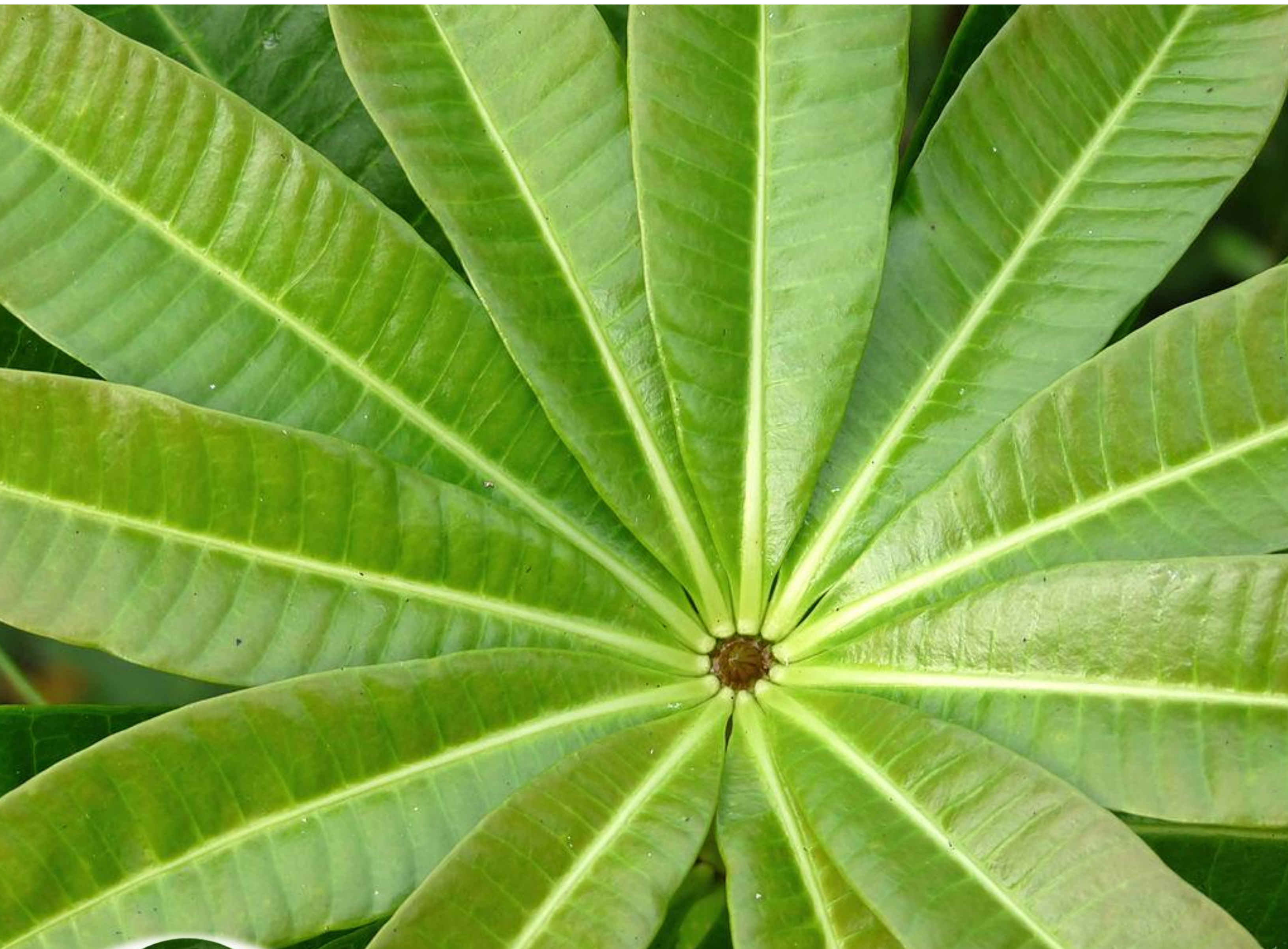
TROPICAL TREES



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TROPICAL TREES

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Going back in time to the final few years of the 20th century, Schaffer *et al*. (1997)[1] grew two mango ecotypes - one evolving from a warm, humid tropical climate, and the other from a cool, dry subtropical region - for 12 months in glasshouses maintained at either 350 or 700 ppm CO_2 in order to determine the effects of atmospheric CO_2 enrichment on the trees' growth and leaf mineral nutrient concentrations. In doing so, they found that in addition to the greater net carbon gains of the CO_2-enriched trees, the elevated CO_2 tended to decrease foliar concentrations of mineral nutrients (N, P, K, Ca, Mg, S, Cl, Fe, Zn, Mn, Cu and B) in both mango cultivars, most likely due to a dilution effect, since atmospheric CO_2 enrichment increased leaf dry mass. But with respect to this latter finding, the scientists who conducted the study wrote that "given the slow rate at which global atmospheric CO_2 concentration is increasing, it is possible that plants will adapt to this phenomenon over time with respect to mineral nutrition," as actually was found to be the case in a prior study of sour orange trees after 85 months of exposure to elevated CO_2 (Penuelas *et al*., 1997).

One year later, Lin *et al*. (1998)[2] measured the ecosystem carbon exchange rate of a 1700-m^3 synthetic rainforest mesocosm that was alternately maintained at atmospheric CO_2 concentrations of either 430 or 740 ppm. This enormous study site, managed by Columbia University, was located within the 1.25-ha naturally-lit Biosphere 2 research "dome," which contained several large synthetic ecosystems enclosed by stainless steel sheets and glass. After the dome's air was stabilized at a treatment CO_2 level for about a week, the rainforest mesocosm was isolated from the rest of the dome for one to three days so its carbon exchange rate could be measured. This work revealed that the 72% increase in atmospheric CO_2 concentration increased the daytime net ecosystem carbon exchange rate of the synthetic rainforest by 79%, without affecting the amount of carbon respired from the soil, which observation indicated that the CO_2-enhanced ecosystem carbon uptake was due primarily to increased canopy net photosynthesis, as the elevated CO_2 had no significant effect on soil respiration.

Contemporaneously, Wurth *et al*. (1998)[3] enclosed upper-canopy leaves of four species of trees located in a semi-deciduous tropical forest near Panama City, Republic of Panama, in small transparent cups enriched with CO_2 to about twice the current ambient concentration, in order to determine the effects of elevated CO_2 on sugar and starch production in the trees' leaves. And "against expectation," as they put it, they determined that the elevated CO_2caused 30 and 100% increases in leaf sugar and starch concentrations, respectively, for all four of the tropical tree species, regardless of whether they were sampled in the morning or evening or under high

[1] http://www.co2science.org/articles/V2/N17/B1.php.
[2] http://www.co2science.org/articles/V1/N3/B4.php.
[3] http://www.co2science.org/articles/V2/N4/B1.php.

or low light intensities, which observations demonstrated that atmospheric CO_2 enrichment can significantly stimulate individual- leaf total nonstructural carbohydrate contents in tropical tree species, even when there is a very large "sink" (the rest of the tree) to which the carbohydrates could readily be exported.

Also working concurrently in Panama were Lovelock *et al*. (1998)[4], who grew ten tropical tree species in open-top chambers situated on the edge of a tropical forest for six months at both ambient and twice-ambient atmospheric CO_2concentrations, in order to determine the effects of elevated CO_2 on them. And this work, too, indicated that the leaf starch concentrations of the trees were approximately doubled in the doubled CO_2 environment.

One year later, Lovelock *et al*. (1999b)[5] enclosed branchlets of 30-m tall *Luehea seemannii* trees in small open-top chambers, suspended within their upper canopies, and exposed them to atmospheric CO_2 concentrations of 360 or 750 ppm for nearly 40 weeks, in order to study the effects of elevated CO_2 on photosynthesis, growth, and reproduction in this deciduous tropical tree. In doing so, they determined that the leaves of branchlets grown in elevated CO_2 had net photosynthetic rates that were approximately 30% greater than those observed in leaves of ambiently-grown branchlets. However, the extra carbohydrates produced by this phenomenon were not used by CO_2-enriched branchlets to increase leaf growth or reproductive efforts. Instead, they were stored away in terminal woody tissues, which finding led the four researchers to speculate that the enhanced carbohydrate storage in terminal branchlets may facilitate greater first-flush leaf growth the following year.

Breaking from experimental work to conduct a mini-review of the scientific literature dealing with subtropical and tropical fruit tree responses to atmospheric CO_2 enrichment to that point in time, Schaffer *et al*. (1999)[6] reported results for a number of parameters, including photosynthesis and biomass accumulation. They found, for example, that exposure to elevated CO_2 concentrations significantly enhanced photosynthesis in leaves of avocado, banana, citrus, mango, and mangosteen trees. After being exposed to an atmospheric CO_2 concentration of 800 ppm for one year, for example, the leaves of mangosteen trees displayed photosynthetic rates that were 40 to 60% greater than rates observed in ambiently grown leaves. In addition, atmospheric CO_2 enrichment increased biomass accumulation in each of these species, and in macadamia trees as well. In most cases, elevated CO_2 also increased total yield and fruit weight. However, when it did not immediately increase yield in avocado, mango, and macadamia, a preferential allocation of carbon belowground to roots was seen, suggesting that "increasing water and nutrient uptake resulting from increased root mass would eventually increase assimilate partitioning to the aboveground organs," ultimately enhancing yield.

Returning to experimental work, Sheu and Lin (1999)[7] grew 50-day-old seedlings of the sub-tropical tree *Schima superba* for six additional months in pots placed within glass chambers maintained at atmospheric CO_2 concentrations of 360 and 720 ppm. In addition, at each CO_2 concentration half of the seedlings were grown at an *optimal* day/night temperature

4 http://www.co2science.org/articles/V2/N4/B2.php.
5 http://www.co2science.org/articles/V2/N19/B1.php.
6 http://www.co2science.org/articles/V2/N22/B5.php.
7 http://www.co2science.org/articles/V3/N2/B1.php.

regime of 25/20°C, while the other half were subjected to a *higher* temperature treatment of 30/25°C. This work revealed that the CO_2-enriched seedlings exhibited photosynthetic rates that were 20% greater than those displayed by ambiently-grown trees at the *original* "optimal" day/night temperatures, but that their photosynthetic rates were fully 40% greater than those displayed by the ambiently-grown trees in the *elevated* temperature regime, thereby *demonstrating* that the optimal growth temperature for this species had to have *increased* with the increasing CO_2 concentration. And as a result, the CO_2-enrichedseedlings displayed total dry weights that were 14 and 49% greater than control seedlings at the lower and higher set of growth temperatures, respectively.

Contemporaneously, Lovelock *et al*. (1999a)[8] grew seedlings of the tropical tree *Copaifera aromatica* for 50 days in pots placed within open-top chambers maintained at atmospheric CO_2 concentrations of 390 and 860 ppm. Additionally, after 14 days of differential CO_2 exposure, half of the seedlings in each treatment were subjected to mechanical defoliation, which removed about 40% of their leaf area, and which enabled the three researchers to study the influence of simulated herbivory on the CO_2 growth response of this species.

During the entire experiment, the seedlings grown in the elevated CO_2 treatment displayed rates of net photosynthesis that were between 50 and 100% greater than those exhibited by plants grown in ambient CO_2, regardless of defoliation, which had little to no impact on photosynthesis in either CO_2 treatment. Mechanical defoliation did, however, temporally reduce seedling leaf area and leaf relative growth rates in both CO_2 environments. But by the end of the experiment, leaf relative growth rates had recovered, and there were no differences between defoliated and undefoliated seedlings in either CO_2 treatment. In contrast, the leaf *area* of defoliated seedlings never recovered to match that of undefoliated controls in either CO_2 treatment. But defoliated seedlings grown at ambient CO_2 were able to ultimately attain leaf areas that were 77% of their un-defoliated controls, while those exposed to elevated CO_2attained leaf areas that were 67% of their respective controls.

In spite of that difference, the defoliated seedlings grown in elevated CO_2 still possessed about 20% *more* leaf area than the defoliated plants grown in ambient CO_2. In addition, final plant dry weight, which better represents the total impact of any stress upon a plant - and which indicates how well a plant is able to deal with a stress - was 15% greater in defoliated seedlings exposed to elevated CO_2 than it was in defoliated seedlings growing in ambient CO_2. And, therefore, even with leaf destruction resulting from herbivory, *Copaifera aromatica* seedlings will likely exhibit increased photosynthetic rates and greater biomass accumulation as the air's CO_2 content continues to rise.

Passing from the 20th to the 21st century, Hoffmann *et al*. (2000)[9] germinated and grew specimens of a tree common to the Brazilian savannah (*Keilmeyera coriacea*) in controlled environment chambers that were maintained at combinations of ambient (350 ppm) and elevated (700 ppm) atmospheric CO_2 concentration and low- and high-strength soil nutrient solutions. In addition, at 10 weeks post-germination, half of the seedlings in each treatment

8 http://www.co2science.org/articles/V3/N7/B4.php.
9 http://www.co2science.org/articles/V3/N28/B2.php.

were clipped to the ground to simulate burning, thus allowing the five researchers to study the interactive effects of elevated CO_2 and soil nutrients on seedling growth and regrowth with and without the presence of a simulated burning event. And what did they find?

In the uncut seedlings, the doubled atmospheric CO_2 treatment increased total dry weight by about 50%, while the high nutrient solution increased it by 22%, with no significant interactions between the two factors. However, in seedlings subjected to the simulated burning event, elevated CO_2 had a significant impact on regrowth, but only in the presence of high soil nutrient availability, when *it stimulated regrowth by nearly 300%!* This observation, coupled with the knowledge that large pulses of nutrients typically become available in soils following burning events, led Hoffmann*et al*. to conclude that "under elevated CO_2, enhanced growth following fire will reduce the time required for individuals to regain the pre-burn size, minimizing the negative effect of fire on population growth." And as a result, they stated that "greater growth rates and higher capacities of regeneration under elevated CO_2 are expected to increase the ability of woody plants to withstand the high fire frequencies currently prevalent in moist savannahs throughout the tropics."

Greater growth rates and higher capacities of regeneration under elevated CO_2 are expected to increase the ability of woody plants to withstand the high fire frequencies currently prevalent in moist savannahs throughout the tropics.

A few years later, Laurance *et al*. (2004) reported accelerated growth in the 1990s relative to the 1980s for the large majority (87%) of tree genera in 18 one-hectare plots spanning an area of about 300 km^2 in central Amazonia. And it was suggested, in the words of Laurance *et al*. (2005), that these "pervasive changes in central Amazonian tree communities were most likely caused by global- or regional-scale drivers, such as increasing atmospheric CO_2concentrations," a theme that was also promulgated by Phillips *et al*. (2004).

Shortly thereafter, from a primary rain forest in Ariuana, Brazil, Hietz *et al*. (2005)[10] collected samples of wood from 37 tropical cedar (*Cedrela odorata* L.) trees that were between 11 and 151 years old in 2001 and from 16 big-leaf mahogany (*Swietenia macrophylla* King) trees that were between 48 and 126 years old at that time, after which they measured the wood samples' cellulose ð^{13}C in 10-year growth increments. This work revealed that cellulose ð^{13}C decreased by 1.3 per mil in *Cedrela* and by 1.1 per mill in *Swietenia* over the past century, with the largest changes occurring during the past 50 years. And based on these data and known trends in atmospheric CO_2 and ð$^{13}CO_2$, they calculated that the intrinsic water-use efficiency of the trees

[10] http://www.co2science.org/articles/V8/N38/B3.php.

increased by 34% in *Cedrela* and by 52% in *Swietenia* over this period, which they said was about the same as what had been deduced from similar measurements of the wood of temperate trees (Freyer, 1979; Bert *et al*., 1997; Feng, 1999). And because, in the words of the three researchers, "water is probably not a strong limiting factor in tropical rain forest trees," they concluded that "the gain in water use efficiency translates mostly to increased carbon assimilation, which may explain the observed increase in tree growth and turnover (Phillips, 1996; Laurance *et al*., 2004)."

Three years later, Phillips *et al*. (2008)[11] synthesized recent observational results from the network of Amazon-forest researchers known as RAINFOR (*Red Amazonica de Inventarios Forestales*), which represented the combined long-term ecological monitoring efforts of 35 institutions from all around the world, with plots that spanned Amazonia "from the driest southeast to the wettest northwest and the least fertile east to the most fertile west." And in doing so, the team of five researchers reported finding evidence for "concerted changes in the structure, dynamics and composition of old-growth Amazonian forests in the late twentieth century," noting that "in the 1980s and 1990s, mature forests gained biomass and underwent accelerated growth and dynamics, all consistent with a widespread, long-acting stimulation of growth" that was "normally distributed" and had "occurred across regions and environmental gradients and through time," indicating "continued biomass sink strength through to the end of the century."

In numerical terms, they indicated that "in the late twentieth century, biomass of trees of more than 10 cm diameter increased by 0.62 t C ha^{-1} yr^{-1} averaged across the basin," which implied "a carbon sink in Neotropical old-growth forest of at least 0.49 Pg C yr^{-1}." And they added that "if other biomass and necromass components are increased proportionally, then the old-growth forest sink here has been 0.79 Pg C yr^{-1}, even before allowing for any gains in soil carbon stocks." This finding, in their words, was "consistent with the evidence from recent global inversions of atmospheric CO_2 measurements and local aircraft measurements of atmospheric CO_2 profiles, showing that the tropics are either carbon-neutral or sink regions, despite widespread deforestation."

What has been driving these changes? This is the question the five researchers asked themselves; and they replied that "the simplest explanation for the ensemble result - more biomass, more stems, faster recruitment, faster mortality, faster growth and more lianas - is that improved resource availability has increased net primary productivity, in turn increasing growth rates." And they concluded that "the only change for which there is unambiguous evidence that the driver has widely changed *and* that such a change should accelerate forest growth is the increase in atmospheric CO_2," because of "the undisputed long-term increase in concentrations, the key role of CO_2 in photosynthesis, and the demonstrated effects of CO_2 fertilization on plant growth rates."

About this same time, Lloyd and Farquhar (2008)[12] - as part of an international workshop held at Oriel College, Oxford, UK, in March of 2007 - prepared a review of the effects of rising

[11] http://www.co2science.org/articles/V11/N19/B1.php.
[12] http://www.co2science.org/articles/V11/N19/B2.php.

temperatures and atmospheric CO_2 concentrations on the productivity of tropical forest trees. And based on their examination of the pertinent scientific literature, and using a mixture of observations and climate model outputs together with a simple parameterization of leaf-level photosynthesis incorporating known temperature sensitivities, they said they could find "no evidence for tropical forests currently existing 'dangerously close' to their optimum temperature range," as is often suggested by climate alarmists. Quite to the contrary, in fact, they indicated they had found that increases in photosynthetic rates associated with increases in ambient CO_2 over forthcoming decades should "more than offset" any decline in photosynthetic productivity due to higher leaf temperatures, leaf-to-air vapor pressure deficits or autotrophic respiration rates. And they affirmed that "the magnitude and pattern of increases in forest dynamics across Amazonia observed over the last few decades are consistent with a CO_2-induced stimulation of tree growth."

Thus, it would appear that not only have *past* increases in the atmosphere's CO_2 content and temperature been a boon to the productivity of Amazonia's tropical forests - as well as all of the world's *other* tropical forests - it would appear from the materials reviewed by these two highly-regarded scientists, as well as their own original research, that the productivity of earth's tropical forests will likely rise even *higher* in response to predicted *future* increases in the atmosphere's temperature and CO_2 concentration.

A subsequent report by Oliver L. Phillips of the UK's University of Leeds and his 65 co-authors (Phillips *et al*., 2009)[13] suggested pretty much the same thing, as the troop of scientists indicated that over the prior quarter-century of intensive region-wide measurements, the productivity of the Amazon rainforest - even in its extreme old age - had been found to be "increasing with time," in support of which statement they cited the comprehensive observational studies of Phillips *et al*. (1998), Nemani *et al*. (2003), Baker *et al*. (2004a), Lewis *et al*. (2004) and Ichii *et al*. (2005). And in their own new study, they determined that although *extremely* severe drought conditions can indeed bring a halt to biomass accumulation in old growth tropical forests - and sometimes even lead to minor *reductions* in biomass due to selective tree mortality - the vast majority of the aged trees are able to regain their photosynthetic prowess and add to their prior store of biomass once the moisture stress subsides, thanks in large measure to the enhanced *growth* and *water use efficiency* that are experienced by nearly all woody plants as the air's CO_2 content rises.

Shifting to another continent, Lewis *et al*. (2009)[14] invested a great amount of time and effort in documenting changes in aboveground carbon storage in 79 permanent sample plots spanning 40 years (1968-2007), located in closed-canopy moist forest, spanning West, Central and Eastern Africa, based on data obtained from more than 70,000 individual trees spread across ten countries. This work revealed, in their words, that "aboveground carbon storage in live trees increased by 0.63 Mg C ha^{-1} $year^{-1}$ between 1968 and 2007," and that "extrapolation to unmeasured forest components (live roots, small trees, necromass) and scaling to the continent implies a total increase in carbon storage in African tropical forest trees of 0.34 Pg C $year^{-1}$."

[13] http://www.co2science.org/articles/V12/N19/EDIT.php.
[14] http://www.co2science.org/articles/V12/N26/EDIT.php.

In discussing these results, the 33 researchers said the observed changes in carbon storage "are similar to those reported for Amazonian forests per unit area, providing evidence that increasing carbon storage in old-growth forests is a pan-tropical phenomenon," and they reported that "combining all standardized inventory data from this study and from tropical America and Asia together yields a comparable figure of 0.49 Mg C ha^{-1} $year^{-1}$," which equates to "a carbon sink of 1.3 Pg C $year^{-1}$ across all tropical forests during recent decades" and could account for roughly *half* of the so-called *missing carbon sink*.

As for what the driving force was that seemed to have breathed new life into old trees, Lewis *et al*. wrote in the concluding sentence of the abstract of their paper that "taxon-specific analyses of African inventory and other data suggest that widespread changes in resource availability, such as increasing atmospheric carbon dioxide concentrations, may be the cause of the increase in carbon stocks, as some theory (Lloyd and Farquhar, 1996) and models (Friedlingstein *et al*., 2006; Stephens *et al*., 2007; Ciais *et al*., 2008) predict."

Meanwhile, back in the Amazon, Laurance *et al*. (2009)[15] were reporting what they had learned while working within 20 one-hectare plots scattered over approximately 300 km^2 of intact rainforests, where they evaluated forest dynamics over the period 1981-2003, based on data obtained from 21,667 individual trees. This work revealed, in their words, that their "large-scale, long-term study appears to illustrate two contrasting patterns: (1) long-term trends in which tree mortality, recruitment, turnover, and basal area are progressively increasing over time in most (80-100%) of our study plots; and (2) shorter-term fluctuations in which strong pulses of tree mortality and poor growth have more transitory impacts on forest dynamics."

With respect to the first of these findings, Laurance *et al*. noted that "the increasing forest dynamics, growth and basal area observed are broadly consistent with the CO_2 fertilization hypothesis," while with respect to the second finding, they said that "tree mortality peaked, and tree recruitment and growth declined during atypically wet periods," and that "tree growth was fastest during dry periods, when reduced cloudiness might have increased available solar

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[15] http://www.co2science.org/articles/V12/N29/B1.php.

radiation." Consequently, it would appear that the historical increase in the atmosphere's CO_2 concentration, driven by the burning of fossil fuels, has actually been *good* for the Amazon's trees, and (very likely) for the rest of the region's plants and animals, even in the face of the local warming of 0.26°C per decade that was reported for the region since the mid-1970s.

In assessing this latter suggestion, Lapola *et al*. (2009)[16] used a potential vegetation model (CPTEC-PVM2) "to analyze biome distribution in tropical South America under a range of climate projections," while taking into consideration the *aerial fertilization* and *transpiration-reducing* effects of atmospheric CO_2 enrichment. In doing so, the Brazilian and German researchers said their modeling work revealed that "if the CO_2 'fertilization effect' indeed takes place and is maintained in the long term in tropical forests, then it will avoid biome shifts in Amazonia in most of the climate scenarios, even if the effect of CO_2 fertilization is halved." In fact, they stated that the CO_2 fertilization effect, "when fully or half considered, overwhelms the impacts arising from temperature (in agreement with Lloyd and Farquhar, 2008) and even some of the precipitation changes projected by most of the global climate models, resulting in higher net primary production by the end of the century."

Still stuck in the same year, Gloor *et al*. (2009)[17] wrote that "analysis of earlier tropical plot data has suggested that large-scale changes in forest dynamics are currently occurring in Amazonia (Phillips and Gentry, 1994; Phillips *et al*., 2004), and that an increase in aboveground biomass has occurred, with increases in mortality tending to lag increases in growth (Phillips *et al*., 1998; Baker *et al*., 2004a,b; Lewis *et al*., 2004)." However, they stated that this conclusion had recently been challenged by what they called an overzealous application of the "Slow in, Rapid out" dictum, which relates to the fact that forest growth is a slow process, whereas mortality can be dramatic and singular in time, such that sampling over relatively short observation periods may miss these more severe events, leading to positively-biased estimates of aboveground biomass trends, when either no trend or negative trends actually exist.

In evaluating this claim, Gloor *et al*. statistically characterized "the disturbance process in Amazon old-growth forests as recorded in 135 forest plots of the RAINFOR network up to 2006," as well as other independent research programs; and they "explored the consequences of sampling artifacts using a data-based stochastic simulator." This work revealed that "over the observed range of annual aboveground biomass losses, standard statistical tests show that the distribution of biomass losses through mortality follow an exponential or near-identical Weibull probability distribution and not a power law as assumed by others." In addition, they said that "the simulator was parameterized using both an exponential disturbance probability distribution as well as a mixed exponential-power law distribution to account for potential large-scale blow-down events," and that "in both cases, sampling biases turn out to be too small to explain the gains detected by the extended RAINFOR plot network." And in light of these findings, Gloor *et al*. concluded that their results lend "further support to the notion that currently observed biomass gains for intact forests across the Amazon are actually occurring over large scales at the current time, presumably as a response to climate change," which in

[16] http://www.co2science.org/articles/V12/N45/B1.php.
[17] http://www.co2science.org/articles/V13/N3/B1.php.

many of their earlier papers is explicitly stated to include the aerial fertilization effect of the historical increase in the air's CO_2 content.

In yet another contemporary paper, Lewis *et al.* (2009)[18] evaluated tropical forest inventory data, plant physiology experiments, ecosystem flux observations, earth observations, atmospheric measurements and dynamic global vegetation models, which "taken together," in their words, "provide new opportunities to cross-validate results." And in doing just that, the five researchers confirmed that both theory and experiments suggest that over the past several decades "plant photosynthesis should have increased in response to increasing CO_2 concentrations, causing increased plant growth and forest biomass." Also in this regard, they found that "long-term plot data collectively indicate an increase in carbon storage, as well as significant increases in tree growth, mortality, recruitment, and forest dynamism." In addition, they confirmed that satellite measurements "indicate increases in productivity and forest dynamism," and that five Dynamic Global Vegetation Models, incorporating plant physiology, competition, and dynamics, all predict increasing gross primary productivity, net primary productivity, and carbon storage when forced using late-twentieth century climate and atmospheric CO_2 concentration data." In addition, they stated that "the predicted increases in carbon storage via the differing methods are all of similar magnitude (0.2% to 0.5% per year)."

"Collectively," therefore, in the words of Lewis *et al.*, "these results point toward a widespread shift in the ecology of tropical forests, characterized by increased tree growth and accelerating forest dynamism, with forests, on average, getting bigger (increasing biomass and carbon storage)," which findings are just the *opposite* of what the world's climate alarmists would like to have everyone believe.

Collectively, these results point toward a wide-spread shift in the ecology of tropical forests, characterized by increased tree growth and accelerating forest dynamism, with forests, on average, getting bigger … which findings are just the opposite of what the world's climate alarmists would like to have everyone believe.

Finally moving ahead a year, Friend (2010)[19] worked with the Hybrid6.5 model of terrestrial primary production, which simulates the carbon, nitrogen, phosphorus, water and energy fluxes and structural changes in terrestrial ecosystems at hourly to decadal timescales, and at spatial

18 http://www.co2science.org/articles/V13/N9/B3.php.
19 http://www.co2science.org/articles/V13/N26/B1.php.

scales ranging from individual plants to the whole earth, while employing the climate change anomalies predicted by the GISS-AOM GCM under the A1B emissions scenario for the 2090s relative to observed modern climate. And with atmospheric CO_2 increased from 375.7 ppm to 720 ppm - a 92% increase - Friend calculated the percentage changes in terrestrial plant production that would occur throughout the world in response to (1) the projected climate changes alone, and (2) the projected *concurrent* changes in climate *and* atmospheric CO_2 concentration. And what were the results?

During this period of warming, they said it was thought by many that earth's tropical ecosystems suffered extensively because mean temperatures are surmised to have exceeded the ecosystems' heat tolerance.

But was that really so? And did the ancient warming of the world truly constitute a major problem for the planet's rainforests?

In response to the projected climate changes between 2001-2010 and 2091-2100, the *net primary production* (NPP) of the entire planet was reduced by 2.5%, with the largest negative impacts occurring over southern Africa, central Australia, northern Mexico, and the Mediterranean region, where reductions of over 20% were common. At the other extreme, climatic impacts were modestly positive throughout most of the world's *boreal forests*, as might have been expected when these colder regions received an influx of welcome heat. But when both climate *and* atmospheric CO_2concentrations were changed concurrently, the story was vastly different, with a mean *increase* in global NPP of 37.3%, driven by mean increases of 43.9-52.9% among C3 plants and 5.9% among C4 species. And in this case of concurrent increases in the globe's air temperature and CO_2 concentration, *the largest increases occurred in tropical rainforests* and C3 grass and croplands.

Contemporaneously, [Jaramillo *et al*. (2010)][20] looked *back* in time - *way* back in time - to the days of the Paleocene-Eocene Thermal Maximum (PETM) of some 56 million years ago, which they noted "was one of the most abrupt global warming events of the past 65 million years (Kennett and Stott, 1991; Zachos *et al*., 2003; Westerhold *et al*., 2009)." It was driven, as they described it, by "a massive release of ^{13}C-depleted carbon (Pagani *et al*., 2006; Zeebe *et al*., 2009)" that led to "an approximate 5°C increase in mean global temperature in about 10,000 to 20,000 years (Zachos*et al*., 2003)." And during this period of warming, they said it was thought

[20] http://www.co2science.org/articles/V14/N4/EDIT.php.

by many that earth's tropical ecosystems "suffered extensively because mean temperatures are surmised to have exceeded the ecosystems' heat tolerance (Huber, 2008)."

But was that really so? And did the ancient warming of the world *truly* constitute a major problem for the planet's rainforests?

In an attempt to answer this important question, the 29 researchers, hailing from eight different countries, analyzed pollen and spore contents and the stable carbon isotopic composition of organic materials obtained from three tropical terrestrial PETM sites in eastern Colombia and western Venezuela; and this work revealed - contrary to the prevailing wisdom of the recent past - that the onset of the PETM was "concomitant with an increase in diversity produced by the addition of many taxa (with some representing new families) to the stock of preexisting Paleocene taxa." And they determined that this increase in biodiversity "was permanent and not transient."

In discussing their findings, Jaramillo *et al*. wrote that "today, most tropical rainforests are found at mean annual temperatures below 27.5°C," and they noted that several scientists have argued that "higher temperatures could be deleterious to the health of tropical ecosystems," citing Huber (2008, 2009) and Tewksbury *et al*. (2008) in this regard. In fact, they reported that tropical warming during the PETM was actually believed to have produced *intolerable* conditions for tropical ecosystems. Nevertheless, they reiterated that at the sites that *they* studied, "tropical forests were maintained during the warmth of the PETM (~31° to 34°C)," concluding that "it is possible that higher Paleocene CO_2 levels (Royer, 2010) contributed to their success."

One year later, Rasineni *et al*. (2011a)[21] introduced their study of the subject by explaining that "excess light limits photosynthesis by photoinhibition, resulting in reduced carbon gain and also causing photo-damage (Oquist and Huner, 1993; Pastenes *et al*., 2003; Allakhverdiev and Murata, 2004; Nishiyama *et al*., 2006)," and they stated that "plants grown in tropical climates usually experience significantly high irradiance leading to the strong midday depression of photosynthesis (Hymus *et al*., 2001)." So how might that problem be overcome, they wondered.

Utilizing two open-top chambers in the Botanical Gardens of the University of Hyderabad, India - each of which contained four six-month-old specimens of the fast-growing tropical *Gmelina arborea* tree, which they maintained at optimum moisture and nutrient levels - the three scientists measured several plant physiological properties and processes related to leaf photosynthesis and photosystem II (PSII) photochemistry and photoinhibition at both ambient and elevated CO_2 concentrations (360 and 460 ppm, respectively), working with "well-expanded and light-exposed leaves randomly chosen from the upper half of the plant canopy."

This work revealed that there were no significant differences in CO_2 assimilation rates between the ambient and elevated CO_2 grown plants during early morning hours; but they discovered that, thereafter, "photosynthesis typically maximized between 0900 hours and 1000 hours in

[21] http://www.co2science.org/articles/V14/N27/B2.php.

both ambient and elevated CO_2-grown plants," which experienced net photosynthetic rates of 20 and 32.5 μmol/m^2/s, respectively, for a stunning CO_2-induced enhancement of 62%, which for the more standard CO_2 enrichment of 300 ppm would be roughly equivalent to an enhancement of 180%. Subsequently, during the following midday period of 1100-1300 hours, the rate of net photosynthesis was still significantly enhanced by about 37% (roughly equivalent to a 300-ppm induced increase of more than 100%) in the elevated CO_2 treatment, after which the difference between the net photosynthetic rates of the two CO_2 treatments once again became insignificant.

Noting that the "elevated CO_2 treatment mitigated PSII-photoinhibition through enhanced electron transport rates and through efficient biochemical reactions in leaves of *G. arborea*," Rasineni *et al*. concluded that their data "demonstrate that future increases in atmospheric CO_2 may have positive effects on photochemical efficiency in fast growing tropical tree species," allowing them to take great advantage of the high-light midday period of potential maximum growth in earth's tropical regions.

About this same time, Bonal *et al*. (2011)[22] wrote that "an increase in tree radial growth increment over recent decades in Amazonian tropical rainforests has been observed, leading to increased above-ground biomass at most study sites," citing the studies of Phillips *et al*. (1998, 2009) and Malhi *et al*. (2004), while noting that "the stimulating impact on photosynthesis of increased CO_2 concentrations in the air (Ca) could explain these growth patterns (Lloyd and Farquhar, 2008)." And in further investigating this phenomenon, the eleven researchers assessed the impacts of historical environmental changes on several leaf morphological and physiological traits of two tropical rainforest species (*Dicorynia guianensis*; *Humiria balsamifera*) that are abundant in the Guiana shield (Northern Amazonia)," working with leaf samples from different international herbariums that covered a 200-year time period (AD 1790-2004).

Once this task was completed, Bonal *et al*. stated that their results revealed "a clear response of leaf physiological characteristics to increasing Ca for both species," which were consistent with previous studies "from different ecosystems (Penuelas and Azcon-Bieto, 1992; Beerling *et al*., 1993; Van de Water *et al*., 1994; Pedicino *et al*., 2002; Penuelas *et al*., 2008), and with data from tree rings in Europe (Bert *et al*., 1997; Duquesnay *et al*., 1998; Saurer *et al*., 2004), Africa (Gebrekirstos *et al*., 2009) and in tropical rainforests (Hietz *et al*., 2005; Silva *et al*., 2009; Nock *et al*., 2011)." More specifically, they indicated that their results pointed to "an increase in water-use efficiency over recent decades of about 23.1 and 26.6% for *Humiria* and *Dicorynia*, respectively," driven mostly by increases in leaf photosynthesis. And they stated that "the range of change in water-use efficiency for these two species was consistent with many results observed not only in tropical forests (Hietz *et al*., 2005; Nock *et al*., 2011), but in boreal (Saurer *et al*., 2004) and temperate forests (Francey and Farquhar, 1982; Penuelas and Azcon-Bieto, 1992; Bert *et al*., 1997; Duquesnay *et al*., 1998)." And so it was that Bonal *et al*. concluded that the responses of the two tree species they studied to increasing Ca appeared to be "simply related to the availability of CO_2 in the air (fertilization effect)," and they indicated

[22] http://www.co2science.org/articles/V14/N39/B2.php.

that "this trend seems to be consistent with recent tree growth patterns in the Amazonian region."

Publishing yet again in the same year, Rasineni *et al*. (2011b)[23] described how they grew well-watered-and-fertilized five-week-old fast-growing *Gmelina arborea* trees out-of-doors at the University of Hyderabad, India, within open-top chambers maintained at ambient and ambient+100 ppm atmospheric CO_2 concentrations throughout the 120 days of that region's spring and summer seasons, while they periodically made numerous measurements of the trees' physical properties and physiological prowess. This work revealed that the trees in the modestly-elevated CO_2 chambers exhibited net photosynthetic rates that were 38% greater than those of the trees growing in ambient air; and aided by a significant CO_2-induced reduction in leaf transpiration rates, the mean instantaneous water-use efficiency of the leaves of the CO_2-enriched trees was 87% greater than that of the ambient-treatment trees. And as a result of these CO_2-induced plant physiological benefits, the above-ground biomass of the CO_2-enriched trees at the end of the growing season was found to be 45% greater than that of the trees growing in ambient air, while their *total* biomass (above and below ground) was 53% higher.

In discussing their findings, Rasineni *et al*. noted that elevated atmospheric CO_2 "persistently enhanced all the growth characteristics in *Gmelina*, including plant height, number of branches, internodes, internodal distance, aerial biomass and total plant biomass." And they suggested that "high sink demand and better growth dynamics" were what led to the huge *sustained* increase in carbon sequestration in the tropical deciduous tree. And so they concluded that their findings pointed to the likelihood that "there are management options for creating short-rotation deciduous tree plantations to achieve increased sequestration of carbon in a future elevated CO_2 environment."

Last of all, we come to the paper of Dick *et al*. (2012)[24], who wrote in their introduction to it that "tropical rain forest has been a persistent feature in South America for at least 55 million years," and who noted that "at times in the past,

In light of these and the many other positive findings of all of the studies reviewed above, therefore, it should be clear that as the air's CO_2 content continues to rise, tropical and sub-tropical trees will likely display enhanced rates of photosynthesis and biomass production, even under conditions of herbivory, water stress and elevated air temperature.

[23] http://www.co2science.org/articles/V14/N48/B1.php.
[24] http://www.co2science.org/articles/V16/N28/B2.php.

Amazon surface air temperatures have been higher than those today," citing Feely and Silman (2010), Hoorn *et al*. (2010), Jaramilo *et al*. (2010) and Haywood *et al*. (2011). They also reported that "experiments show that tropical plants can photosynthesize and maintain a positive carbon balance under higher temperatures than those occurring today (Krause *et al*., 2010; Way and Oren, 2010)." So the question naturally arises: How high can Amazon temperatures rise and its trees still survive?

In broaching this question, Dick *et al*. hypothesized that "the older the age of a species prior to the Pleistocene, the warmer the climate it has previously survived," noting that Pliocene and late-Miocene air temperatures of 2.6-5 million years ago (Ma) and late-Miocene air temperatures of 8-10 Ma across Amazonia were "similar to AD 2100 temperature projections under low and high carbon emission scenarios, respectively." In fact, they reported that "some 56.3 Ma during the Paleocene-Eocene Thermal Maximum (PETM), global mean temperature increased by 5-6°C over a period of <= 20 ka," citing Haywood *et al*. (2011). And they affirmed that "fossil pollen from the PETM showed an increase in tree diversity in three South American rainforest sites with abundant rainfall (Jaramillo *et al*., 2010)." Thus, they used comparative phylogeographic analyses to determine the age of the tropical tree *species* that are currently found in Amazonia. And by these means, the four researchers determined that "9 of 12 widespread Amazon tree species have Pliocene or earlier lineages (>2.6 Ma), with seven dating from the Miocene (>5.6 Ma) and three >8 Ma."

As a result of these several findings, Dick *et al*. concluded that "the remarkably old age of these species suggests that Amazon forests passed through warmth similar to AD 2100 levels [as predicted by climate models] and that in the absence of other major environmental changes, near-term high temperature-induced mass species extinction is unlikely."

In light of these and the many other positive findings of all of the studies reviewed above, therefore, it should be clear that as the air's CO_2 content continues to rise, tropical and sub-tropical trees will likely display enhanced rates of photosynthesis and biomass production, even under conditions of herbivory, water stress and elevated air temperature. And as a result, greater sequestration of carbon will also likely occur within earth's tropical and sub-tropical forests, as *the greening of the earth continues*.

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