead to increased nitrogen mineralisation and consequently increased availability for uptake by plants. Increased carbon input in litter meant that more carbon would have to be lost through decomposition before critical C : N ratios were reached in organic matter and excess nitrogen could be mineralised.

The nutrient cycle was closed through litter production by the shedding of plant parts, such as roots, bark, branches and, most importantly, foliage. Litter was assumed to be produced as a constant fraction of live biomass pools. In addition, foliage was shed during drought or when canopies became too dense. Litter was then added to the organic matter pools from where carbon was eventually lost and nitrogen became available again as inorganic mineral nitrogen.

CO_2 sensitivity was calculated based on the biochemically-based model of Farquhar and co-workers (Farquhar et al., 1980; Farquhar and von Caemmerer, 1982) in the brief form given by Kirschbaum (1994):

$$A_{max} = A_{Vj}(c_i - \Gamma_*)/(c_i + 2\Gamma_*), \quad (1)$$

where A_{Vj} is the RuBP regeneration rate at a given temperature, c_i is the intercellular CO_2 concentration and Γ_* is the CO_2 compensation point in the absence of non-photorespiratory respiration, which can be calculated in dependence on temperature with an equation given by McMurtrie et al. (1992).

Photosynthetic carbon gain was assumed to have a temperature dependence based on a hump function such that:

$$A_{Vj} = 0 \quad \text{if } T_{day} \leqslant T_{min} \quad (2a)$$

$$A_{Vj} = A_{opt}(T_{day} - T_{min})/(T_{opt1} - T_{min}) \quad \text{if } T_{min} < T_{day} < T_{opt1} \quad (2b)$$

$$A_{Vj} = A_{opt} \quad \text{if } T_{opt1} \leqslant T_{day} \leqslant T_{opt2} \quad (2c)$$

$$A_{Vj} = A_{opt}(T_{max} - T_{day})/(T_{max} - T_{opt2}) \quad \text{if } T_{opt2} < T_{day} < T_{max} \quad (2d)$$

$$A_{Vj} = 0 \quad \text{if } T_{day} \geqslant T_{max} \quad (2e)$$

where T_{min} and T_{max} are the minimum and maximum temperatures that allow any photosynthesis, T_{opt1} and T_{opt2} are lower and upper temperature bounds that allow optimum photosynthetic rates and T_{day} is mean daytime temperature.

In addition A_{opt} could be reduced through scorch or frost damage on current or preceding days. Scorch damage was assumed to occur when daily maximum temperatures exceeded a scorch threshold temperature, S_0, and frost damage was assumed to occur when daily minimum temperatures fell below a frost threshold temperature, F_0.

Stomatal conductance was calculated based on the original Ball/Berry formulation (Ball et al., 1987) as:

$$g_s = kAr_h/c_a, \quad (3)$$

where g_s is stomatal conductance (mol m^{-2} s^{-1}), A is assimilation rate (μmol m^{-2} s^{-1}), r_h is relative humidity (dimensionless) and c_a is atmospheric CO_2 concentration (mol mol^{-1}). This allowed the intercellular CO_2 concentration to be calculated as:

$$c_i = c_a[1 - 1.6/(kr_h)]. \quad (4)$$

The term "k" was calculated depending on plant water status so that:

$$k = k_d + W_{lim}(k_w - k_d), \quad (5)$$

where k_d are stomatal factors for (notionally) completely dry stands and k_w for stands with adequate water and W_{lim} a water limitation factor in the range of 0 when all plant available water had been utilised and 1 when soil water was not limiting. More complete details of all calculations are given by Kirschbaum (1999b).

The model had been parameterised and tested against data from a *P. radiata* plantation growing at the Biology of Forest Growth (BFG) experimental site near Canberra, Australia. Modelled woody biomass over 4 years and 5 treatments closely agreed with observations over all years and experimental treatments (Fig. 2). Complete model and data descriptions and more comprehensive comparisons between model and observations are given in Kirschbaum (1999b).

3. Simulation details

The same parameters were used as determined by Kirschbaum (1999b). Parameters of particular relevance to assess the response to climate change are shown in Table 1.

Simulations were run by using a twenty-year climate sequence observed at the BFG site, Canberra, Australia. For longer runs, this 20-year

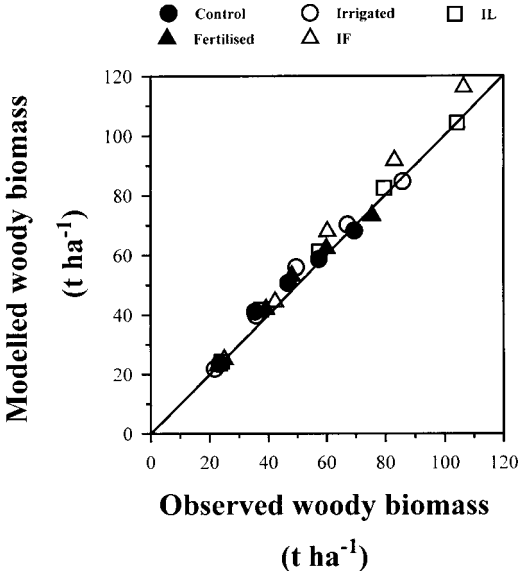

Fig. 2. Observed versus modelled total woody biomass. Different symbols refer to different experimental treatments as given in the figure. The solid line is a 1:1 relationship which explains 97.4% of observed variation. "Control" refers to untreated plots; "Irrigated" refers to plots receiving only irrigation; "Fertilised" refers to plots receiving solid fertiliser; "IF" refers to plots receiving irrigation and solid fertiliser; "IL" refers to plots receiving irrigation and liquid fertiliser supplied monthly throughout the experimental period. This figure has been redrawn from Kirschbaum (1999b).

Table 1. *Some parameters of particular relevance for the forest growth response*

T_{min}	5°	minimum temperature for photosynthesis
T_{opt1}	15°	lower optimum temperature for maximum photosynthesis
T_{opt2}	20°	upper optimum temperature for maximum photosynthesis
T_{max}	30°	maximum temperature for photosynthesis
S_0	35°	temperature threshold for scorch damage
F_0	0°	temperature threshold for frost damage
k_d	8.2	stomatal factor in the Ball/Berry equation for notionally dry stands
k_w	16.4	stomatal factor in the Ball/Berry equation for stands with non-limiting water availability
N_{atm}	2.5 kg ha^{-1} yr^{-1}	input of atmospheric nitrogen

sequence was used repeatedly. For "current CO_2 concentration", a value of 360 µmol mol^{-1} was used.

To simulate fertilised conditions, 400 kg N ha^{-1} were added every 5 years. Added fertiliser was solubilised as soon as rain or irrigation water was available, and it was available for plant uptake up to a maximum determined by the size of trees and the degree of nitrogen under-saturation. Excess nitrogen was partly incorporated into soil organic matter, leached when drainage occurred or remained in the soil as mineral nitrogen. Under the conditions simulated here, the added nitrogen from the second application onwards was more than sufficient to satisfy plant requirements so that foliar nitrogen concentrations in fertilised plants were at the maximum given by plant physiological limits. For simulating irrigation, an amount of water was added every 3 days that was sufficient to bring soil moisture of the whole profile up to 99% of field capacity.

For constructing a response surface of growth response under increased temperature or CO_2 concentration, a one-year climate sequence typical of conditions at the BFG site was used and repeated for each year. The model was run for 20 years and the average growth increment over the last five years of the run were used to construct the response surface. Different moisture and nutrient limitations were simulated by daily adding a supplemental amount of rain water or annually adding an amount of fertiliser as specified in the figures.

For simulating the effect of gradually increasing CO_2 concentration, the concentration was increased annually by 2 µmol mol^{-1} yr^{-1}. This compares with an annual increase of about 1.5 µmol mol^{-1} over the 1980s and early 1990s and an anticipated increase of up to 700 µmol mol^{-1} during the 21st century (Schimel et al., 1996).

For assessing the effect of changing both CO_2 and temperature, the observed climate at Canberra was modified by the global temperature anomaly as observed over the past 40 years (Jones, 1994)

and extrapolated for the next 40 years according to the IPCC 92a scenario. Similarly, the CO_2 concentration was changed to reflect the changes over the past 40 years and extrapolated over the next 40 years.

For assessing the effect of increasing temperature, both daily minimum and maximum temperatures were increased by the same increase in temperature so that the diurnal temperature range was not changed. Those modified temperatures were then used to calculate absolute humidity (as saturated humidity at the overnight minimum temperature) and vapour pressure deficit and relative humidity from the saturated vapour pressure at mean daytime temperature. Incident radiation was used as observed at Canberra, and was not changed for climate change runs.

Simulations were run for the Control condition at the BFG site, with tree performance under natural rainfall, and with nutrient requirements being met out of mineral nitrogen supply from the decomposition of organic matter observed in the soil under normal conditions. Simulations were also run for conditions receiving irrigation, fertiliser addition or receiving both irrigation and fertiliser (IF). These simulation conditions were chosen to emulate tree responses under naturally occurring water and/or nutrient-limited conditions and under conditions when neither of those are limiting.

Simulated growth was calculated as current annual increment (CAI) as that is the growth measure most relevant to forestry. It was calculated as the growth increment in stem wood in the 12 months preceding particular dates. This calculation was performed monthly to always describe the growth increment over the preceding 12 months.

In most instances, CAI was expressed relative to that in the current climate. This was calculated as the CAI under particular climate change assumptions relative to the simulated CAI in the current climate. Both current and changed climate simulations were run based on the same soil, base climate and initial stand conditions.

Relative responses in CAI were generally similar to relative responses in net primary production, but they additionally reflect shifting allocation patterns in response to climate change. Aboveground allocation was assumed to increase with increasing foliar nitrogen status so that any increase in foliar nitrogen concentration as an indirect consequence of the imposed climate change scenario also led to increased allocation of net primary production to stem wood production. The converse applied where climate change indirectly led to reduced foliar nitrogen concentration.

4. Results and discussion

To investigate the response of growth to the different aspects of climate change, the following shows responses to step changes in climatic conditions under different combinations of water and nutrient limitations. Responses of current annual increment are shown for all runs, and that is supplemented by additional information where that is relevant to understand the reasons for observed responses. These individual runs are also expressed as responses surfaces across ranges in water and nutrient limitations. The simulations conclude with a set of simulations under gradually increasing CO_2 concentration and gradually changing CO_2 concentration and temperature.

4.1. Response to step change in climatic conditions

Fig. 3 shows the response of current annual increment (CAI) with current climate, under doubled CO_2 concentration or with increased temperature by 2°C. The third panel of the Fig. shows the simulated CAI, and the bottom panel the CAI relative to that simulated with current CO_2 and temperature. Hence the bottom panel gives the response directly attributable to the effect of the changed climate. A relative CAI of "1" in the bottom panel means that the CAI under altered climatic conditions would be the same as in the current climate.

The figure illustrates the strong dependence of growth on rainfall at this site, with more than 3-fold variations in rainfall leading to corresponding more than three-fold variations in CAI.

Currently observed temperatures varied inversely with rainfall, but over the fairly narrow range of variation, this was unlikely to have had much effect on CAI. This is borne out by the simulations with increased temperature by 2°C in which CAI showed little response, with only a slight decrease in some seasons and a slight

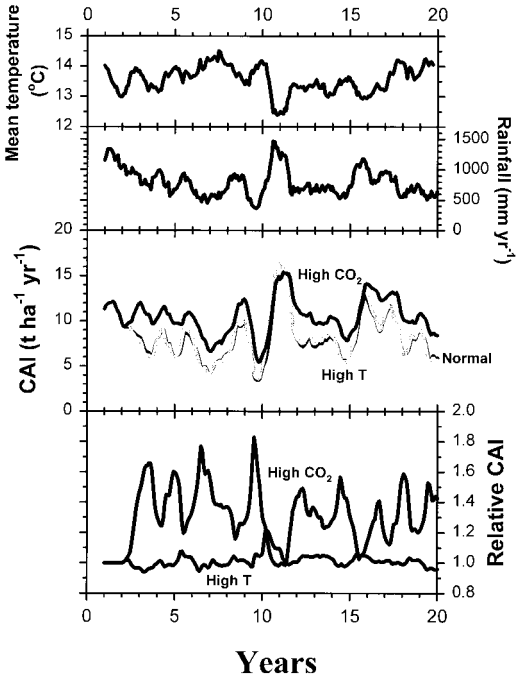

Fig. 3. Observed 12-monthly mean temperature, cumulative rainfall and simulated current annual increment (CAI) in the control condition for current climate and under increased temperature or increased CO_2 concentration. In the bottom panel, CAI relative to that simulated in the current climate is shown. Climate change was imposed from year 2. High CO_2 refers to doubling CO_2 concentration from 360 to 720 μmol mol^{-1}, and high T refers to increasing temperature by 2°C. CAI was calculated as the wood increment over the preceding 12 months, recalculated monthly. Mean temperature and cumulative rainfall similarly refers to the relevant values over the preceding 12 months.

increase in others. The greatest growth enhancement was observed in the wettest year which was also the coolest year within the sequence.

In contrast, there was a large response to increasing CO_2 concentration, with growth enhanced by up to 80% in the driest year. In wet years, the growth response was smaller. In dry years, growth was essentially limited by water use, and water use efficiency was much enhanced under the higher CO_2 conditions. In wet years, when water availability was not limiting, the response to CO_2 was more modest because only the direct photosynthetic response to CO_2 gave a benefit. This benefit was further reduced by some nitrogen being tied up by the higher previous carbon production and subsequently increased litter fall. Following an increase in both temperature and CO_2 concentration, the response in CAI was essentially that which would have been expected from adding the responses to the two climatic perturbations separately (data not shown).

Fig. 4 shows current annual increment with fertiliser addition for current climate and with increased CO_2 concentration or increased temperature. As was observed for the Control condition, there was little response to increasing temperature but a large increase in CAI in response to increased CO_2 concentration. In response to doubled CO_2 concentration, CAI was increased by more than 80% in the driest year, and was enhanced by more than 50% on average (Fig. 4). As for the Control condition, growth was essentially limited by water availability and thus by the efficiency with which a limited supply could be used. Under doubled CO_2 concentration, transpiration efficiency could be substantially increased and that greatly stimulated growth.

The response observed under irrigated conditions (Fig. 5) was fundamentally different from the responses under water-limited conditions. When nutrition was the primary limitation, there was a positive growth response to increasing temperature. That response increased for about 10 years

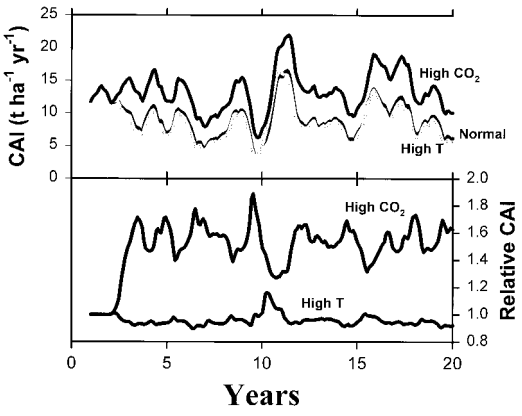

Fig. 4. Current annual increment (CAI) with fertiliser addition simulated with current climate or under increased temperature or increased CO_2 concentration. In the top panel, simulated CAI is shown. In the bottom panel, CAI is expressed relative to that in the current climate. Climate change was imposed from year 2.

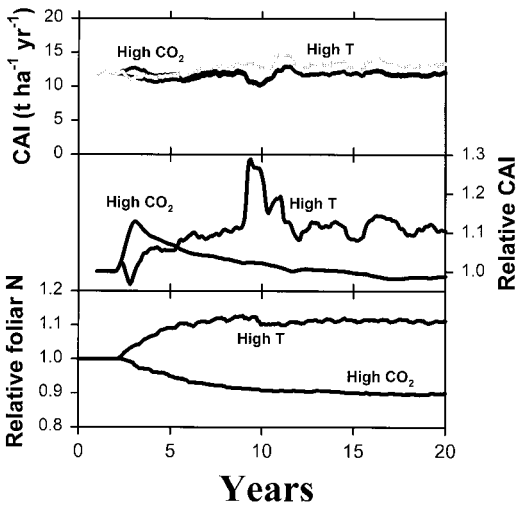

Fig. 5. Current annual increment (CAI) under irrigated conditions simulated under current climate or under increased temperature or CO_2 concentration. In the top panel, simulated CAI is shown. In the middle panel, the CAI relative to that in the current climate is shown. Note that the scales used on the vertical axes are different from those in Figs. 3, 4. The bottom panel shows total foliar nitrogen content relative to that in trees under current climate.

and then stabilised at an approximate 10% increase in CAI, but with considerable year-to-year variation. The greatest positive response was seen in year 9, when an unusual number of winter frosts caused some damage that could be prevented by a 2°C temperature increase.

In response to increasing CO_2 concentration, there was an initial increase in CAI over the first few years. However, that initial response almost completely disappeared after ten or more years. At the end of the 20-year simulation run, CAI was even marginally less than that of trees under current CO_2 concentration (Fig. 5).

The small response to increasing CO_2 concentration was due firstly to the fact that water use efficiency was unimportant under these conditions, and therefore the response to CO_2 concentration was even initially not large. The transient growth increase then led to increased litter production, and increased litter carbon immobilised nitrogen in the soil and reduced subsequent availability of mineral nitrogen to trees. Consequently, trees subject to increased temperature had up to 10% more nitrogen in their foliage, whereas trees in increased CO_2 concentration had 10% less nitrogen (bottom panel in Fig. 5). As growth was strongly limited by nitrogen availability under these conditions, this had a significant effect on subsequent growth.

Furthermore, the proportion of carbon allocated to stem growth was also increased with nutrient status, so that in trees in higher temperature, a greater proportion of fixed carbon was allocated to stem growth, and in trees subject to increased CO_2 concentration, a reduced proportion was allocated to stem growth.

Under irrigated and fertilised (IF) conditions, responses were dominated by the direct physiological effects attributable to either CO_2 concentration or temperature (Fig. 6). In response to increasing CO_2 concentration, there was an approximate 15–20% increase in growth, and that increase was sustained over time. The magnitude of that increase was consistent with the magnitude of the direct photosynthetic response to doubled CO_2 concentration (Kirschbaum, 1994). Hence, there was neither the very large response possible under water-limited conditions, nor the small response observed under irrigated conditions which was caused by the tying up of nitrogen in soil organic matter that was the principal growth limiting factor under those conditions.

There was little consistent response to increasing temperature by 2°C. The positive response to increasing temperature in some years was caused

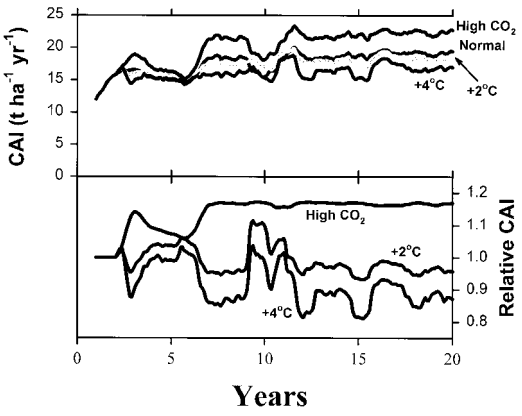

Fig. 6. Current annual increment (CAI) of stands receiving irrigation and fertilisation (IF) simulated under current climate and under increased temperature by 2 or 4°C, or under doubled CO_2 concentration. In the top panel, simulated CAI is shown. In the bottom panel, the CAI relative to that in the current climate is shown.

by the alleviation of frost damage (assumed to occur at night-time temperatures below 0°C) in the years when that was particularly severe. However, temperature increases then also began to cause increased heat damage (assumed to occur at day-time temperatures above 35°C) and reduced growth in years that already had high summer temperatures.

To investigate the response to temperature more fully, a simulation was also run with a 4°C increase in temperature. In response to increasing temperature by 4°C, there was a similar pattern as for a 2°C increase. However, at this site, the problem of frost damage could be almost completely overcome by a temperature increase by just 2°C so that further increases could lead to no further gain. Heat damage, on the other hand, became increasingly more pronounced with further increasing temperature so that temperature increases beyond 2°C had an increasingly detrimental effect on growth.

4.2. *Summary of responses to step changes*

Fig. 7 summarises the growth responses to temperature under the four different conditions. Under irrigated conditions, there was the most positive response to increasing temperature because the greatly enhanced nitrogen mineralisation rate was an important advantage under those growth conditions.

Under the Control conditions there was some positive response to increasing temperature. That was caused by increasing nitrogen mineralisation which in turn increased foliar nitrogen concentrations and led to slightly increased carbon gain and preferential allocation of carbon to shoots rather than roots.

Under fertilised and IF conditions, there was very little response to increasing temperature. There was no positive effect through stimulated nitrogen mineralisation as these trees had adequate nutrition. Under fertilised but unirrigated conditions, there was a slight negative effect through increased evaporative demand, but this had only a small effect on overall growth.

Fig. 8 summarises growth responses to increasing CO_2 concentration under the four different conditions. Under fertilised conditions, there was the largest growth responses of greater than 80% in driest years. The growth response was more moderate in wetter years. This large growth response was possible because nutritional feedbacks played no role under these conditions, whereas enhanced water use efficiency could be of greatest benefit.

Under Control conditions, there was a similar response to that under fertilised conditions, with the same large year-to-year variations, but an overall slightly lower response. While stands under Control conditions gained the same benefit from increasing transpiration efficiency as under fertilised conditions, these stands were also affected by nutrient limitations that reduced growth, especially in the wettest years. In dry years, when

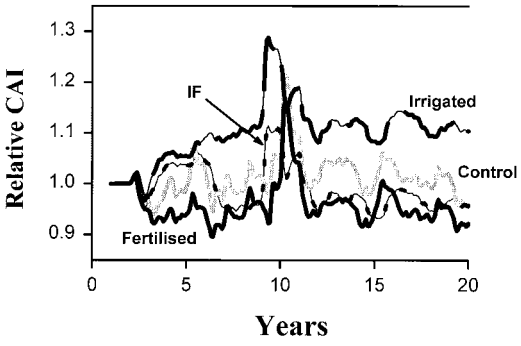

Fig. 7. Relative current annual increment in response to increased temperature in the four conditions, Control, fertilised, irrigated as well as fertilised and irrigated (IF). This figure summarised the temperature responses shown in Figs. 3–6.

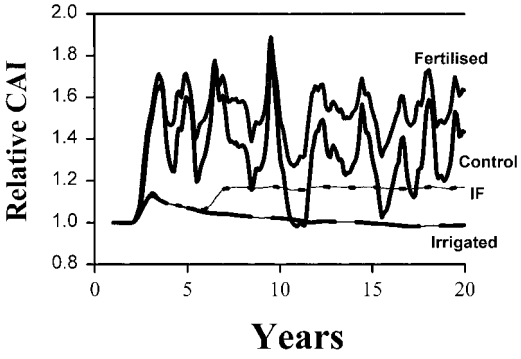

Fig. 8. Relative current annual increment in response to increased CO_2 concentration under the four conditions, Control, fertilised, irrigated as well as irrigated and fertilised (IF). This figure summarises the CO_2 responses shown in Figs. 3–6.

growth was overwhelmingly limited by water availability, the growth response was similar to that in the fertilised stand.

Under irrigated conditions there was the least response to increasing CO_2 concentration, with virtually no growth enhancement after 20 years. This was caused by the negative feed-back from transiently enhanced growth which subsequently reduced nutrient availability.

The stand receiving both irrigation and fertiliser addition showed moderate growth enhancements by increasing CO_2 concentration. As it was not water limited, it showed only moderate initial responses to increasing CO_2 concentration that were much less pronounced than those under unirrigated conditions which gained the benefit from increasing transpiration efficiency. Because nutrients were supplied in large quantities every five years, the negative feed-back that reduced growth under irrigated conditions did not operate, and growth increases were sustained.

It is also interesting to note that the large year-to-year variations in response to increasing CO_2 that were very pronounced under unirrigated conditions were not apparent under these irrigated conditions. The relative responsiveness to increasing CO_2 was strongly dependent on the degree of water limitation which varied markedly with natural variations in rainfall, but that variation disappeared with the application of irrigation. Year to year variations in responsiveness to increasing temperature, on the other hand, were apparent under all conditions (Fig. 7). They were caused by direct physiological responses, such as the alleviation of frost damage in winters that were particularly cold and when damage thresholds were exceeded.

Table 2 summarises the responses observed under the four conditions. Under current climatic conditions, growth responded only slightly to fertiliser addition, somewhat more to irrigation, but maximal responses were only achieved when both irrigation and fertiliser were applied together (Table 2). Under current climatic conditions and without irrigation and fertiliser, CAI was only 40% of that which could be achieved with unlimiting water, nutrition and doubled CO_2 concentration. Essentially the same response pattern to irrigation and fertiliser addition was also observed under increased temperature.

Under doubled CO_2 concentration, however, CAI was only marginally higher under irrigated than Control conditions, whereas CAI under fertilised conditions considerably exceeded that under irrigated conditions. Increasing CO_2 concentration thus enables plants to make much more efficient use of supplied fertiliser. However, even with these enhancements, CAI in plants under IF conditions still greatly exceeded that which could be achieved without the addition of both irrigation and fertiliser under even the most favourable climatic changes (Table 2).

Table 2. *Summary of growth responses to increasing CO_2 concentration and temperature under different limiting conditions*

	Current conditions	Increased temperature (2°C)	Doubled CO_2 concentration
control	8.9 (40.7%)	9.2 (41.9%)	11.0 (50.4%)
fertilised	9.5 (43.7%)	9.3 (42.3%)	14.3 (65.4%)
irrigated	12.0 (54.7%)	13.4 (61.3%)	11.9 (54.5%)
IF	18.8 (85.8%)	18.3 (83.6%)	21.9 (100%)

Shown are average CAI ($t\,ha^{-1}\,y^{-1}$) over the last 10 years of the runs shown in Figs. 3–8. Numbers in brackets give the percentage relative to the biological maximum for that site and species taken to be the CAI simulated for the IF condition under doubled CO_2 concentration.

4.3. *Response surfaces across nutrient and water limitation ranges*

The growth response to doubling CO_2 concentration or increasing temperature by 2°C at the end of a 20-year acclimation period is shown in Figs. 9 and 10. In response to increasing CO_2 concentration, the weakest response was observed when large amounts of water were added but no additional fertiliser. On the other hand, the responsiveness was greatest with no additional water but large additions of fertiliser.

In response to increasing temperature, the most negative growth response was observed when much fertiliser and an intermediate amount of water were added (Fig. 10). Growth under those conditions was almost 10% less than under current temperatures. Positive growth responses were seen when no fertiliser was added but at least moderate amounts of additional water. Under those conditions, the positive effect on nutrient

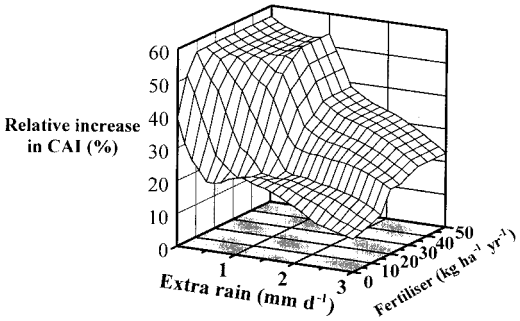

Fig. 9. Relative annual increment in response to doubled CO_2 concentration with different combinations of water and fertiliser added.

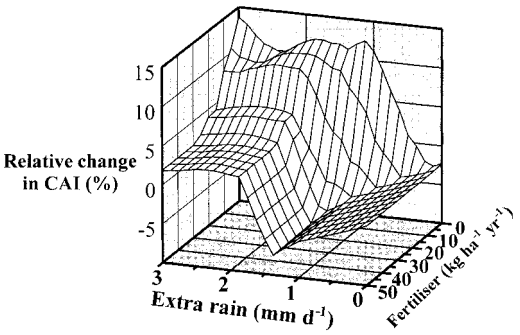

Fig. 10. Relative annual increment in response to increasing temperature by 2°C with different combinations of water and fertiliser added. Note that water and fertiliser additions are scaled in the opposite direction from those in Fig. 9.

mineralisation caused a positive overall growth responses to increasing temperature.

In addition to this broad pattern, there was also a considerable amount of complex small-scale variation. These were not artefacts, but reflected the complex range of temperature-related factors that affect growth. Under the base conditions, growth was also restricted by both cold temperature in winter and hot conditions in summer. These physiological limits were not very important when water was the over-riding limitation, and they interacted in complex ways with nutrient limitations. Hence, under each combination of water and nutrient limitation, a different set of growth limitations attained greater or less importance, and hence the overall growth response to increasing temperature showed numerous smaller ups and downs.

The most intriguing pattern was observed in the temperature response surface which showed a pronounced valley at an intermediate water addition and across a range of moderate to high fertiliser additions (Fig. 10). This was caused by an interaction between the low temperature thresholds for growth and water use in winter. When water was limiting, increasing temperature had a detrimental effect on growth because higher temperature led to faster water use and consequently increased the degree of water limitation. When more than a threshold amount of water was added (more than about 2 mm d^{-1}), the effect via water use efficiency was no longer operative and growth responded more positively to increasing temperature.

Increasing temperature in winter also meant that temperature limitations to growth could be overcome at that time of year and more water could be utilised at a time of the year when it could be utilised with higher efficiency than in summer when high vapour pressure deficits caused inefficient use. This effect diminished with increasing water addition, hence there was a slight decrease in the growth response to temperature with increasing water addition. When enough water was added to overcome water limitations altogether, the effect via water use in different seasons disappeared and only the larger effect of growth responses in water-limited versus non-limited conditions remained and the overall growth response become more positive by almost 10% (Fig. 10).

4.4. *Gradual change*

The responses shown above were responses to an instantaneous doubling of CO_2 concentration. Such illustrations are useful in illustrating the response of different systems and highlighting the nature of important feed-back processes. However, such responses are unrealistic as the CO_2 concentration in reality is increasing more gradually. Hence, simulations were also run with gradually increasing CO_2 concentration (Fig. 11).

Consistent with the patterns observed in Fig. 8, there was little growth enhancement (about 1% after 50 years) under irrigated conditions, a moderate enhancement with irrigation and fertilisation (about 6–7%), a larger responses in the Control

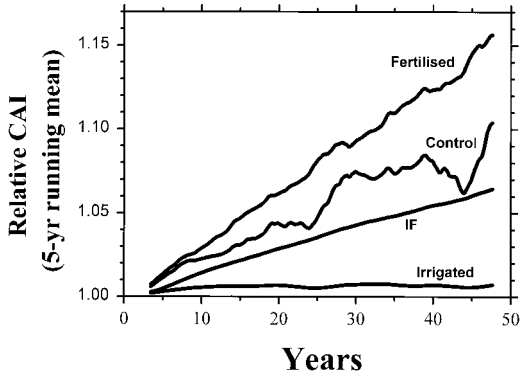

Fig. 11. Relative current annual increment in response to gradually increasing CO_2 concentration (by 2 μmol $mol^{-1}\,yr^{-1}$) under the four conditions, Control, fertilised, irrigated as well as irrigated and fertilised (IF). Results are expressed as 5-year running means.

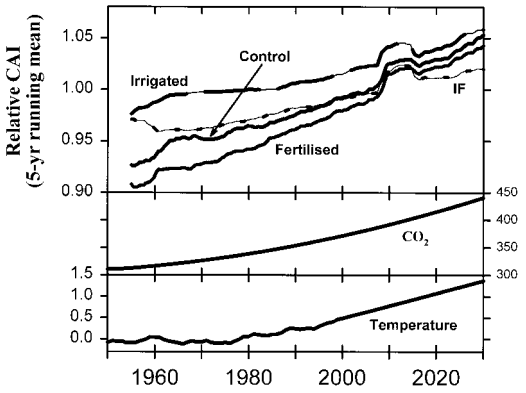

Fig. 12. Relative growth responses to gradually increasing CO_2 concentration and temperature under the four different conditions. Relative CAI is expressed relative to that under the same respective conditions, but at constant current CO_2 concentration (360 μmol mol^{-1}) and temperature. Changes in CO_2 concentration and temperature correspond to changes since 1950 and an extrapolation to 2030 based on the IPCC 92a scenario as shown in the bottom 2 panels.

(about 10–11%) and the largest under fertilised conditions (about 16% after 50 years).

The reasons are the same as for the responses to step increases in CO_2 concentration described above, with trees under water limited conditions benefiting most from increases in CO_2 concentration through improved water use efficiency. Under water adequate but nutrient-limited conditions, on the other hand, benefits are smallest because of feed-back effects via the nutrient cycle that reduce ultimate growth responses.

In reality, both temperature and CO_2 concentration are changing simultaneously, and their combined effects on tree growth are illustrated in Fig. 12.

Growth under all conditions was increased by climate change over the 80-year period, but the reasons differed between conditions. Under irrigation, there was some overall increase in growth by some 8% over the 80-year period, with most of the increase over the latter years, when temperature increased relatively more than CO_2 concentration. This was caused by a slight beneficial effect of increasing CO_2 concentration and a more important beneficial effect of increasing temperature that made more mineral nitrogen available to plants.

Under conditions with both irrigation and fertilisation (IF), there was a slightly smaller growth increase, with the increase mainly being due to the direct photosynthetic response to increasing CO_2 concentration. Under Control conditions, there was an overall growth enhancement of about 13%, caused both by significant growth enhancements by increasing CO_2 concentration under water limited conditions and the enhanced mineralisation of soil nitrogen that helped to alleviate any nutrient limitations as well.

The largest effect was found under fertilised conditions, reflecting the strong growth enhancement by increasing CO_2 concentration under water-limited conditions. As stands under these conditions suffered the most severe water limitations, the response to increasing CO_2 concentration was the strongest under any of the conditions.

4.5. *Effects on soil organic matter*

Apart from its effect on forest growth, the effect of climate change on the storage of soil organic carbon is also of great importance as any loss of carbon with climate change would act as a positive feed-back by adding CO_2 to the atmosphere and bringing about further warming whereas an increase in carbon storage would be a stabilising negative feed-back (Kirschbaum, 1999a).

Under Control conditions, increasing CO_2 concentration led to an increase in carbon storage of about 3–4 t ha^{-1} (about 10%) over 20 years.

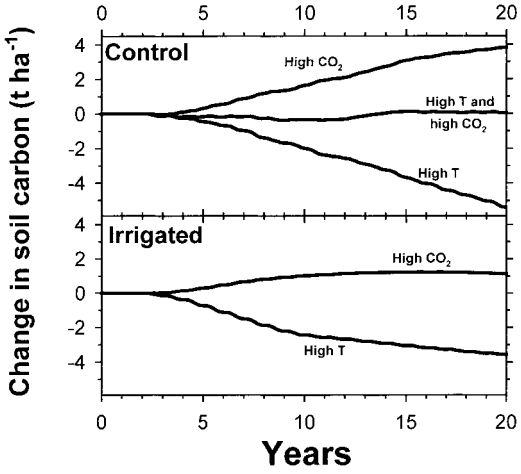

Fig. 13. Changes in soil organic carbon in response to increasing CO_2 concentration and temperature in the Control and irrigated conditions. Climate change was imposed at year 2, and the curves show the change in soil organic matter relative to that in the current climate. For the Control conditions, the response to the combined increase in both temperature and CO_2 concentration is also shown. The soil contained about 37 t ha^{-1} soil organic matter at the start of the current simulation run which corresponds with that measured at the BFG site for which the model had been parameterised.

Increasing temperature, on the other hand, led to a loss of about 5 t ha^{-1} (13%) over the same period, and on-going further losses over longer periods. In response to a combined increase in both temperature and CO_2 concentration, there was little change over 20 years (Fig. 13).

Under these conditions, climatic changes led to relatively large and on-going changes in soil carbon because nutrition was no significant growth constraint under these conditions so that feed-back effects via increased or decreased soil organic carbon in reducing or increasing the availability of inorganic nitrogen were only partially effective. Under irrigation, on the other hand, changes in soil carbon were smaller because of nutritional feed-backs (Fig. 5, bottom panel), and the response saturated in less than 20 years (Fig. 13, bottom panel).

When nutrition is limiting growth, changes in soil fertility can constitute a powerful feed-back effect that can prevent any large changes in soil carbon (see Kirschbaum, 1999a). In response to increasing CO_2 concentration, increased soil carbon immobilised soil nitrogen and prevented on-going increases in growth (Fig. 5), thus not leading to increased carbon input in the longer term. The converse applied in response to increased temperature, with stimulated nitrogen mineralisation rate making more nitrogen available for plant growth, stimulating growth and carbon input to the soil, and thus reducing soil carbon losses.

As previous work has shown (Kirschbaum, 1993, 1995, 1999a; Wang and Polglase, 1995), the response of soil organic matter trends is highly dependent on the base case from which a change occurs, with changes in CO_2 concentration being relatively more important in warm regions and increases in temperature being relatively more important in cool regions. Hence, the indication that changes in CO_2 concentration might cancel the effect of changes in temperature on soil organic carbon storage is only valid for the BFG site and only for the magnitude of the changes used for this simulation, but they would be different under different initial climatic condition or under different climate change scenarios.

5. General discussion

The question of ecosystem responses to climate change remains one of the key research challenges for the future. A great deal of experimental work has been done on subjecting plants to altered climatic conditions, especially elevated CO_2, yet no consensus has emerged as to likely overall growth responses.

The present work illustrates part of the reason for these diverging findings: the response of plant growth is highly dependent on the conditions under which the response to climate change is investigated. It is to be expected on theoretical grounds, and has been observed in several experimental studies, that plants are most responsive to increasing CO_2 concentration under water-limited conditions (Gifford, 1979; Allen, 1990). Increased water use efficiency has been observed in long-term experimental studies (Wang and Kellomäki, 1997) and inferred from carbon isotope discrimination in wood rings formed during the period of increasing CO_2 concentration this century (Bert et al., 1997). The connection to water availability was also evident in the present study which showed

the greatest growth enhancements under water-limited conditions, especially when nutrients were supplied in non-limiting quantities.

In contrast, when growth was limited by nutrition rather than water availability then only minor responses to increasing CO_2 concentration were observed because transiently enhanced growth led to greater litter production and subsequent immobilisation of mineral nitrogen in soil organic matter which acted as a negative feed back and reduced subsequent growth. This was reflected in the present work in the limited response under irrigation in which the moderate initial response was reduced to a response of only a few percent after ten or more years.

This negative feed-back was investigated in greater detail by Comins and McMurtrie (1993) and Kirschbaum et al. (1994, 1998) who formalised this feed-back effect, and showed how the extent of the feed-back effect was dependent not only on the details of physiological and soil interactions (Kirschbaum et al., 1994) but also on the nature of the environment in which the feed backs operate (Kirschbaum et al., 1998). Hence, systems with more open nutrient fluxes, such as those in which large amounts of nutrients are lost in fires or through effective nutrient removals in growing stems, can benefit more from increasing CO_2 concentration than systems with tightly closed nutrient cycles such as those without fires or where stems are shorter-lived and where nutrients are more readily turned over and recycled (Rastetter et al., 1997; Kirschbaum et al., 1998).

In contrast to the response to increasing CO_2 concentration, the response to temperature is even more complex (Fig. 10) because numerous plant internal factors and interactions between plants and their environment are affected. Increasing temperature:

1. increases evaporative demand;
2. increases high-temperature damage;
3. may increase carbon losses in respiration;
4. may reduce growth in summer if current temperatures are already near the upper optimum;
5. may increase cool season growth if current temperatures are below lower optimum limits;
6. may decrease frost damage (if plants are experiencing it currently);
7. increases the rate of nitrogen mineralisation in the soil.

The first 4 of these factors reduce growth, whereas the last three can increase it. It is therefore quite possible for individual responses to increasing temperature to be either negative or positive depending on the current temperature relative to the species' optimum temperature and temperature damage thresholds and depending on the principal growth limiting factors under specific conditions.

It is possible to make only a few generalisations:

- Plants predominantly limited by water availability can be negatively affected by increasing temperature because of its effect on increasing evaporative demand and unfavourable effect on water-use efficiency. This negative growth effect may not eventuate if increasing temperature is accompanied by increasing rainfall.
- Systems predominantly affected by nutrient availability can be positively affected by increasing temperature because of the enhanced rate of nitrogen mineralisation. It must be recognised, however, that it constitutes an effective mining of the soil for organic nitrogen, and is thus an unsustainable cause for increased growth. Increased growth is possible while more nitrogen is taken out of the soil than is returned through mortality and litter fall. Eventually, the system will find a new equilibrium when nitrogen inputs and outputs are matched and when growth again diminishes.
- If the current temperature at a site is low relative to a species' physiological range, it will be beneficially affected by increasing temperature as any potential harm from high-temperature damage will be low and potential benefit of reduced frost damage high. The converse applies if the current temperature at a site is already high relative to the species' physiological range. Any further temperature increases will then be harmful and reduce growth.

To what extent increasing temperature will lead to increased respiration rate is under debate within the scientific literature (Amthor, 1994; Gonzalez-Meler et al., 1996). The traditional view was that respiration rate did increase with temperature as can be readily observed in short-term measurements (Gifford, 1994, 1995; Lavigne and Ryan, 1997).

However, there is considerable evidence that acclimation takes place so that in response to permanently raised temperatures, there is only a weak, if any, dependence of respiration rate on temper-

ature (Amthor, 1994; Gifford, 1994, 1995; Körner, 1996; Waring et al., 1998). Other evidence, however, suggests that respiration rate and its temperature dependence can be fundamentally important in determining the way in which plant growth responds to temperature (Criddle et al., 1997).

Whether respiration rate responds to long-term transfer to high-temperature environments in the same way as it does to short-term exposure is of great significance in anticipating any response to climate change. In the present simulations, respiration rate was simply included as a constant fraction of photosynthesis, but it is recognised that the true interaction between temperature and respiration rate is more complex and may deviate from a simple constant fraction. Basing simulations on the short-term temperature response of respiration without considering acclimation, however, would give an unduly negative effect of temperature increase on plant growth.

It is interesting to compare the climate change simulations presented here with those reported by Ryan et al. (1996b), in which a number of the leading forest growth simulation models (BIOMASS, Biome-BGC, Century, HYBRID, MBL-GEM, PnET-CN and Q) were run for the BFG site and tested for their response to increases in both temperature and CO_2 concentration. The different models gave diverging simulation results which could usually be related to the particular model structure and the inclusion or omission of particular processes that accounted for the observed patterns.

BIOMASS showed a negative response to increasing temperature under irrigation. As BIOMASS did not model the cycling of soil nutrients (Ryan et al., 1996a), it lacked the most significant reason for the positive response to warming observed in the present study so that the observed response in the BIOMASS simulation reflected only the direct physiological response. The model HYBRID similarly lacked representation of below-ground processes, yet showed several responses similar to those obtained in the present work. However, without the negative feed-back associated with build-up of soil carbon under increased CO_2 concentration, growth responses to increasing CO_2 were large under irrigated conditions and similar to those in the IF conditions.

In the CENTURY simulation, on the other hand, growth did respond positively to increased temperature as procedures for handling the turnover of soil organic matter are the key feature of that model. However, responses to increasing CO_2 concentration were very large ($> 80\%$) and even larger in the IF condition. These large responses are probably related to the simple photosynthetic modules employed in that model (Ryan et al., 1996a) and may not be realistic.

BIOME-BGC simulated unrealistically large increases in soil organic matter during simulation runs under any growth conditions, which pointed to some obvious problems with its parameterisation. MBL-GEM showed some climate change responses of carbon and nitrogen dynamics that were similar to those reported here. However, it used a very simple water flux routine so that transpiration could not realistically respond to climate change, leading to essentially the same predicted growth responses in both the Control and irrigated conditions. PnET-CN showed very large growth responses to increasing CO_2 concentration in excess of 100% under not only the Control conditions, where they may be realistic, but also in the IF and irrigated conditions which are more difficult to understand. This may have been due to the simple photosynthetic scheme employed in these simulations (Ryan et al., 1996a).

Climate change affects tree growth in a variety of different ways, and ultimate responses reflect a combination of direct and indirect effects. Many initial effects can lead to system-internal feed-back responses that can greatly modify the initial effect. It is important to understand how climate change may affect forest growth, but models that do not account for the whole range of possible interacting factors cannot give reliable guidance as to likely effects on forest growth.

6. Conclusions

It is becoming apparent that in trying to assess the responsiveness of different ecosystems to increasing CO_2 concentration and temperature, it is necessary to include considerations of all the various feed-back effects that interact with temperature and CO_2 concentration in determining an ultimate growth response to an initial perturbation.

There is unlikely to be a general responsiveness of systems to increasing CO_2 concentration. Some

systems are likely to be highly responsive to increasing CO_2 concentration while others are likely to be quite unresponsive. There is a need to further refine our understanding of the factors that increase or reduce the CO_2 responsiveness of different systems, and then apply that understanding individually to different sites. Only by adding the responses of all different systems can we hope to come to an understanding of the global response of plant growth to climate change.

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