

Tropical rainforest canopies and climate change

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Abstract There is less certainty about the impact of climate change on tropical rainforests than on temperate forests because of the comparative lack of background data and because few large scale experiments have been, and are being, carried out in tropical rainforests. Many of the factors critical to the future of tropical rainforests concern canopies, the key processes that take place there, and the roles and interactions of canopy biodiversity. In particular there are almost no data on how forest canopies and processes are changing with increased carbon dioxide levels. The implications of elevated carbon dioxide, climatic stress and related changes in water-use efficiency, nutrient availability and other such changes are discussed particularly with references to Australia's tropical rainforests.

Key words: tropical rainforests, canopy, climate change, elevated carbon dioxide, forest hydrology, tree physiology, forest fluxes, transpiration, FACE

INTRODUCTION

In a recent synthesis of temperate and tropical forest canopy research, Ozanne *et al.* (2003) stressed the importance of this forest layer as the interface between the atmosphere and the biosphere and its vital role in many key ecological processes. Although we know that rainforests have a major influence on the world's climate what is less clear is how rainforest canopies are being affected and will be affected by climate change, and how rainforest canopies are affecting and will affect climate. The present paper explores this issue further with an emphasis on Australia's tropical rainforests. We further examine the need for studies examining both natural changes in the carbon balance in tropical rainforests and those due to climate change and more particularly due to elevated carbon dioxide levels on forests and forest canopies.

Moist tropical rainforests cover approximately 6–7% of the surface of the globe and typically occur in a band about 15–20° either side of the equator in places that receive more than 2000 mm precipitation a year and where there is no prolonged dry season. Rainforests are renowned for their immense biodiversity. It is often said that tropical rainforests house more than half of the world's biodiversity. At least 44% of the world's vascular plants and 35% of the world's vertebrates (Sechrest *et al.* 2002) are endemic to 25 'global

biodiversity hotspots' (Myers *et al.* 2000) more than half of which are rainforest sites. Much less is known about the diversity of non-vertebrate animals in tropical rainforests although some would consider that there are many millions of species in tropical rainforests (May 2000; Novotný *et al.* 2002).

In Australia approximately 21.4% of the land mass is covered by forest, most of this occurring on the Eastern seaboard, in Queensland, Northern Territory, New South Wales, Tasmania and Victoria. Of this about 0.55% is tropical rainforest and this is largely restricted to a narrow belt about 400 km long where the Great Dividing Range meets the Coral Sea from 15°30'S to almost 19°25'S. The so-called 'Wet Tropics' is vitally important for its unique and rich biodiversity, for the ecosystem services it provides and because it is the last vestige of what was an ancient and extensive ecosystem covering perhaps a third of Australia (Bowman 2000).

PREDICTED CLIMATE CHANGE SCENARIOS

Increasing concentrations of greenhouse gases in the atmosphere, together with other forces, both positive and negative (Rotstayn *et al.*, 2007) have led to an increase in the mean global temperature by 0.6°C over the last century (Jones *et al.* 2001). The latest Intergovernmental Panel on Climate Change forecast (IPCC 2001a) suggests that this warming will continue for at least the next hundred years regardless of

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advances to reduce future emissions, due to a lag in ocean heat uptake. We note at the outset that there is a range of IPCC scenarios for emissions and future atmospheric concentrations of greenhouse gases. Further, different models have different climatic responses to greenhouse forcing. The A1F1 scenario has a rapid future growth of CO₂ equivalent emissions reaching about 1000 ppm by 2100. By contrast, the B1 scenario includes the adoption of green energy alternative, and the lowest likely concentration of greenhouse gases is 500 ppm. Models using the A1F1 scenario suggest that mean global temperature could increase by up to 5.8°C by 2100 and increasing sea surface temperatures could lead to a more El Niño-like mean state in the tropical western Pacific (IPCC 2001a; Cai 2003). Generally, it is predicted that there will be an increase in atmospheric water vapour and precipitation, more frequent and intense storms in the lower latitudes, and drier conditions in the mid latitudes (IPCC 2001a; Vecchi *et al.* 2006).

Over the last century the Australian continental mean annual temperature has increased by approximately 0.8°C, mostly in winter and spring, and rainfall has increased slightly, although on a continent-wide basis the trend is not statistically significant due to the high inter-annual variability (Hughes 2003). However, since 1976 the frequency and intensity of El Niño events has increased, and there is a possibly related decrease in rainfall along the east coast, mostly in the summer and autumn months (Salinger *et al.* 2000; IPCC 2001a; Hughes 2003; Bureau of Meteorology web site: <http://www.bom.gov.au>). Like many other rainforest regions on Earth, the tropical climate of the Wet Tropics of north-east Queensland exhibits distinct seasonality and relatively high variability in climate and hydrological processes over time scales from months to decades and beyond.

The average temperature in the north-east Queensland region is predicted to increase by up to 5.2°C by 2070 under the A1F1 scenario (Walsh *et al.* 2002), with greater warming inland and less along the coastal strip (CSIRO 2001; Cai *et al.* 2003). Rainfall projections for north-east Queensland are varied depending on location and influence from systems such as El Niño southern oscillation (ENSO), but are expected to change by -5% to 15% from December to February, and -15% to 5% for March to November (Whetton 2003). Nevertheless, increases in the intensity and frequency of extreme rainfall events have been modelled across Australia and found to be highest in mountainous terrain (such as the Wet Tropics), with an average increase in intensity of 20% to 40% by 2040 (Abbs 2004) and return period for an 80 mm per day event dropping from 40 years down to 20 years (CSIRO 2001). In the tropical rainforests of Northern Australia, increase in the frequency of El Niño events, and the resulting reduction in available moisture, may

lead to an increase in drought and the frequency of fire. The result of repeated fire would be a shift from fire-sensitive rainforest vegetation to fire-tolerant species (Kershaw 1985; Mayle *et al.* 2004) as even small surface fires reportedly impact heavily on tropical forests, in one instance killing up to 48% of trees and 49% of the living tree liana biomass (Laurance 2003).

Already the tropical rainforest regions of the world have experienced a high rate of warming ($0.26 \pm 0.05^\circ\text{C}$ per decade since the mid 1970s), and, surprisingly, a decline in precipitation (1% per decade $\pm 0.8\%$) (Malhi & Wright 2004). However, this precipitation decline is in the Northern hemisphere tropics, and there has been little change in the Southern Hemisphere tropics (New *et al.* 2001). The disparity may relate to the greater increase of aerosols levels in the Northern Hemisphere (Rotstayn *et al.*, 2007).

Several studies have recorded a poleward and altitudinal shift of species and changes to the distribution, migration, reproduction and abundance of both plants and animals in response to climate change (e.g. IPCC 2001b; Walther *et al.* 2002; Parmesan & Yohe 2003; Primack & Corlett 2005). These trends are expected to continue altering species abundance, composition and dominance, and reducing favourable habitats to the point of extinction in some cases (Thomas *et al.* 2004). In tropical forests fingerprinting techniques have been developed to ascertain the magnitude of ecosystem change which may be attributed to temperature, precipitation, solar radiation and climatic extremes (Lewis *et al.* 2004). Australian ecosystems, and in particular the World Heritage reef and rainforest areas, are considered particularly vulnerable to climate change due to the possible increase in the frequency of El Niño events, resulting in decreases in rainfall along the east coast, and increases in cyclone and rainfall intensity (IPCC 2001b; Anonymous 2005). Although the diverse ecology of the Wet Tropics rainforest is partly the result of such a variable climate, one that has encouraged diversity and yet is stable enough to maintain habitat for species evolving over evolutionary time scales, the rate of future anthropogenic climate change is considered more akin to the catastrophic changes responsible for mass species extinction (Colinvaux 1989).

In mountainous areas increases in temperature may both lift the cloud base, depriving upland rainforest of water stripped from clouds (Foster 2001), and reduce the extent of montane rainforest by up to 95% (2°C of warming) forcing cool adapted species further up the mountains (O'Neill 1999). Existing lowland forests in North Queensland are expected to increase in area while highland rainforest will decrease by up to 50% with 1°C of warming (Hilbert *et al.* 2001). An estimated 74% of rainforest birds in the region are predicted to become threatened (including 26 critically

endangered species) (Shoo *et al.* 2005) and vertebrate species distribution will decrease by more than 50% on average (Meynecke 2004) by 2100 as a result of mid-range warming. The entire range of all 65 endemic vertebrate species would disappear with an increase in temperature of 7°C (Williams *et al.* 2003). Although somewhat different approaches are needed in assessing the impact of climate change on the flora and fauna, in all cases the predicted geographical distributions of plants and animals depend on temperature increases. In the rainforest there can be substantial differences in temperature in different parts of the canopy and between the canopy and the ground (Anhuf & Szarzynski 2001). Similarly, there may be large differences in temperatures between different areas of rainforest depending upon slope, soil type, etc. To realistically assess the effects of climate change on rainforests and rainforest canopies, temporally and spatially resolved microclimatic datasets will be required for significant forest types. The overlay of this fine scale detail on the broader landscape level climate change will be necessary to predict likely species changes in complex forest and community structures.

The total number of tropical cyclones has decreased in the Australian region since the late 1960s (probably due to changes in ENSO); however, the number of stronger cyclones has increased slightly (Plummer *et al.* 1999). Recent studies (e.g. Walsh & Ryan 2000; Knutson & Tuleya 2004) are reinforcing the findings that cyclones will become more intense, with an expected increase in wind speeds of 5–10%, peak rainfall increases of 15–30%, and an increase in the number of category five cyclones. Future tropical cyclones in the north-east Queensland region are projected to increase in maximum intensity but show little change in their region of formation or number (Walsh *et al.* 2002). Projected increases in cyclone intensity are expected to impact heavily on the shallow rooted, tall rainforest trees that are susceptible to uprooting, breakage and defoliation (Primack & Corlett 2005), and an increase in the intensity of rainfall events will lead to higher erosion and sedimentation (IPCC 2001b).

FLORISTICALLY COMPLEX FOREST CANOPIES WILL RESPOND IN COMPLEX WAYS

Of all the aspects of climate change, the most certain is that levels of atmospheric CO₂, the most significant anthropogenic greenhouse gas, are rising. Currently they are at 380 ppm, some 20% more than 50 years ago and are predicted to reach at least 500 ppm, and possibly 1000 ppm, by the end of the century. Although there have been many notable studies involving

manipulations of CO₂ levels to assess impacts of increased CO₂ on temperate forests, there is a complete absence of comparable empirical data for tropical rainforests. In a synthesis paper Malhi and Phillips (2004) developed arguments for expected changes in tropical forest growth and carbon balance as a result of elevated CO₂ levels, but as yet we have little understanding about how tropical rainforests will respond to such increases and how these responses might interact with other aspects of climate change such as changes in temperature, precipitation and frequency/severity of cyclones/hurricanes. It is surprising that tropical forests are not covered by the international network of Free Air CO₂ Enrichment (FACE) experiments, undoubtedly the best available technology for observing system level responses in difficult-to-model, spatially variable, natural ecosystems. In the only tropical FACE experiment so far conducted, the Australian Savanna FACE experiment (OzFACE), large annual differences were reported in the responses of perennial C₄ grasses and C₃ tree seedlings to enhanced CO₂ concentrations in an ecosystem in which water and nutrient limitations are of differential importance during the annual seasonal cycles (Stokes *et al.* 2003, 2005). By enabling above- and below-ground responses to be integrated over whole growing seasons, FACE permitted examination of plant production consumption and decay, nutrient cycling, soil carbon storage, tree–grass and plant–insect interactions, and soil hydrology.

The response of tropical trees and vines to elevated CO₂ may be initially positive where water is non-limiting, although, as with the response to changing moisture regimes, it is likely to vary considerably across species. There is already some evidence of a general increase in forest biomass in the Amazon Basin possibly attributable to the anthropogenic rise in atmospheric CO₂ concentrations over the last century (Phillips *et al.* 1998; Phillips *et al.* 2002a; Baker *et al.* 2004), although this trend may not be universal, and may prove to be short-lived (Körner 2004; Körner *et al.* 2005; Beerling & Mayle 2006). It is assumed that rainforests such as those of the Wet Tropics are also storing carbon because of the high precipitation, high insolation and reasonable nutrient status of the soils. Initial analyses of carbon fluxes at one of the wettest places in North Queensland at the Cape Tribulation Crane site where mean annual precipitation is 3900 mm, suggest that in the drought years of 2002 (2400 mm rainfall) and 2003 (2500 mm rainfall) this forest was in balance for carbon for the whole year or a net source compared with the wetter years of 2001 (3100 mm) and 2004 (4900 mm) when it was a net carbon sink (M. Liddell, unpubl. 2006). These results are complementary to those found in temperate eucalypt forests in Australia (Leunig *et al.* 2005) and in Europe under strong drought conditions (Ciais *et al.* 2005).

Global climate change and increasing atmospheric CO₂ concentration are closely coupled, but the relationship between the two is complex. Nonetheless, tropical forests will be impacted by changes in both climate and elevated CO₂, so both must be considered during experimentation, analysis and prediction. The floristically complex nature of tropical rainforest canopies ensures that their response to elevated CO₂ and any change in climate will be non-uniform (Körner 1998). This is due to inherent physiological differences between major taxonomic groups and plant structural forms. A strong indication of change in mature tropical forest structure is the increase in stem turnover reported at the end of the 20th century (Phillips & Gentry 1994). Altered tree communities in central Amazonia have also been reported as a 'signature' of increasing forest productivity associated with global or regional scale changes due to factors such as increasing atmospheric CO₂ levels or elevated nutrient deposition from ash produced by regional forest fires (Laurance *et al.* 2005).

At a physiological level, trees of contrasting root structure, such as deep *versus* shallow, will be differentially affected by changing soil moisture regimes, with drier conditions favouring deeper rooted species with access to more reliable groundwater sources (Jackson *et al.* 1995, 1999; Meinzer *et al.* 1999; Drake & Franks 2003). Deeper rooted rainforest species may even perform a crucial role in drier periods by redistributing water from depth to roots in the upper soil zone via hydraulic lift (Oliveira *et al.* 2005), a mechanism usually associated with drier ecosystems (Caldwell *et al.* 1998). Stokstad (2005) reports that some of the emergent trees died in a drought experiment after 4 years of reduced water in a Brazilian rainforest but gave no indication as to how deep-rooted these were.

Different stem hydraulic properties between trees and vines (Gartner *et al.* 1990; McCulloh & Sperry 2005) and angiosperms *versus* gymnosperms (Feild & Brodribb 2001) impart contrasting water-use qualities leading to partitioning of canopy water fluxes. In one study of several species of angiosperms and conifers it was found that, for trees of comparable size, angiosperms used more water than conifers (Meinzer *et al.* 2005). The highly conductive xylem of woody vines supports transpiration rates that may exceed the rates in canopy trees (Fichtner & Schulze 1990; Ewers *et al.* 1991; Tyree & Ewers 1996), further partitioning canopy water flux between trees and vines. However, the nature of this partitioning may shift with different sensitivities of tree species and vines to changing environmental moisture conditions, or increasing CO₂ concentrations. In some Amazonian forests, vines are reported to be increasingly dominant (Phillips *et al.* 2002b), a trend supported by physiological studies on vines exposed to elevated

CO₂ concentration (Granados & Körner 2002; Zotz *et al.* 2006).

The plant hydraulic system is an integral component of the mechanism through which stomata control transpirational water loss (Meinzer & Grantz 1990; Meinzer 2002; Franks 2004; Franks & Brodribb 2005) and a growing body of evidence suggests close coupling between plant hydraulic and photosynthetic capacity (Sober 1997; Brodribb & Feild 2000; Santiago *et al.* 2004; Franks 2006). At the leaf level there is considerable physiological diversity in response to environmental perturbation that is linked to hydraulic constraints inherent to different plant functional groups (Franks & Farquhar 1999; Brodribb *et al.* 2005). Different hydraulic properties between species, including xylem conductivity, water storage and susceptibility to drought-induced xylem embolisms, contribute to diverse modes of daily gas exchange regulation and response to climate change. In tropical forest the architectural diversity of trees also influences canopy physiology, adding to the difficulty of predicting overall physiological responses of tropical forests. By comparison, temperate coniferous forests are much more architecturally constrained and therefore less physiologically complex.

Increasing levels of atmospheric carbon dioxide are expected to increase forest productivity by increasing photosynthesis, but to reduce the digestibility and quality of vegetation (Ceulemans 1996) as leaf toughness and leaf defence compounds (such as tannins) increase and nitrogen phosphorus ratios and proteins decrease (Wang & Polglase 1995; O'Neill 1999; Kanowski 2001; Williams *et al.* 2003). These changes may have important consequences for canopy vertebrates and invertebrates. For example, Kanowski (2001) has suggested that changes in leaf palatability and defence compounds could impact on folivores that balance these competing forces. Similarly, Blüthgen *et al.* (2004a,b) have shown that there may be a fine balance in the sugars, proteins and nutrient content of fluids that dominant species of ants harvest from plants or bugs that feed on plants.

Elevated CO₂ concentration tends to reduce stomatal conductance to water vapour and CO₂, but because photosynthesis may be enhanced at higher ambient CO₂ concentrations, the net effect can be an increase in carbon assimilated per unit water transpired, that is, an increase in transpiration efficiency. Reduced canopy conductance under elevated CO₂ concentrations could significantly reduce rates of transpiration from forests, thus dramatically altering catchment water balance. This has recently been implicated on a continental scale, with researchers identifying direct response of stomata to CO₂ as possibly the primary mechanism underlying increased continental river runoff in the twentieth century (Gedney *et al.* 2006). In Australia the Wet Tropics rainforest

catchments are the source of about 5% of all Australian runoff and contribute about 40% of the runoff to the Great Barrier Reef lagoon. The Amazon is the largest river system on the planet and is responsible for delivering approximately 1/5 of the total volume of freshwater to the oceans of the world. Any change to the transpiration rates of tropical rainforests then has considerable importance in both the Australian and global context as it will not only dramatically alter the rainforest ecosystems but also the associated marine ecosystems.

Differences in physiological response between above- and below-ground components of forest ecosystems could lead to complex transients in the terrestrial carbon budget. In a coupled carbon-climate model Cox *et al.* (2000) predicted that initially an increase in atmospheric CO₂ concentration would increase both vegetation and soil carbon, producing a net increase in terrestrial carbon. However, as CO₂ increased further, terrestrial carbon would decrease, switching the land biosphere from sink to source, as photosynthesis saturated while soil respiration continued to increase with temperature. The interaction between soil moisture and soil respiration is also significant. In regions where rainfall diminishes, soil carbon emissions may decrease due to the effect of reduced moisture on microbial activity (McLain & Martens 2006).

Widely differing forecasts of the responses of plants in the tropics to increases in atmospheric CO₂ concentrations and temperature, altered light levels, rainfall regimes and storm severity illustrate the limited predictive power of even recent models (Lewis *et al.* 2005, 2006; Wright 2005). This poor predictive capability reflects the complexity of rainforest ecosystems, with their mix of species and the interactions between them, let alone the connections and feedbacks with below-ground processes. In particular, such models are generally silent about the couplings between plants and other trophic levels, such as herbivores, detritivores and soil micro-organisms. For example, the allocation of resources to defence compounds is difficult to predict, as is competition between soil micro-organisms and plants for limited nutrients.

CONCLUSIONS

It is evident that we should expect large-scale changes to tropical forest composition and structure as these forests adapt to changing climates. Associated with this will be changes to forest canopies and the organisms that live there and provide essential biological services. As Laurance *et al.* (2005) have suggested it is not sufficient to rely on studies in temperate forests to predict how rainforests are responding and will

respond to increased levels of atmospheric CO₂. A tropical FACE experiment in mature rainforest at one of the few rainforest canopy cranes where the infrastructure is in place to access the canopy easily on a daily basis would help to fill this gap in our knowledge. It is clear that such a study would need to be run for at least 10 years and would need to examine the range of plant and associated animal responses to such increases in CO₂ and their interactions. Such experiments will be difficult to carry out because of the requirement of large amounts of high quality CO₂ amounting to more than 2 t per day and the technical difficulties in managing gas flow at the required quantities to all parts of the canopy of the experimental trees. However, such considerations should not prevent the commencement of these essential tests.

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