

REVIEW

A review of the possible impacts of climate change on forests in the humid tropics

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Abstract: Increased anthropogenic emissions of greenhouse gases (GHGs) have led to gradual warming of the earth's atmosphere. It is predicted that by the year 2100, the average annual global air temperature will increase by 1.1 – 6.4 °C. This has triggered a series of long-term changes in the atmospheric and soil environments. As forests form a key component of humid tropical ecosystems, the objective of this review is to synthesize the currently available experimental results and offer insights into how forests in the humid tropics would respond and adapt to different aspects of climate change. The atmospheric CO₂ concentration (C_a), which is currently at 386 μmol mol⁻¹, is expected to reach at least 600 μmol mol⁻¹ by 2100. As CO₂ is an input in the photosynthetic process, increasing C_a increases photosynthetic rates of all plants. In C₃ herbs and woody plants, which dominate humid tropical forests, this is translated into average biomass increases of 45% (maximum 240%) and 48% (maximum 260%) respectively, leading to increased net primary productivity at the ecosystem level. Increasing air temperatures could either enhance or dampen the growth stimulation due to higher C_a, depending on the magnitude of temperature increase relative to the optimum temperature for maximum ecosystem productivity. The ability of humid tropical forests to acclimate and adapt to future temperature changes are considered to be lower than that of temperate forests because of the narrower range of seasonal temperatures experienced by forests in the humid tropics. Increasing C_a and temperatures could also influence forest ecosystems through significant changes in the soil environment and in the plant-water relations. In all the above-described responses to increased C_a and temperature, there is substantial species-to-species variation. Studies on the capacity of tropical forests to sequester carbon and reduce future increases of C_a have indicated a substantial capacity for forests in the humid tropics. However, reductions of this capacity have been observed during years of warmer temperatures and lower precipitation resulting from *El Niño* Southern Oscillation.

Keywords: Carbon dioxide, carbon sequestration, forest ecosystems, net primary productivity, photosynthesis, temperature.

INTRODUCTION

Climate is the totality of the above-ground environment and its variation over time. The term 'climate change' has different connotations and interpretations. For example, the Inter-governmental Panel for Climate Change (IPCC) defines climate change as 'the long-term change in the above-ground environment due to human activity or natural variability'. On the other hand, the United Nations Framework Convention for Climate Change (UNFCCC) specifically identifies the human influence and excludes the natural variability in its definition of climate change as 'change of climate attributed directly or indirectly to human activity that alters the composition of global atmosphere'.

There is increasingly conclusive evidence that long-term, human-induced climate change is taking place (Jones & Mann, 2004; IPCC, 2007). Climate change is triggered by increased atmospheric concentrations of greenhouse gases (GHGs), leading to a continuous, gradual warming of the atmosphere and thereby setting in motion a complex chain of changes in the climate. Although some of these changes have made their presence felt in recent times through increased frequency of extreme climatic events such as hurricanes, floods and droughts, many of the changes in climate are initiated by increased GHGs that occur over longer time scales (i.e. decades and centuries). Forests are extremely important ecosystems because of their multiple functions in biodiversity conservation, ensuring long-term environmental stability while providing a variety of economically-important products and services. Forest ecosystems will definitely experience the gradual, long-term changes in climate because of their long life spans. However, there is only limited research information on the potential impacts of

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climate change on individual plant species in forests and their functioning or on the processes and functioning of forests as ecosystems. A large portion of the limited information that is available is on temperate and boreal forests and their component plant species (Saxe *et al.*, 1998, 2001). Therefore, the present review aims to provide a synthesis of the possible impacts of long-term climate change on forests in the humid tropics. However, because of the paucity of empirical data on tropical forests, we have had to rely on the basic principles of plant physiology and ecology and supporting data, which are predominantly from experiments on temperate plant species.

MAJOR ASPECTS OF LONG - TERM CLIMATE CHANGE

Some of the major aspects of long-term climate change that are likely to influence forest ecosystems are briefly described below:

Increasing concentrations of greenhouse gases in the atmosphere

Greenhouse gases are those that have the ability to absorb certain wavelengths of longwave radiation (i.e. wavelengths greater than 0.7 μm). Carbon dioxide, water vapour, methane, nitrous oxides and halogenated carbons are the GHGs in the earth's atmosphere. Most of the shortwave radiation coming from the sun passes through the earth's atmosphere. However most of the longwave radiation emitted from the earth's surface is absorbed by the GHGs. This leads to a gradual warming of the earth's atmosphere and this phenomenon is the well-known greenhouse effect (Houghton, 1997). Actual measurements and estimations from proxy sources have shown that the atmospheric concentrations of most GHGs have been rising steadily during the last three centuries, leading to an up-regulation of the greenhouse effect (called the *enhanced greenhouse effect*) (Houghton, 1997). These increases are beyond the range of fluctuations that these GHGs have shown over longer time scales of thousand/million years. The current atmospheric levels of GHGs are higher than those at any time during the last 650,000 years (Siegenthaler *et al.*, 2005) and they are increasing at a rate of 2.3 $\mu\text{mol mol}^{-1}$ of CO_2 equivalents per year (IPCC, 2001; Stern, 2007).

Carbon dioxide is the GHG, which contributes most to the enhanced greenhouse effect. Atmospheric CO_2 concentration (C_a) was stable around 280 $\mu\text{mol mol}^{-1}$ for several thousand years up to the beginning of the industrial revolution around 1750. Since then, C_a has shown an exponential increase (Figure 1) up to the

present level of around 386 $\mu\text{mol mol}^{-1}$. During the period between 1975 and 2010, C_a in the tropics has increased by 14% from 330 to 377 $\mu\text{mol mol}^{-1}$ (Clark, 2007; IPCC, 2007). In comparison, C_a did not exceed 300 $\mu\text{mol mol}^{-1}$ during the 420,000 year period before industrialization (Petit *et al.*, 1999). As CO_2 is an essential component in photosynthesis, this rise in C_a has profound implications on the functioning of forest ecosystems. Hence, the impacts of increasing C_a will form a major part of this review.

Increasing air temperatures

When the increases of all GHGs are taken into account, some recent studies have predicted an increase of global mean temperature by 2 – 5 °C by 2030-2060 (Wigley & Raper, 2001; Murphy *et al.*, 2004) (Table 1), which would bring the earth to a global average temperature that has not been reached during the last three million years (Hansen *et al.*, 2006). Moreover, there is a 20% probability of a temperature rise greater than 5 °C by 2050 and a warming of 3-10 °C by 2100 (Meinshausen, 2006; Stern, 2007). Global warming predictions of the Fourth Assessment Report of the IPCC (IPCC, 2007) are given in Table 2. During the 30-year period between 1975 and 2005, temperatures in the tropical regions have increased at a rate of 0.26 ± 0.05 °C per decade (Malhi & Wright, 2004). Although the tropics are expected to experience a slightly lower warming than the mid and high latitudes (Stern, 2007), such increases in air temperatures would influence the rates of a wide range of temperature-dependant processes in plants and soils with profound implications for forests in the humid tropics.

Increased frequency of droughts and other extreme climatic events

Warmer air temperatures will accelerate the hydrologic cycle with significant shifts in the amount and temporal distribution of rainfall. Although there is uncertainty about whether annual total rainfall in the tropical zone would change significantly (Stern, 2007), there is increasing evidence that the same annual rainfall will come in a fewer, more intense rainfall events (Wetherald & Manabe, 2002; Huntington, 2006). On the other hand, annual rainfall is predicted to decrease significantly in Mediterranean climates (Stern, 2007). Globally, the percentage of land area under moderate drought at a given time is expected to increase from the current level of 25% to 50% while the corresponding percentage for extreme drought is projected to increase from 3% to 30% (Burke *et al.*, 2006). Hence, forests in the humid tropics could experience drought of greater intensity and longer duration. During the last three decades,

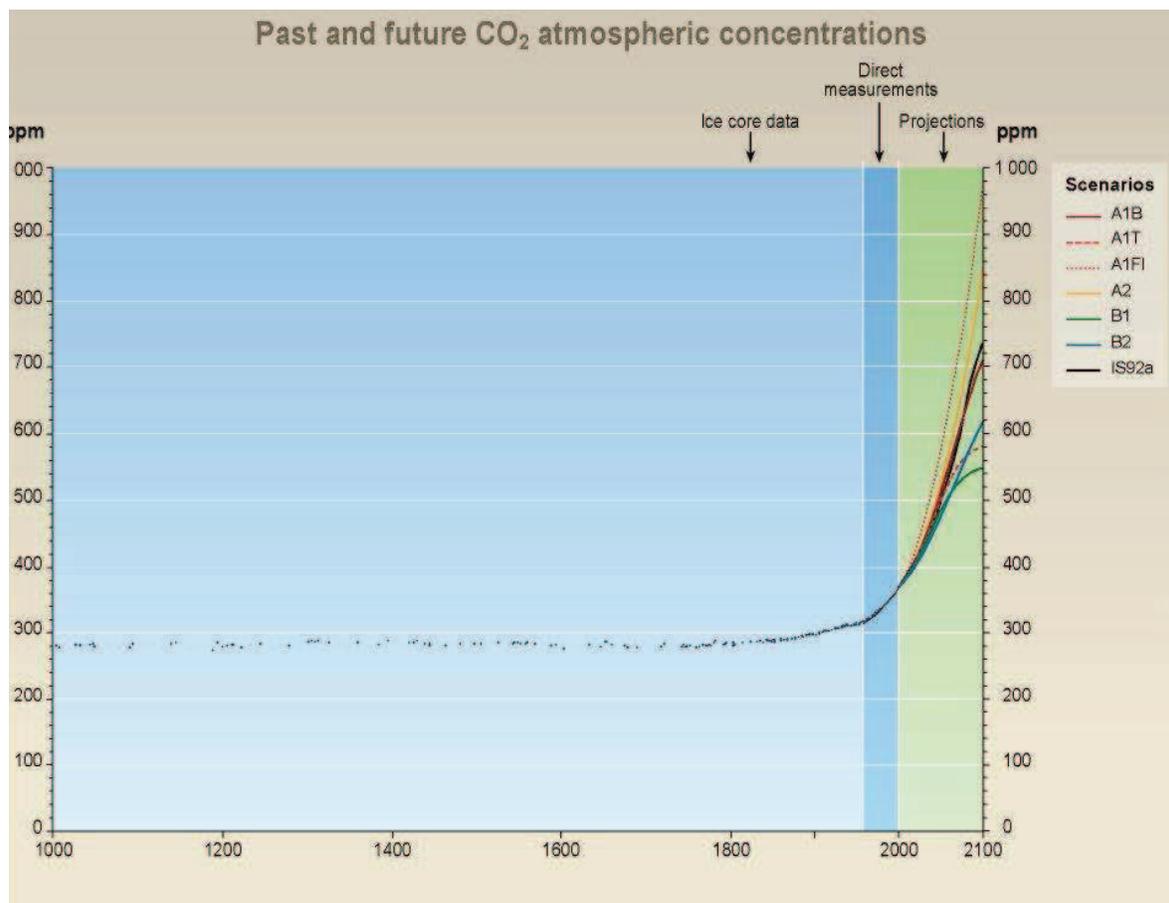


Figure 1: Long-term variation of the atmospheric carbon dioxide concentration along with predicted increases under different emission scenarios: A1 – Rapid economic growth, with convergence between different regions of the world. A1F – Economic growth with high dependence on fossil energy sources; A1T – Economic growth with non-fossil energy sources; A1B – Economic growth with a balanced mixture of energy sources; A2 – Regionally-oriented and unevenly-distributed (i.e. divergent) economic growth, which is slower than in A1; B1 – Convergent world which is rapidly moving global solutions to economic, social and environmental sustainability with the introduction of clean and resource-efficient technologies; B2 – Intermediate rates of economic development focusing on environmental protection and social equity, but with emphasis on local solutions and less rapid and more diverse technological change than in B1 and A1; IS92a – ‘Business-as-usual’ scenario.

(Sources: <http://www.ipcc.ch/present/graphics.htm>; Nakicenovic & Swart, 2001; Metz *et al.*, 2001).

there have been decreases in rainfall over some tropical regions, with tropical Asia recording a marginal decrease while tropical North Africa showing a 3-4% decrease (Houghton *et al.*, 2001; Malhi & Wright, 2004) and Amazonia showing no significant variation (Malhi & Wright, 2004). Furthermore, there has been an increase in the intensity of *El Niño* events, causing episodes of

significant drought and high temperatures. This has also increased the frequency of regional scale forest fires releasing significant quantities of aerosols into the atmosphere and causing up to 65% reduction of incident photosynthetically active radiation in South East Asia (Kobayashi *et al.*, 2005) and Amazonia (Nepstad *et al.*, 2004).

Table 1: Projected increases of global average temperature in response to increasing atmospheric carbon dioxide at various levels of stabilisation

Stabilisation level (ppm CO ₂ equivalent)	Temperature increase at equilibrium relative to pre-industrial (°C)		
	IPCC TAR 2001†	Hadley Centre Ensemble‡	Eleven Studies*
400	0.8 – 2.4	1.3 – 2.8	0.6 – 4.9
450	1.0 – 3.1	1.7 – 3.7	0.8 – 6.4
500	1.3 – 3.8	2.0 – 4.5	1.0 – 7.9
550	1.5 – 4.4	2.4 – 5.3	1.2 – 9.1
650	1.8 – 5.5	2.9 – 6.6	1.5 – 11.4
750	2.2 – 6.4	3.4 – 7.7	1.7 – 13.3
1000	2.8 – 8.3	4.4 – 9.9	2.2 – 17.1

†Third Assessment Report of the Intergovernmental Panel for Climate Change (Wigley & Raper, 2001), ‡Murphy *et al.* (2004), *Meinshausen (2006).

Table 2: Predicted increases in global mean annual temperature by 2100 under the four SRES† scenario families

Distribution of future development	Nature and emphasis of future development	
	More economic focus	More environmental focus
Globalization (Homogeneous world)	A1 Rapid economic growth 1.4 – 6.4 °C	B1 Global environmental sustainability 1.1 – 2.9 °C
Regionalization (Heterogeneous world)	A2 Regionally-oriented economic development 2.0 – 5.4 °C	B2 Local environmental sustainability 1.4 – 3.8 °C

(Source: http://en.wikipedia.org/wiki/IPCC#IPCC_Fourth_Assessment_Report:_Climate_Change_2007), †IPCC (2001).

PREDICTION OF THE IMPACTS OF CLIMATE CHANGE ON FOREST ECOSYSTEMS

Experimental approaches

The present review will focus on the impacts of increasing C_a and air temperatures (T_a) and varying water availability on forests in the humid tropics. The type and magnitude of climate change impacts on a given forest ecosystem is partly determined by the environmental factors that control its functioning and productivity. Under the current climatic conditions, for forests in the humid tropics, radiation receipt and temperature are the main factors of control as water and nutrient availability

are unlikely to be limiting (Churkina & Running, 1998; Nemani *et al.*, 2003; Running *et al.*, 2004).

It is important, at the outset, to appreciate the practical experimental difficulties involved in collecting valid research data on the impacts of climate change on a complex ecosystem such as a forest. The slow, gradual nature of climate change necessitates observations over a long time period to detect its impacts on a forest ecosystem, which itself is likely to have a rather long response time. Hence, alternative approaches, which would yield valid predictions within a shorter period of time need to be sought. Such an approach is to quantify the response of seedlings of key plant species to certain

specified increases of C_a and T_a , which are expected to occur during the next 50-100 years. Accordingly, for C_a , elevated levels have ranged from 570 $\mu\text{mol mol}^{-1}$ (a 200 $\mu\text{mol mol}^{-1}$ increase, which is expected to occur in another 40-50 years, IPCC, 2007; Stern, 2007) to 700 $\mu\text{mol mol}^{-1}$ (a doubling of the current ambient C_a , which is expected by 2100) while the temperature elevations have ranged from 2 °C to 4 °C (which are expected in the next 40–70 years, IPCC, 2007; Stern, 2007). Plants growing under elevated C_a have been compared with those growing at the current ambient levels of C_a , with the implicit assumption that the response of plants within this range of C_a is linear. It is already known that response of plant processes to increasing tissue or air temperature is 'bell-shaped' (Saxe *et al.*, 2001) with increasing rates of processes up to an optimum temperature followed by a decrease. Hence, a combination of these trends is used in predicting the impacts of increasing C_a and T_a .

In the majority of experiments, CO_2 enrichment to achieve the required elevation of C_a has been carried out on seedlings growing in open top chambers (Whitehead *et al.*, 1995; Norby *et al.*, 1997; De Costa *et al.*, 2003), which are ventilated enclosures with an open top and transparent side walls to simulate 'near natural' conditions. A limited number of experiments on forest plants have been conducted in closed top chambers (CTCs) with re-circulation of air (Beerling & Woodward, 1996; Forstreuter, 1996; Tingey *et al.*, 1996). Free Air CO_2 Enrichment (FACE) is a more expensive method of enriching a larger, un-enclosed (open) area with CO_2 to simulate completely natural conditions (Hendrey *et al.*, 1999). A limited number of FACE studies have been carried out on temperate forest stands, but none on tropical forests. Responses to increased T_a has been carried out either in open top chambers heated with heating coils, temperature gradient chambers or in completely enclosed growth chambers.

Quantification of the ecosystem response

Even the few FACE systems are established on monocultures of forest stands. Open top chambers and enclosed growth chambers can only house potted individual seedlings of trees. Extrapolation of plant growth responses obtained under such experimental conditions to predict the response of a complex and multi-species ecosystem such as a forest in the humid tropics is difficult and questionable. A more valid alternative would be to quantify the response of basic plant and soil processes to the different aspects of climate change and use this information to synthesize the ecosystem response (Landsberg, 2003; Mäkelä, 2003). Hence, this approach is followed in the present review. However, even with this approach, the results on many key processes are not

unequivocal (Boisvenue & Running, 2006) and therefore, extrapolations, generalizations and predications can be made only with extreme caution (Luo *et al.*, 1999; Beier, 2004). Furthermore, climate change involves the variation of several environmental factors (i.e. C_a , T_a and water availability) simultaneously and complex interactions in their effects. Therefore, the net result of overall climate change on a given forest ecosystem could be site- and environment-specific (Norby & Luo, 2004).

Inter- and intra-species variation in the magnitude of responses

A review of experimental results on the response of trees to different aspects of climate change show clear differences among species and also among provenances/populations/families within a species (Eamus & Jarvis, 1989; Poorter, 1993; Berryman *et al.*, 1994; Battaglia *et al.*, 1996; Beerling, 1996; Basso & Bazzaz, 1998; Faria *et al.*, 1998; Atkin *et al.*, 1999; Jablonski *et al.*, 2002; Arulmageswaran *et al.*, 2003; De Costa *et al.*, 2003; Poorter & Navas, 2003; Körner *et al.*, 2005). These variations have to be taken into consideration when reconstructing ecosystem response from studies on individual processes of single plants.

INFLUENCE OF ELEVATED CARBON DIOXIDE AND TEMPERATURE ON BASIC PLANT AND SOIL PROCESSES

An overview of the inter-connected network of key plant and soil processes that can be influenced by climate change is given in Figure 2.

Response of photosynthesis, respiration and biomass production to increased C_a

Photosynthesis is one of the key processes affected by increasing C_a because CO_2 is an essential input for it. A wide body of evidence has shown that the net photosynthetic rate per unit leaf area (P_n) increases with increasing C_a (Eamus & Jarvis, 1989; Curtis, 1996; Drake *et al.*, 1997; Saxe *et al.*, 1997; Wullschleger *et al.*, 1997; Luo *et al.*, 1999; Nowak *et al.*, 2004). This is primarily because of two reasons. Firstly, a greater CO_2 concentration in the outside air would allow a greater air-leaf CO_2 concentration gradient and thereby increase the rate of CO_2 uptake in to the leaves. If the leaves do not have a limitation of photosynthetic structures (i.e. chlorophyll, components of the electron transport pathway, thylakoid membranes etc.) increased uptake of CO_2 would lead to a greater production of primary carbohydrates (i.e. glucose, fructose, sucrose, starch, etc.) through gross photosynthesis. This is called the ' CO_2 fertilization effect'. Secondly, the greater CO_2 concentration at the

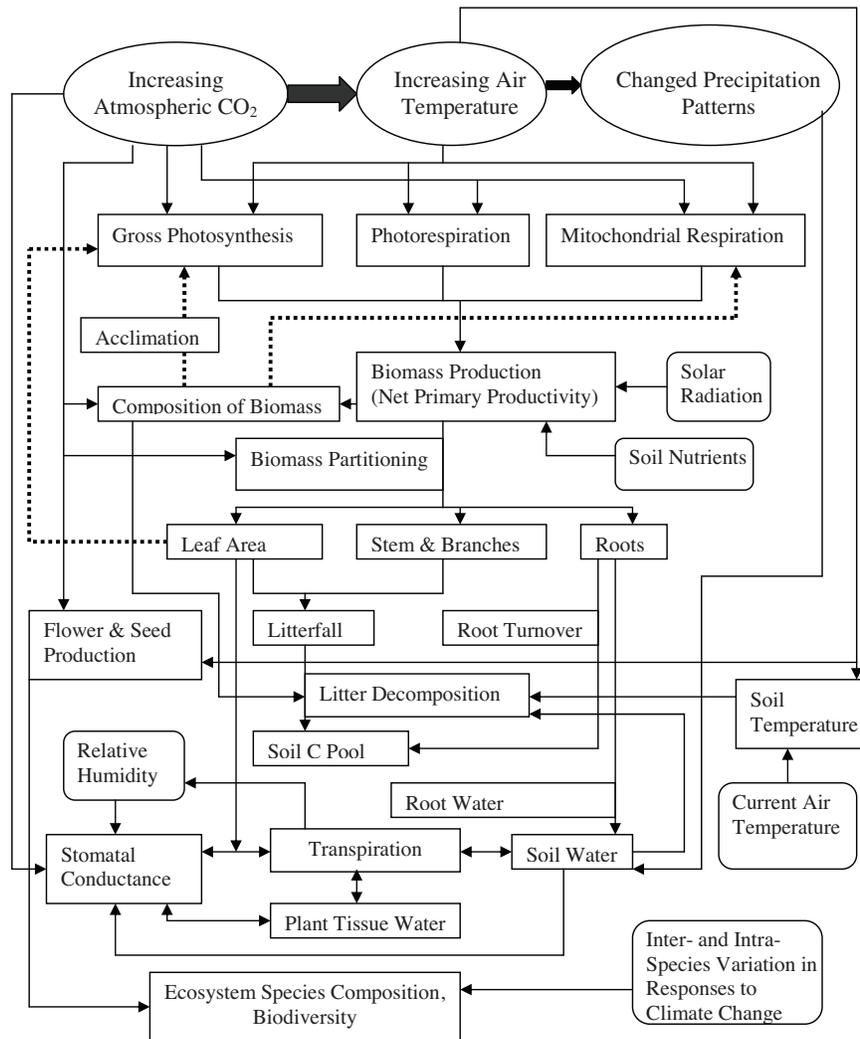


Figure 2: Network of plant- and soil processes (given within squares) in a forest ecosystem influenced by climate change. Main drivers of climate changes are given within ellipses. Factors modifying the magnitude of response are given within rounded squares. Arrows indicate the direction of influence. Key feedbacks are shown by dotted arrows.

chloroplast partly suppresses photorespiration (Drake *et al.*, 1997) and thereby channels a greater percentage of the absorbed CO₂ through photosynthesis, thus increasing P_n. Compilations of responses of a wide range of plant species have shown a significant species-to-species variation in the magnitude of increase of P_n in response to a doubling of C_a. Among the tree species, Saxe *et al.* (1998) showed that long-term photosynthetic stimulation by elevated C_a was slightly higher for conifers (62%) than for deciduous tree species (53%). Specifically for a selected set of tropical tree species growing in Sri Lanka,

De Costa *et al.* (2003) observed increases of P_n ranging from 18% to 224% in response to an increase in C_a from 370 to 570 μmol mol⁻¹ (Table 3).

This stimulation of photosynthesis by increasing C_a has been shown to be greater for C₃ than for C₄ plants (Drake *et al.*, 1997; Long *et al.*, 2004). Kranz anatomy and the consequent increase of internal CO₂ concentration within the C₄ leaves makes CO₂ a lesser limitation for C₄ photosynthesis (Sage, 2001). In addition to the decrease of photorespiration (R_p), there is considerable evidence

Table 3: Response of leaf net photosynthetic rate (P_n) to elevated C_a in seedlings of selected tropical tree species growing in open top chambers at different times after CO_2 enrichment (CE). Plants were grown with adequate water and nutrients. P_n was measured under saturating light in the youngest fully expanded leaf.

Species	P_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$) after 75 days of CE		P_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$) after 105 days of CE	
	C_a at 370 $\mu\text{mol mol}^{-1}$	C_a at 570 $\mu\text{mol mol}^{-1}$	C_a at 370 $\mu\text{mol mol}^{-1}$	C_a at 570 $\mu\text{mol mol}^{-1}$
<i>Artocarpus heterophyllus</i>	3.62	9.14	5.99	7.08
<i>Swietenia mahogany</i>	12.90	16.96	13.42	11.83
<i>Swietenia macrophylla</i>	3.68	6.73	3.98	12.90
<i>Tectona grandis</i>	2.47	3.80	10.65	21.77

(Source: De Costa *et al.*, 2003).

that mitochondrial respiration (R_d) also decreases with increasing C_a (Griffin *et al.*, 1996; Bunch, 1997; Drake *et al.*, 1997; Drake *et al.*, 1999). A review of existing literature incorporating all types of plants has shown that R_d decreases by an average of 17-20% for a doubling of C_a (Eamus & Jarvis, 1989; Drake *et al.*, 1999). This has been attributed to a CO_2 -induced reduction of the activity of two key enzymes of the respiratory pathway (i.e. cytochrome oxidase and succinate dehydrogenase) (González-Meler *et al.*, 1997) and reduced respiratory cost for tissue synthesis under elevated C_a (Wullschlegel *et al.*, 1994; Amthor, 1997). Reductions in R_d in different forest tree species have been observed in several studies (Stewart & Hoddinott, 1993; Karnosky *et al.*, 1999; McDowell *et al.*, 1999). However, CO_2 -induced reduction of R_d is not as conclusive as the decrease of R_p because there is also evidence against a significant reduction of R_d (Saxe *et al.*, 1998; Ceulemans *et al.*, 1999; Amthor, 2000). For example, Overdieck (1993), Pontailler *et al.* (1994) and Saxe *et al.* (1998) have observed increases in R_d due to elevated C_a in *Pinus sylvestris* (13-19%) and *Fagus sylvatica* (53-84%). An increase in R_d under elevated C_a is possible because of increased carbohydrate availability due to increased P_n (Amthor, 1995). Moreover, even if specific R_d (i.e. dark respiration rate per unit plant biomass) may be reduced with increasing C_a , the greater plant biomass produced under elevated C_a could increase total plant R_d because of increased maintenance respiration. In contrast, Martin *et al.* (1994) concluded that there is no direct effect of elevated CO_2 on woody tissue respiration because of the higher CO_2 concentrations (i.e. 1%) in wood. However, Carey *et al.* (1996) observed an increase in R_d per unit volume of stem wood due to elevated C_a . Hence, a clear scientific consensus has not emerged yet on the direction or magnitude of response of R_d to CO_2 enrichment (Amthor, 1997; Saxe *et al.*, 1998; Ceulemans *et al.*, 1999).

It is also possible that the response of R_d to elevated C_a depends on the type of tissue. Ryan *et al.* (1996) showed that in stems and coarse roots, R_d was positively correlated with biomass (resulting in an increase of R_d under elevated C_a) whereas in foliage and fine roots, R_d was directly correlated with N concentration (causing a reduction of R_d with increasing C_a). It is notable that in trees R_d of leaves constitutes more than 50% of total R_d . There is fairly clear evidence that root respiration is greater at elevated C_a (Johnson *et al.*, 1994; Voce *et al.*, 1995; Rouhier *et al.*, 1996). Mousseau (1996) quoted that in model ecosystems, elevated C_a decreased leaf R_d by 28%, increased stem R_d by 40% and reduced root R_d by 13%, when all R_d values are expressed on a per unit dry weight basis. The total stand respiration was increased by 52% primarily because of a 75% increase in total biomass.

Another reason for the conflicting results obtained could be variation in the respiratory response at different stages of tree growth. Wullschlegel *et al.* (1995) observed an increase in R_d in response to increased C_a only during periods of leaf growth. Out of the 111% increase in R_d observed under elevated C_a during the active growing period, a higher proportion was attributed to increased growth respiration. The direction and magnitude of change in total plant respiration in a future climate will partly determine whether forests would act as a sink or source of atmospheric CO_2 . Therefore, more research is urgently needed to resolve the uncertainties involved in this response.

The net result of the increased gross photosynthesis and decreased R_p under elevated C_a is an increase in biomass production in plants. A possible reduction of R_d would further increase this stimulation of plant growth at increased C_a . Inter-species variation in the magnitudes

of stimulation of P_n and reductions of R_p and R_d means that a considerable species-to-species variation could be expected in the stimulation of biomass production by elevated C_a . When plants are growing with adequate water and nutrients, for C_3 woody plants, the growth stimulation with a doubling of C_a has ranged from 0 to 260% with an average of 48% while for C_3 herbs, it has ranged from 0 to 240% with an average of 45%. These values were obtained in a meta-analysis of experimental data for 160 woody plants and 144 herbs (Poorter & Navas, 2003). Curtis and Wang (1998) and Idso (1999) have reported biomass increases up to 30-50% with woody species subjected to long-term CO_2 enrichment. Specifically, the inter-species variation in the growth stimulation due to increased C_a for seedlings of some tropical forest tree species is shown in Figure 3. Schlesinger and Lichter (2001) observed that carbon accumulation in the forest floor was also greater under elevated C_a as compared to ambient. Moreover, Naumburg and Ellsworth (2000) showed that shaded leaves of saplings under elevated C_a maintained greater rates of P_n for longer periods than those of saplings under ambient C_a , indicating that the contribution from the lower vegetation strata of a forest to carbon accumulation could increase in a future climate.

In an analysis of experimental data from different sources, Novak *et al.* (2004) concluded that the observed increases in tree biomass production in response to elevated C_a , which are largely based on observations on

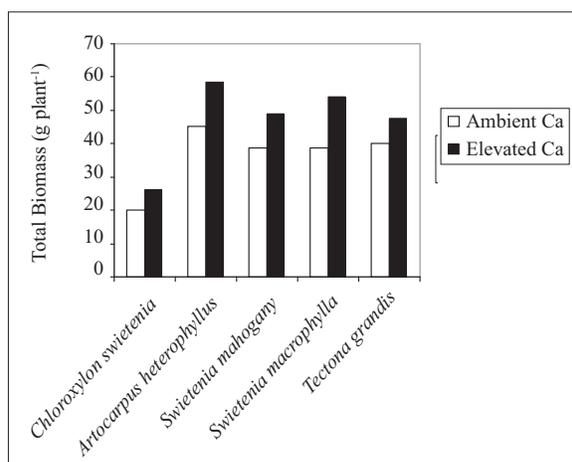


Figure 3: Response of biomass production of seedlings of selected tropical forest tree species to elevated C_a provided over a period of 105 days. Plants were grown in pots and kept within open top chambers. Ambient C_a - $370 \mu\text{mol mol}^{-1}$; Elevated C_a - $570 \mu\text{mol mol}^{-1}$. (Source: De Costa *et al.*, 2003).

seedlings growing in open top chambers, are adequately supported by observations on mature trees growing under FACE. However, they emphasize that both species composition and resource availability play important roles in determining the magnitude of response. The CO_2 -induced growth stimulation of trees occurs because of both increased photosynthetic rate per unit leaf area and increased leaf area per plant (Norby *et al.*, 1992; Ceulemans *et al.*, 1995; Norby *et al.*, 1995).

Implications of the stimulation of biomass production under increased C_a

Comparison of the inter-species variation in growth stimulation due to increased C_a has shown that the stimulation is 30% greater for fast-growing plant species (i.e. mainly pioneers in the succession process) as compared to slow-growing species (i.e. mainly late-succession species) (Poorter, 1993; Lovelock *et al.*, 1998; Atkin *et al.*, 1999; Winter & Lovelock, 1999; Poorter & Navas, 2003). This would have important implications for the species composition of forests in the humid tropics. Hence, a discernible shift in species composition in favour of fast-growing pioneers could be expected. As most of the alien invasive species are fast-growing, there could be a greater probability of invasive species degrading the humid tropical forests. This could also result in greater rates of extinction for threatened and endangered species. With the proportion of fast-growing species in the ecosystem increasing, the species turnover in the forest could be faster.

Review of species responses to elevated C_a has also shown that the photosynthetic and growth response is clearly greater for C_3 plants than for C_4 plants. In the meta-analysis of Poorter and Navas (2003), the estimated biomass increase in response to a doubling of C_a was only 12% (an average from 40 C_4 species) in C_4 plants as compared to 45% (an average from 160 C_3 species) in C_3 plants. Therefore, over longer time scales, the proportion of C_4 species in a forest ecosystem could decrease along with an increase in the proportion of C_3 species.

A widely-observed response of plants growing under elevated C_a is that a higher proportion of increased biomass is partitioned to roots (Rogers *et al.*, 1994), especially increasing the fine root biomass (Norby *et al.*, 2000; Pregitzer *et al.*, 2000). In addition, there is greater root branching in trees under elevated C_a (Ceulemans *et al.*, 1999). These responses increase the capacity of the tree root systems to explore a greater volume of soil and absorb more soil resources such as nutrients and water. Although forests in the humid tropics do not

experience substantial shortages of water or nutrients under the current climate, C_a -induced increases in root absorption capacity will enable them to better withstand any shortages of these soil-based resources (especially, the soil water) in a future climate.

Photosynthetic and growth response to elevated C_a under non-optimum growing conditions

The question of whether the above reported stimulation of P_n and biomass production by increased C_a under optimum conditions (i.e. when plants are grown with adequate water and nutrients under light and temperature regimes to which they are best-adapted), would occur to the same extent under non-optimum growing conditions have been investigated. A review of results by Poorter and Pérez-Soba (2001) shows that there is a reduction of the photosynthetic and growth stimulation under low nutrient availability and low temperatures. The average magnitude of reduction was 20-22% as compared to the growth stimulation under optimum conditions. Interestingly, Poorter and Navas (2003) show that under low nutrient availability, the greater CO_2 -induced growth stimulation of C_3 plants as compared to C_4 plants is nullified. The only exception here is the C_3 legumes, which maintain an advantage over C_4 species because of their N-fixing ability. In an analysis of data from a FACE experiment, with C_a elevated up to $550 \mu\text{mol mol}^{-1}$, CO_2 -induced stimulation of net primary productivity (NPP) of *Pinus taeda* were 27% and 19% under high and low N availability (Finzi *et al.*, 2002; Norby *et al.*, 2005). In contrast, growth stimulation due to increased C_a occurred to the same magnitude under conditions of lower water availability, shade and salinity. However, Oren *et al.* (2001) concluded that C_a -induced increases in NPP would be minimum or zero under prolonged water deficits on poor soils. Generally, forests in the humid tropics do not experience nutrient shortages because of their closed and efficient recycling of nutrients. Low temperatures would be experienced only in those forests in the humid tropics, which are located at higher elevations. Therefore, it is highly likely that humid tropical forests would show greater rates of biomass production and NPP in a future climate of increased C_a (Melillo *et al.*, 1993; Field *et al.*, 1998). This is also likely to increase their capacity for carbon sequestration.

Long-term acclimation of photosynthesis to elevated C_a

Analysis of the biochemical composition of plant tissue produced under elevated C_a has shown a clear increase in the proportion of carbohydrates, and more importantly, a clear decrease in the concentration of nitrogen and hence

of proteins (Drake *et al.*, 1997; Cotrufo *et al.*, 1998). In leaves, a reduction in the protein content would mean a reduction of essential photosynthetic enzymes such as Rubisco (ribulose 1,6-bis phosphate carboxylase oxygenase), thus down-regulating the photosynthetic capacity (Gunderson & Wullschleger, 1994; Curtis, 1996). Therefore, if P_n of plants grown under elevated C_a throughout is measured at ambient C_a , its P_n would be lower than that of a plant grown at ambient C_a throughout. This is called *photosynthetic acclimation*. In addition to a reduction in the concentration of Rubisco, a reduction of its activity has also been observed under elevated C_a (Tissue *et al.*, 1996). Photosynthetic acclimation is thought to occur because of the inability of a plant to utilize the extra carbohydrates produced by photosynthetic stimulation under elevated C_a (Long & Drake, 1992). As trees have a large capacity for storage of extra carbon in their woody tissue and a large number of growing points, which can act as sinks for additional photosynthates (Wullschleger *et al.*, 1997; Janssens *et al.*, 1999), it is argued that photosynthetic down-regulation is rare in trees (Ceulemans *et al.*, 1999). This is supported by the findings of Idso *et al.* (1991) who did not observe any down-regulation in either P_n or growth in field-grown orange trees subjected to long-term CO_2 enrichment. The meta-analyses by Curtis (1996) and Curtis and Wang (1998), which involved a wide range of tree species, found only 10% down-regulation. In a review of 16 FACE studies involving different vegetation types, Novak *et al.* (2004) found that while elevated C_a reduced leaf N in herbaceous species, there was little change in leaf N in most of the woody species.

In spite of any down-regulation of photosynthetic capacity, the gross and net photosynthetic rates would still be increased under elevated C_a , as compared to ambient C_a , because of the greater magnitude of the CO_2 fertilization effect and suppression of photorespiration. However, the altered biochemical composition of plant tissues produced under elevated C_a would definitely alter the rates of litter decomposition and nutrient release and thereby influence the nutrient recycling process (Swift *et al.*, 1979; Cotrufo *et al.*, 1994; Berntson & Bazzaz, 1996). Several studies have shown increased C/N (Köner, 2000) and lignin/N ratios in tissues grown under elevated C_a resulting in lower rates of litter decomposition (Coûteaux *et al.*, 1991; Cotrufo *et al.*, 1994; Boerner & Rebeck, 1995; Scherzel *et al.*, 1998; De Angelis *et al.*, 2000). On the other hand, Hirschel *et al.* (1997) found that elevated C_a had no significant effect on litter decomposition rates of tropical rainforest species. Feeding behaviour and the population of leaf-eating insects could also be affected by the changed leaf biochemical composition (Lindroth *et al.*, 1993). Carbon

inputs to the soil through litter fall and rhizodeposition will increase because of increased biomass production under elevated C_a (Ceulemans *et al.*, 1999).

Some pertinent questions on the predicted increase of forest growth under increased C_a

While predicting an increase of P_n , biomass production and NPP under elevated C_a , some pertinent questions need to be raised as these predictions are based largely on responses observed in seedlings growing in open top or closed chambers. Firstly, the down-regulation of photosynthetic capacity raises several questions of the sustainability of photosynthetic and growth stimulation of elevated C_a in a perennial ecosystem such as a forest: (a) Will there be a point (i.e. a ceiling level of C_a) in a future climate at which the photosynthetic stimulation due to increasing C_a would be limited by the amount of photosynthetic machinery available in leaves?, (b) As a consequence, will the growth stimulation level-off at a certain level of C_a ?, (c) As stimulation of growth has to be supported by increased capture of essential growth resources (i.e. light, water and nutrients), will resource capture be a limitation to further stimulation of growth at a certain point of C_a in the future?

Answers to questions (a) and (b) have to be sought on the physiological basis of photosynthetic acclimation. As the internal CO_2 concentration at the site of photosynthesis (i.e. chloroplast), C_p , is sub-optimal in C_3 plants (because of the relatively lower CO_2 concentration in the atmosphere and the absence of a CO_2 concentrating mechanism such as that found in C_4 plants), a greater amount of photosynthetic enzymes (primarily Rubisco) has to be present in the chloroplast to achieve appreciable rates of photosynthesis (Drake *et al.*, 1997; Long *et al.*, 2004). With the elevated C_a increasing the air-leaf CO_2 concentration gradient and thereby increasing C_p , the essential photosynthetic enzymes need not be present at higher concentrations to achieve higher rates of photosynthetic carboxylation. Biosynthesis of proteins require greater respiratory energy (and a greater amount of photosynthates for respiration) than biosynthesis of carbohydrates (Penning de Vries *et al.*, 1974). Hence, with the reduced requirement of photosynthetic enzymes (i.e. proteins) under elevated C_a , allocation of photosynthates in leaves shifts from proteins to carbohydrates, thus causing photosynthetic acclimation. This follows that if the essential photosynthetic enzymes become a limiting factor to achieve the required rates of photosynthesis to utilize the increased CO_2 uptake at a future point, the plants should be able to re-adjust and allocate more photosynthates again to protein synthesis. Hence, it is likely that photosynthetic acclimation may not impose

a ceiling on growth stimulation in response to increasing C_a . However, as stated earlier, it is possible that resource limitation [question (c)], especially nutrients, could curtail CO_2 -induced growth stimulation, especially in non-leguminous species.

A second pertinent question is whether the growth stimulation observed in the seedlings, which are at the juvenile stage, would be reproduced in fully-grown trees that have come to the reproductive stage. The few FACE studies have shown that the growth stimulation due to increased C_a does occur in fully-grown trees as well. On the other hand, fully-grown trees have a much greater respiration cost (especially maintenance respiration) in order to maintain their large biomass. Therefore, whether mitochondrial respiration is reduced or not by elevated C_a would be a critical factor in determining the magnitude of growth stimulation in fully-grown trees.

RESPONSE OF PHOTOSYNTHESIS, RESPIRATION AND BIOMASS PRODUCTION TO INCREASED AIR TEMPERATURES (T_a)

Long-term, gradual increase of C_a is accompanied by an increase of T_a because of the enhanced greenhouse effect. Hence, plants and their internal processes respond simultaneously to increases of both C_a and T_a . Generally, all plant physiological and metabolic processes respond in a similar manner to increasing T_a (Figure 4) (Johnson & Thornley, 1985). When the tissue temperatures (which are closely correlated with T_a) increase from low levels, rates of processes increase (often linearly) until an optimum temperature (T_o) is reached. This is because the reaction molecules would have a greater kinetic energy at higher temperatures. When T_a increases beyond T_o , process rates decrease primarily because of the gradual denaturation of enzymes (Berry & Björkman, 1980) and other effects of heat stress such as damage to thylakoid membranes (Méthy *et al.*, 1997).

Therefore, the direction and magnitude of photosynthetic and growth response to a simultaneous increase of T_a and C_a would be determined by the respective T_o and the magnitude of increase of T_a in relation to T_o . If the increase of T_a occurs within the sub-optimal range of temperatures for photosynthesis and biomass production, the rates of these processes would be further stimulated by increased T_a . This is most likely to occur in the forests of the humid tropics, which are located at higher altitudes (situation *a* in Figure 4). In a review of 27 studies of temperature effects on net photosynthesis of different tree species, Saxe *et al.* (2001) concluded that the temperature increases that are expected to occur during this century would increase the net photosynthesis

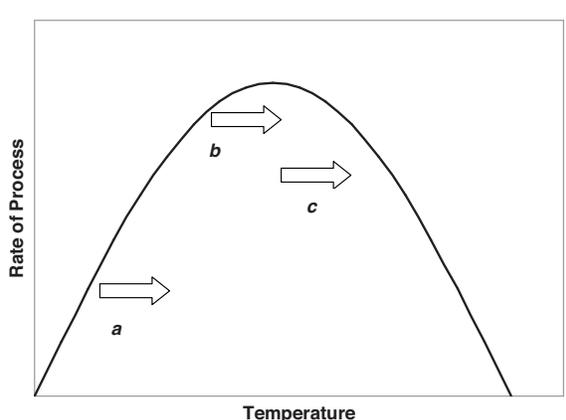


Figure 4: Generalized response pattern of plant physiological and metabolic processes to temperature. Refer to the text for further explanations

of 66% of the 27 studies reviewed. This review largely focused on species growing in temperate environments, which are equivalent to high altitudes of humid tropics, at least in terms of the temperature regime.

On the other hand, if the future increases of T_a occur around T_o , increased T_a would not cause a significant change in process rates with only the growth stimulation due to C_a occurring (situation *b* in Figure 4). However, if the T_a is pushed beyond T_o during future warming of the atmosphere, increased T_a would have a negative effect on the rates of photosynthesis and biomass production. Therefore, in a future climate where C_a is increased along with an increase of T_a above T_o , the direction and magnitude of change in the rates of photosynthesis and biomass production would be determined by the relative magnitudes of the positive effect of increasing C_a and the negative effect of increasing T_a (situation *c* in Figure 4). For most processes of tropical plant species, T_o is within the range of 25 – 32 °C (Squire, 1990). At present, most lowland forests within the humid, tropical zone experience an average air temperature of about 26 – 28 °C throughout the year. This is just below or near the T_o for most physiological processes responsible for plant growth. Therefore, it is likely that increases in T_a in the near future (i.e. the next 10–20 years) may not cause significant changes in the biomass production rates of forests located at lowlands in the humid tropics. During the same period increasing C_a is likely to cause an increase in growth rates (situation *b* in Figure 4). However, it is also highly probable that at some point of time in the future (i.e. probably in the next 50–60

years), the T_a would be pushed significantly beyond T_o , bringing the lowland humid tropical forests into situation *c* in Figure 4. Several global ecosystem process models (White *et al.*, 2000; Cramer *et al.*, 2001; Fung *et al.*, 2005) have predicted that the productivity of tropical forests would decrease with increasing T_a . There are also predictions of substantial die-off of tropical forests from mid-century onwards (Jones *et al.*, 2003; Cowling *et al.*, 2004). Leverenz *et al.* (1999) have shown that even in temperate tree species, photosynthesis could be decreased when the increase in T_a is greater than 2–3 °C above the summer ambient.

On the other hand, because the increase in T_a is gradual, plant processes and ecosystems can adapt to increasing T_a to a certain extent. For example, Battaglia *et al.* (1996) showed that T_o for maximum light-saturated photosynthesis (P_{max}) of *Eucalyptus* can be increased by up to 10 °C due to acclimation to high temperatures. If this happens the majority of plant species in forests of the humid tropics could remain in situations *a* or *b* for a longer period. Increasing T_a in the range between 20° and 30 °C has been reported to have positive impacts on tree photosynthesis by increasing the contents of photosynthetic pigments (Ormrod, 1999) and increasing the apparent quantum yield of photosynthesis (i.e. net photosynthetic rate per unit of radiation absorbed) (Wang *et al.*, 1996; Lewis *et al.*, 1999; Saxe *et al.*, 2001).

It is also important to note that the response of photosynthesis to temperature involves interactions with other environmental factors such as vapour pressure deficit and irradiance and plant factors such as leaf temperature and stomatal conductance. For example, Bassow and Bazzaz (1998) showed that variation of photosynthesis in four temperate deciduous tree species was only weakly correlated with variation in leaf temperature and that when averaged over a season, temperature variations explained only a small percentage of the variation in photosynthesis. Beyond certain thresholds, both higher and lower temperatures could lead to partial stomatal closure (Jarvis, 1976). When combined with high irradiance, lower stomatal conductance could lead to formation of reactive oxygen species and phototoxic damage to the photosynthetic tissue (i.e. photoinhibition) (DeLucia *et al.*, 1991; Saxe *et al.*, 2001). Increases in T_a could also cause stomatal closure due to increased water deficits in leaves (Jarvis, 1976) and thereby reduce photosynthesis and accelerate photoinhibition. However, some tree species already have the capability of evolving photo-protection mechanisms to avoid photoinhibition (Faria *et al.*, 1998) and avoid potential adverse effects of higher T_a .

Inter-species variation in T_o and the magnitude of response to increasing T_a and its implications

Experimental work has shown considerable species-to-species variation in T_o and temperature-sensitivity (Table 4) (Saxe *et al.*, 2001; Battaglia *et al.*, 1996; Mebrahtu *et al.*, 1991; Sun & Sweet, 1996; Arulmageswaran *et al.*, 2003). Very often, plant species that are adapted to grow at higher temperatures (i.e. low altitudes in the tropics) have higher T_o values than those that are adapted to grow under cooler temperatures (i.e. higher altitudes in the tropics). This inter-species variation in T_o could modify or shift the responses shown in Table 4. A higher T_o for species growing in a lowland forest would make them less vulnerable to future increases in T_a as it would take a longer duration for T_a to be pushed significantly above T_o . On the other hand, a lower T_o for species growing in high altitude forests would make them more vulnerable to future increases of T_a as T_a could be increased above T_o within a shorter period.

Inter-species variation in T_o within a given forest ecosystem would mean that with time, the ecosystem composition would shift in a such way that the proportion of species adapted to warmer temperatures (i.e. having higher T_o) would increase at the expense of those adapted to relatively cooler temperatures (i.e. having lower T_o), which may become threatened and endangered. Accordingly, the ecosystem boundaries could also shift, with especially the high altitude forests shrinking in area.

However, the capacity of an individual species or a whole ecosystem to adapt to environmental change should

not be discounted. As the increase of T_a due to enhanced greenhouse effect occurs at a very gradual rate, at least some individual species and ecosystems may have the capacity to adapt to the gradually-increasing temperatures. However, in this regard, it has been shown that tropical forest species have a lower capacity for adaptation to higher temperatures than temperate forest species (Cunningham & Read, 2003). This is not surprising as temperate species experience a much greater fluctuation in temperature, both within a 24-hour day and during a year, even at present. Therefore, temperate species have developed internal mechanisms and adaptations to withstand these temperature fluctuations. In contrast, such mechanisms and adaptations are largely absent in tropical species, which experience only a narrow range of temperatures both diurnally and annually.

INFLUENCE OF INCREASING C_a AND T_a ON PLANT WATER RELATIONS

Both increasing C_a and T_a have important influences on water relations of forests in the humid tropics. However, it should be noted that under the current climatic conditions water is not a serious limiting factor for forest growth, reproduction and ecosystem function in humid tropics where rainfall exceeds evapotranspiration almost throughout the year. However, with the predicated increase in the frequency of high rainfall episodes and the associated probability of longer rainless periods in a future climate, forests in the humid tropics could also experience water deficits for at least short periods of the year. Hence, the effects of C_a and T_a on processes determining the water balance of forest plants could increase in importance in a future climate.

Table 4: Response of absolute and relative growth rates to a 4 °C increase in air temperature in seedlings of selected tropical tree species growing in controlled environmental growth chambers. Plants were grown with adequate water and nutrients. Growth rates were computed for a 100 - day (=100 day period) period from the time of imposing temperature treatments.

Species	Absolute growth rate (g d ⁻¹)		Relative growth rate (g g ⁻¹ d ⁻¹)	
	28 °C	32 °C	28 °C	32 °C
<i>Chloroxylon swietenia</i>	8.71	31.5	5.45	11.99
<i>Artocarpus heterophyllus</i>	30.59	1.02	4.19	-0.16
<i>Swietenia mahogany</i>	186.04	173.30	15.41	15.16
<i>Swietenia macrophylla</i>	48.71	107.80	4.77	8.46
<i>Tectona grandis</i>	99.10	86.33	8.85	8.01

(Source: Arulmageswaran *et al.*, 2003).

Both C_a and T_a primarily influence plant water relations by influencing the rate of transpiration. As transpiration occurs through the stomata, stomatal conductance (i.e. a measurement of how easily water is able to move through the stomata in the vapour phase) has a direct relationship with transpiration rate. Stomatal conductance (g_s) is determined by the stomatal density (i.e. the number of stomata per unit leaf area) and the degree of stomatal opening. Increasing C_a has been shown to decrease g_s in a range of tree species (Mousseau & Saugier, 1992; Berryman *et al.*, 1994; Field *et al.*, 1995). However, the magnitude of reduction of g_s has been found to be lower in trees (i.e. around 20%, Field *et al.*, 1995) as compared to herbaceous plants in which the reduction is around 40% (Morison, 1987). Moreover, the magnitude of CO_2 -induced change in g_s has shown considerable variation between species (Field *et al.*, 1995; De Costa *et al.*, 2003; Norby & Luo, 2004) with the g_s of some species showing no response (Curtis, 1996; Eamus, 1996) or even an increase (Barton *et al.*, 1993; Heath & Kerstiens, 1997). A significant contribution to the above decreases of g_s has been the reduction of stomatal densities with increasing C_a . Analysis of fossilized plant samples that grew several hundred to thousand years ago at a lower C_a has shown higher stomatal densities as compared to those grown in recent times at higher C_a (Woodward, 1987; Van de Water *et al.*, 1994; Beerling, 1996; Heatherington & Woodward, 2003). However, further studies have shown that stomatal densities are much less sensitive to increases of C_a from the current ambient levels upwards than they have been to historical increases in C_a (Woodward & Bazzaz, 1988). However, g_s could still decrease with future increases of C_a through reduced stomatal apertures as a direct response of guard cells to increased intercellular CO_2 concentration (Morison, 1987; Mansfield *et al.*, 1990; Mott, 1990). Interestingly, different ecotypes of a given species or genus growing across an altitude gradient have shown a gradient in stomatal density and g_s with both showing an increasing trend with increasing altitude (Woodward *et al.*, 2002). This has been shown to be a response to the natural decrease of C_a with increasing altitude.

Actual measurements have shown that reduced g_s at increased C_a results in a parallel decrease in transpiration rate per unit leaf area (E_l) (De Costa *et al.*, 2003). However, a reduction in E_l may not necessarily decrease total transpiration, either on per tree or per unit land area basis, because of the associated increase of leaf area per tree under elevated C_a (Ellsworth *et al.*, 1995; Lindroth, 1996; Ceulemans *et al.*, 1999). In situations where the proportional reduction in g_s is lower than the proportional increase of leaf area, total transpiration could even increase under elevated C_a .

As elevated C_a causes a simultaneous increase of the net photosynthetic rate per unit leaf area (P_n), transpiration efficiency, i.e. the ratio between P_n and E_l and sometimes called water use efficiency, is increased with increasing C_a (Morison, 1993; Drake *et al.*, 1997). Significant increases in water use efficiency with increasing C_a have been shown for forest trees growing under natural conditions (Fernandez *et al.*, 1998; Feng, 1999). This means that at elevated C_a , plants are able to produce more biomass per unit of water used as transpiration, thus increasing their ability to tolerate water-limited periods.

While increasing C_a reduces transpiration rates, simultaneous increases of T_a tend to increase E_l . This is primarily because of the increased leaf-to-air vapour pressure gradient at increased T_a . As increases of T_a beyond T_o could also decrease P_n , the predicted increases of transpiration efficiency with increasing C_a would be dampened down by the simultaneous increase of T_a . Here again, this dampening down of transpiration efficiency is most likely to be felt by the forests in the lowlands of humid tropics, which already experience T_a levels that are closer to T_o . Because of the inherent ability of C_4 plant species to function at higher temperatures, CO_2 -induced increases of transpiration efficiency of C_4 plants (which is higher than that of C_3 plants at the current levels of C_a and T_a) are less likely to be reduced by increasing T_a .

INFLUENCE OF INCREASING C_a AND T_a ON REPRODUCTIVE BIOLOGY

Effects of climate change on reproductive biology of plant species in a forest will have important implications for possible long-term shifts in the species composition of the ecosystem. A meta-analysis by Jablonski *et al.* (2002) using the wide range of plant species has shown that increasing C_a within the range of 500 – 800 $\mu l l^{-1}$ (ppm by volume) has increased flowering by an average of 19%, fruiting by 18% and seed production by 16%. The individual seed weight also has shown an average increase of 4%. Although these increases in the reproductive effort were proportionately lower than the 31% increase observed for the total biomass of the same set of species used in the meta-analysis, long-term increases in C_a are likely to have a positive influence on the reproductive biology of plants, irrespective of the species. Notably, with the exception of leguminous species, the seed nitrogen concentration decreased with increasing C_a , by an average of 14%.

While the influence of increasing C_a on reproductive biology appears to be positive, increasing T_a could have both positive and negative effects. All plants have to complete a specific, genetically-determined thermal

duration before flowers or other forms of reproductive structures are initiated (Roberts *et al.*, 1997; Saxe *et al.*, 2001). With increasing T_a , this specific thermal duration requirement would be fulfilled within a shorter period of time. In plant species, which flower seasonally, this could prompt earlier flowering than at present. Hence, flowering and fruiting periods for different species within a humid tropical forest ecosystem could undergo temporal shifts in a future, warmer environment. This could set off a chain of events by influencing the behavioural patterns of the fauna, which depend on the fruits of different plant species within the ecosystem.

In addition to its influence on the thermal duration requirement, increasing T_a could influence the processes of flower development, pollination and seed/fruit formation. Generally, these stages are highly sensitive to supra-optimal temperatures. Therefore, increasing T_a beyond a genetically-determined optimum could adversely affect the development of reproductive structures. However, there can be substantial variation in the degree of heat tolerance between different species. Accordingly, species with a relatively greater heat tolerance, especially at the reproductive phase, could increase proportionately and change the composition of future forest ecosystems in the humid tropics.

INFLUENCE OF INCREASING C_a AND T_a ON SOIL PROCESSES

Soil is the major source of nutrients to plants in a forest ecosystem and nutrient recycling plays a major role in supporting the rich diversity of flora and fauna in forests of the humid tropics. Several processes related to nutrient recycling are affected by increasing C_a and T_a . The increased biomass production under elevated C_a will increase the addition of organic material to the soil through litter fall (Ceulemans *et al.*, 1999). Proportionately greater stimulation of root biomass by elevated C_a would increase the organic matter inputs to the soil through root exudates and through root decomposition and turnover (Norby, 1994). However, decomposition rates of litter produced under higher C_a would be slower because of its greater carbon and lower nitrogen concentrations (i.e. higher C:N ratio) (O'Neill & Norby, 1996). In lowland forests of the humid tropics, where the temperatures are higher, slowing down of the litter decomposition may be an advantage because it would lead to slower release of nutrients and lower leaching losses caused by higher rainfall. However, the increase of T_a that accompanies the increase of C_a would ultimately result in soil temperatures (T_s) also increasing. This, in turn, will increase the rates of litter decomposition in forests of the humid tropics located at all altitudes. Increased T_s would also result in

greater mineralization rates for nutrients (i.e. N and P) that are fixed in soil minerals. The resulting increase in nutrient availability in the soil could support the increased nutrient demand required for CO_2 -induced stimulation of photosynthesis and biomass production. These changes in the soil environment could also modify its microbial population and their activity (O'Neill, 1994; Sadowsky & Schortemeyer, 1997). Because of the longer time scales involved, there could be many positive and negative feedbacks between these interacting processes.

POTENTIAL FOR CARBON SEQUESTRATION BY FORESTS IN THE HUMID TROPICS

The longevity and favourable conditions for plant growth of forests in the humid tropics allows significant potential for carbon sequestration in their biomass and soil in a future high C_a environment (Dixon *et al.*, 1994; Grace *et al.*, 1995; Naburrs & Mohren, 1995; Lloyd & Farquhar, 1996; Chambers *et al.*, 1998; Phillips *et al.*, 1998; Prentice *et al.*, 2001; Schimel *et al.*, 2001) and slow down the pace of climate change (Cramer *et al.*, 2001; Clark, 2004a; Thompson *et al.*, 2004). In fact, Phillips *et al.* (1998) showed that increased biomass in tropical forests during the last 40 years accounted for 40% of the missing carbon in the carbon balance of the entire world. Therefore, afforestation and prevention of deforestation have been identified as measures for mitigation of climate change (IPCC, 2007). However, there have been uncertainties on the capacity of tropical forests as carbon sinks (Pearce, 1999; Clark, 2002, 2004b; Houghton, 2003, 2005). Firstly, carbon sequestration capacity may be reduced when forest ecosystems approach the mature, climax stage (Pregitzer & Euskirchen, 2004) and when the ontogenetic development is accelerated by elevated C_a (Hättenschwiler *et al.*, 1997). Some experiments have shown that the CO_2 -induced growth stimulation of forests is transient and diminishes when trees transfer from juvenile to mature stage (McConnaughay *et al.*, 1996; Tissue *et al.*, 1997). Secondly, increasing deforestation and burning of biomass in the tropics could add significant amounts of CO_2 to the atmosphere. Moreover, on re-analyzing Phillips *et al.* (1998)'s data, Clark (2002) contends that the data do not indicate a significant biomass carbon sink in old-growth forests of the humid Neotropics.

Analyzing the results of four FACE experiments on temperate forest stands, Norby *et al.* (2005) showed a $23 \pm 2\%$ median increase in NPP in response to elevated C_a up to $550 \mu\text{mol mol}^{-1}$ and concluded that this response is highly conserved across a broad range of productivity. Norby *et al.* (2005) further showed that at low canopy leaf area index (LAI) values (i.e. juvenile forests), elevated C_a

increases NPP by increasing LAI and thereby increasing the amount of photosynthetically-active radiation (PAR) captured. On the other hand, after the LAI reaches a maximum (i.e. mature forests), elevated C_a increases NPP by increasing the efficiency at which absorbed PAR is converted to biomass (i.e. Radiation or Light Use Efficiency). The measured NPP increase of Norby *et al.* agreed closely with the predicted average increase of 22% for six dynamic global vegetation systems in response to an increase of C_a up to 550 $\mu\text{mol mol}^{-1}$ expected to occur by 2049 (Houghton *et al.*, 2001). The observation by Körner *et al.* (2005) that physiological responses (i.e. photosynthesis, leaf N and non-structural carbohydrate concentrations) to CO_2 enrichment of older and larger trees were similar to younger trees adds support to the view that carbon sequestration capacity is maintained in mature forests as well. In a review involving results from 49 studies on the impacts of climate change (i.e. increased C_a and T_a and changes in precipitation, incident solar radiation and various other atmospheric and soil factors) during the last 55 years on forest productivity, Boisvenue and Running (2006) showed an increasing trend in NPP in 37 of the studies. They further showed that the combination of changes in various climatic factors since the middle of the 20th century has had a positive impact on forest productivity when water is not limiting. As water is rarely a limiting factor in forests of the humid tropics, this analysis confirms the predictions based on fundamental physiological processes. Four (Phillips *et al.*, 1998; Malhi & Grace 2000; Baker *et al.*, 2004; Lewis *et al.*, 2004) out of the five tropical forest ecosystems considered in the study of Boisvenue and Running (2006) had shown increases in NPP or net biome production (NBP) in response to climate change that had occurred during the latter half of the 20th century. In fact, Nemani *et al.* (2003) estimated that tropical ecosystems accounted for a major portion of the 6% increase in global NPP that occurred during the period from 1982-1999, with the Amazon accounting for 42%. This increased NPP in tropical forest ecosystems is attributed to increased C_a and T_a (Lewis *et al.*, 2004) and decreased cloud cover (Wielicki *et al.*, 2002; Wild *et al.*, 2005) in these radiation-limited forest ecosystems (Graham *et al.*, 2003).

However, despite the overall increasing trend in NPP in tropical forests during the last 50 years, lower tree growth rates have been recorded in years with higher temperatures (Clark & Clark, 1994; Clark *et al.*, 2003; Clark, 2004b). These warmer years have coincided with the *El Niño* Southern Oscillation (ENSO), which is a major determinant of temperature and precipitation variation in the tropics (Nemani *et al.*, 2003). Episodes of ENSO have also caused substantial tree mortality,

especially larger trees, which store a greater proportion of carbon, due to drought and forest fires (Williamson *et al.*, 2000; Clark, 2004b).

In addition to the NPP, the partitioning of CO_2 -induced increases of biomass also determines the capacity of a forest ecosystem for carbon sequestration and mitigation of climate change (Dufresne *et al.*, 2002; Luo *et al.*, 2003). Biomass partitioned to above-ground vegetation can be sequestered in stem wood while that partitioned to roots can ultimately be stored as soil C. Chambers *et al.* (1998) have shown that some of the trees in the Amazon that have lived well over a millennium have been capable of growth and carbon sequestration for over 1,400 years. Idso (1999) has cited data that suggest that even after 100 years of exposure to elevated C_a , trees will still be removing more carbon from the air than they would be able to do if atmospheric C_a remained at the current level. Similarly, the soil C that gets sequestered in the recalcitrant soil C pool has residence times of the same scale as that of wood C (Leavitt *et al.*, 1994; Parton *et al.*, 1994). Studies at the single species level show a clear preference for greater partitioning of CO_2 -induced biomass to roots (Rogers *et al.*, 1994). However, available experimental results and model predictions at the ecosystem level do not show any consistent preference in C sequestration towards either vegetation or soil. In the study by Norby *et al.* (2005) percentage NPP gain partitioned to stem wood ranged from 11% to 93%. In global productivity models (Dufresne *et al.*, 2002), the fraction of C stored in vegetation has varied from 35% to 85%. On the other hand, Post and Kwon (2000) concluded that in the terrestrial ecosystems of the Northern Hemisphere, the potential for carbon sequestration in vegetation biomass is much greater than in soil.

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