

# INTERACTIVE EFFECTS OF CO<sub>2</sub> AND TEMPERATURE ON WOODY PLANT GROWTH



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# INTERACTIVE EFFECTS OF CO<sub>2</sub> AND TEMPERATURE ON WOODY PLANT GROWTH

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As the atmosphere's CO<sub>2</sub> concentration continues to rise, most trees will likely exhibit increased rates of photosynthesis and biomass production, which can subsequently lead to an increase in the amount of timber that will likely be required to meet the growing needs of earth's expanding human population. However, some individuals have predicted that CO<sub>2</sub>-induced global warming will counteract the growth-promoting effects of atmospheric CO<sub>2</sub> enrichment and actually *reduce* tree growth. Therefore, in order to determine if this widely-trumpeted claim has any validity, we turn to the peer-reviewed scientific literature to both report and summarize the results of several CO<sub>2</sub>-enrichment studies that were designed to reveal the concurrent effects of elevated CO<sub>2</sub> and air temperature on the growth of trees and other woody plants.

Before progressing, however, we highlight the fact that the optimum growth temperature for several plants has already been shown to rise substantially with increasing levels of atmospheric CO<sub>2</sub> (Berry and Bjorkman, 1980; Stuhlfauth and Fock, 1990; McMurtrie *et al.*, 1992; McMurtrie and Wang, 1993). This phenomenon is described at length by Long (1991), who calculated from well-established plant physiological principles that most C<sub>3</sub> plants should increase their optimum growth temperature by approximately 5°C in response to a 300 ppm increase in the atmosphere's CO<sub>2</sub> concentration. Subsequently, Cowling and Sykes (1999) produced a review of the pertinent scientific literature, demonstrating that this was indeed the case for a number of plants. Thus, one would logically expect plant photosynthetic rates to rise in tandem with concomitant increases in the air's CO<sub>2</sub> concentration and temperature, as previously documented by Idso and Idso (1994). Hence, we here proceed to see if these positive CO<sub>2</sub> x temperature interactions have been validated in the scientific literature of the past couple of decades for various tree species.

*The optimum growth temperature for several plants has already been shown to rise substantially with increasing levels of atmospheric CO<sub>2</sub>.*

In the study of [Kellomaki and Wang \(2001\)](http://www.co2science.org/articles/V4/N29/B1.php)<sup>1</sup>, birch seedlings were grown at atmospheric CO<sub>2</sub> concentrations of 350 and 700 ppm in combination with ambient and elevated (ambient plus 3°C) air temperatures; and after five months of treatment, they reported that the photosynthetic rates of the CO<sub>2</sub>-enriched seedlings were 21 and 28% greater than those displayed by their ambiently-grown counterparts at both ambient and elevated air

<sup>1</sup> <http://www.co2science.org/articles/V4/N29/B1.php>.

temperatures, respectively. In another study, [Carter et al. \(2000\)](#)<sup>2</sup> observed that a 300 ppm increase in the air's CO<sub>2</sub> content allowed leaves of sugar maple seedlings to remain green and non-chlorotic when exposed to air temperatures 3°C above ambient air temperature, while seedlings fumigated with ambient air exhibited severe foliar chlorosis when exposed to the same elevated air temperatures, which results indicate that at elevated air temperatures, rates of photosynthesis are greater and foliar health is typically better in CO<sub>2</sub>-enriched as opposed to ambiently-grown trees.

Many other studies report similar results. [Sheu et al. \(1999\)](#)<sup>3</sup>, for example, grew a sub-tropical tree at day/night temperatures of 25/20 (ambient) and 30/25°C (elevated) for six months and found that seedlings exposed to 720 ppm CO<sub>2</sub> displayed photosynthetic rates that were 20 and 40% higher, respectively, than those of their ambiently-grown controls. In addition, the CO<sub>2</sub>-induced increases in total dry weight for this species were 14 and 49%, respectively, at the ambient and elevated air temperatures. Likewise, [Maherali et al. \(2000\)](#)<sup>4</sup> found that a 5°C increase in ambient air temperature increased the CO<sub>2</sub>-induced biomass enhancement resulting from a 750 ppm CO<sub>2</sub> enrichment of ponderosa pine seedlings from 42 to 62%. In addition, [Wayne et al. \(1998\)](#)<sup>5</sup> reported that a 5°C increase in the optimal growth temperature of yellow birch seedlings fumigated with an extra 400 ppm CO<sub>2</sub> increased the CO<sub>2</sub>-induced increase in biomass from 60% to an amazing 227%. Thus, the beneficial effects of elevated CO<sub>2</sub> on tree photosynthesis and growth is often *further* enhanced by elevated air temperatures, which phenomenon can also be assessed during natural seasonal temperature changes, as documented by [Hymus et al. \(1999\)](#)<sup>6</sup> for loblolly pine and [Roden et al. \(1999\)](#)<sup>7</sup> for snow gum seedlings.

In some cases, however, there appear to be little interactive effects between elevated CO<sub>2</sub> and temperature on photosynthesis and growth in tree species. For example, when [Tjoelker et al. \(1998a\)](#)<sup>8</sup> grew seedlings of quaking aspen, paper birch, tamarack, black spruce and jack pine at atmospheric CO<sub>2</sub> concentrations of 580 ppm, they reported an average increase in photosynthetic rates of 28%, irrespective of air temperature, which varied from 18 to 30°C. And after analyzing the CO<sub>2</sub>-induced increases in dry mass for these seedlings, [Tjoelker et al. \(1998b\)](#)<sup>9</sup> further reported that dry mass values were about 50 and 20% greater for the deciduous and coniferous species, respectively, again irrespective of air temperature.

But the list of recent studies of woody plants that experience a CO<sub>2</sub>-induced enhancement of growth in response to environmental *warming* goes on and on, starting with [Hamerlynck et al. \(2000\)](#)<sup>10</sup>, who grew seedlings of the evergreen perennial shrub *Larrea tridentata* in glasshouses

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<sup>2</sup> <http://www.co2science.org/articles/V3/N15/B1.php>.

<sup>3</sup> <http://www.co2science.org/articles/V3/N2/B1.php>.

<sup>4</sup> <http://www.co2science.org/articles/V3/N14/B3.php>.

<sup>5</sup> <http://www.co2science.org/articles/V1/N4/B4.php>.

<sup>6</sup> <http://www.co2science.org/articles/V2/N18/B1.php>.

<sup>7</sup> <http://www.co2science.org/articles/V2/N19/B3.php>.

<sup>8</sup> <http://www.co2science.org/articles/V1/N4/B6.php>.

<sup>9</sup> <http://www.co2science.org/articles/V2/N7/B3.php>.

<sup>10</sup> <http://www.co2science.org/articles/V4/N18/B1.php>.

maintained at atmospheric CO<sub>2</sub> concentrations of 360, 550, and 700 ppm for one year, while half of the seedlings had water withheld from them for three months prior to a nine-day high-temperature treatment. This work revealed that elevated CO<sub>2</sub> largely offset the detrimental effects of drought and high temperature on water relations and photosynthesis in this particular species. And averaged across the entire experiment, the photosynthetic rates of seedlings grown at 550 and 700 ppm CO<sub>2</sub> were 31 and 90% greater, respectively, than rates displayed by the ambiently-grown control plants.

[Usami et al. \(2001\)](#)<sup>11</sup> grew two-year-old saplings of *Quercus myrsinaefolia*, an evergreen broad-leaved oak species, in controlled environment chambers having various atmospheric CO<sub>2</sub> concentrations and air temperatures for approximately one year, in order to study the interactive effects of elevated CO<sub>2</sub> and temperature on the development and growth of this important tree, which is widely distributed throughout Laos, Vietnam, China, Taiwan, South Korea and southwestern Japan. And in doing so, they found that in *ambient* air, 3 and 5°C increases in air temperature boosted final sapling biomass by 53 and 47%, respectively, while at elevated CO<sub>2</sub> concentrations that were either 1.5 or 2 times greater than the ambient CO<sub>2</sub> concentration, the same 3 and 5°C increases in air temperature enhanced final biomass by 110 and 140%, respectively.

[Turbull et al. \(2002\)](#)<sup>12</sup> manipulated day/night air temperatures around 4-m-tall cottonwood (*Populus deltoides* Bartr. Ex Marsh) trees growing within large experimental enclosures in order to study the effects of temperature on carbon relations. This work revealed that a 6°C increase in daytime temperature, coupled with a 10°C increase in nighttime temperature, enhanced rates of net photosynthesis by 64% and rates of dark respiration by a larger 77%. On an *absolute* scale, however, the photosynthetic carbon gains due to the daytime temperature increase were nearly *an order of magnitude greater* than the nocturnal carbon losses caused by the greater increase in nighttime temperature. Consequently, if the earth were to begin to warm again, carbon uptake by cottonwood trees should significantly increase.

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<sup>11</sup> <http://www.co2science.org/articles/V4/N48/B2.php>.

<sup>12</sup> <http://www.co2science.org/articles/V6/N5/B2.php>.

[Peltola et al. \(2003\)](#)<sup>13</sup> constructed closed chambers around 20-year-old Scots pine (*Pinus sylvestris* L.) trees growing on a low-nitrogen-containing soil; and for three years thereafter, the trees in the chambers were fumigated with air containing either 350 or 700 ppm CO<sub>2</sub> at either ambient or elevated air temperatures (about 4°C above ambient temperatures), in order to study the effects of elevated CO<sub>2</sub> and air temperature on stem development in this coniferous species when growing on a soil low in nitrogen. And what did they find? After three years of treatment, cumulative stem diameter growth in the CO<sub>2</sub>-enriched trees grown at ambient air temperature was 57% greater than that displayed by control trees grown at ambient CO<sub>2</sub> and ambient air temperature. But the trees subjected to elevated CO<sub>2</sub> *and* elevated air temperature exhibited cumulative stem-diameter growth that was 67% greater than that displayed by trees grown in ambient air at ambient air temperatures.

Working with Scots pine as well as Norway spruce (*Picea abies* (L.) Karst.), [Sallas et al. \(2003\)](#)<sup>14</sup> grew seedlings of both species for 50 days in computer-controlled environmental growth chambers in air of ambient or twice-ambient CO<sub>2</sub> concentration (normal or elevated (EC) treatments) at day/night temperature combinations of 19/12°C or 23/16°C (normal or elevated (ET) treatments), while making a host of measurements on them. And in doing so, they found that the seedlings of both species accumulated the most biomass in the combined EC + ET treatment.

[Hymus et al. \(2003\)](#)<sup>15</sup> studied net ecosystem exchange (NEE) of CO<sub>2</sub> in a scrub-oak ecosystem - 85-90% of the aboveground biomass of which was comprised of three oak species (*Quercus myrtifolia*, *Quercus geminata* and *Quercus chapmanii*) - on Merritt Island within NASA's Kennedy Space Center on the coast of central Florida (USA). This ecosystem was completely burned in January of 1996, after which sixteen open-top chambers (OTCs) were placed upon it in the spring of that year, half of which were maintained at the ambient atmospheric CO<sub>2</sub> concentration while the other half were maintained at ambient plus 350 ppm, with routine measurements being started in June 1999 and continued for 25 months through July 2001. This effort revealed that (1) the extra CO<sub>2</sub> supplied to the CO<sub>2</sub>-enriched OTCs "increased maximum NEE and the apparent quantum yield of the NEE during the photoperiod," and that (2) the magnitude of the stimulation of maximum NEE, expressed per unit ground area, "was seasonal, rising from 50% in the winter to 180% in the summer," in accord with what is known about the interactive effects of atmospheric CO<sub>2</sub> enrichment and daily, seasonal and multi-year warming.

[Turnbull et al. \(2004\)](#)<sup>16</sup> studied four- to five-meter-tall cottonwood trees (*Populus deltoides* Bartr.) that had been grown for three years in air of different CO<sub>2</sub> concentrations (420, 800 and 1200 ppm) in the three bays of the Biosphere 2 facility near Tucson, Arizona, USA, where the trees were maintained at three different nocturnal temperatures (15, 20 or 25°C) and a single constant daytime temperature (31 ± 1°C) in a short-term experiment in which *maximum photosynthesis* (A<sub>max</sub>) rates at growth CO<sub>2</sub> concentrations were routinely measured. This work revealed that as nocturnal air temperature rose from 15 to 25°C, subsequent daytime A<sub>max</sub>

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<sup>13</sup> <http://www.co2science.org/articles/V6/N9/B3.php>.

<sup>14</sup> <http://www.co2science.org/articles/V6/N27/B1.php>.

<sup>15</sup> <http://www.co2science.org/articles/V7/N7/B2.php>.

<sup>16</sup> <http://www.co2science.org/articles/V7/N22/B2.php>.

increased by 16% in air of 420 ppm CO<sub>2</sub>, 12% in air of 800 ppm CO<sub>2</sub> and 4% in air of 1200 ppm CO<sub>2</sub>, leading them to conclude that "at future elevated night temperatures suggested by global climate monitoring and modeling, net photosynthesis at elevated CO<sub>2</sub> may be increased," although it appears that the response could saturate at a CO<sub>2</sub> partial pressure somewhat in excess of 1200 ppm CO<sub>2</sub>, the latter of which values, however, is *far* greater than anyone is suggesting will *ever* be reached as a consequence of mankind's burning of fossil fuels.

But what if air temperatures get *really* hot, for some as yet unknown reason? In an earlier study that sheds some important light on this subject, [Idso et al. \(1995\)](#)<sup>17</sup> grew well watered and fertilized sour orange (*Citrus aurantium* L.) trees from the seedling stage out-of-doors at Phoenix, Arizona (USA) in clear-plastic-wall open-top chambers that were continuously maintained at mean atmospheric CO<sub>2</sub> concentrations of either approximately 400 or 700 ppm for 5.5 years, while during the warmest parts of some of the hottest days of summer, rates of net photosynthesis of fully-expanded outer-canopy sunlit leaves and the temperatures of those leaves were concurrently measured.

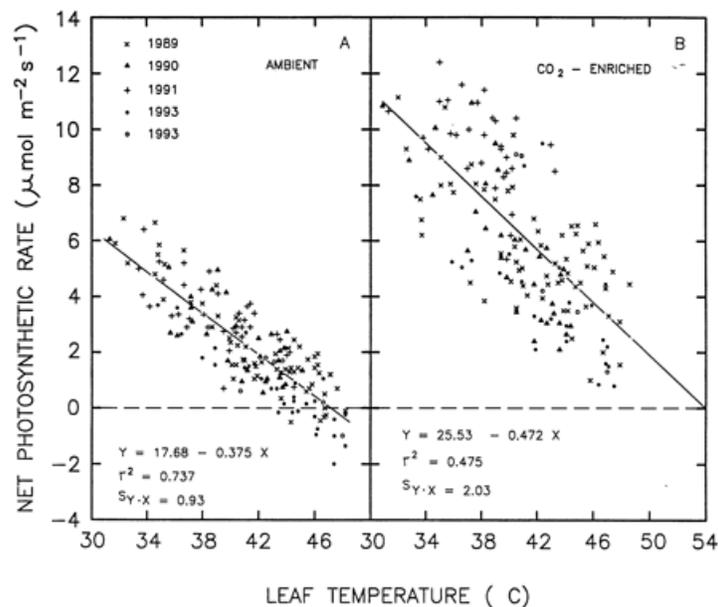
The figure below portrays the results of plotting their net photosynthesis measurements against leaf temperature. Based on the linear regression lines fit to the data, it can be determined that the 75% increase in the air's CO<sub>2</sub> content led to a 75% enhancement of leaf net photosynthesis at a leaf temperature of 31°C, a 100% enhancement at a leaf temperature of 35°C, and a 200% enhancement at 42°C. At higher leaf

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<sup>17</sup> <http://www.co2science.org/articles/V10/N14/B2.php>.

temperatures, it can also be seen that the net photosynthetic rate of the foliage growing in ambient air dropped all the way to zero at 47°C (making the CO<sub>2</sub>-induced enhancement of photosynthesis at that point essentially *infinite*), and that it actually became negative thereafter (which condition, if prolonged, would ultimately lead to plant *death*).

In the CO<sub>2</sub>-enriched trees, on the other hand, the net photosynthetic rate of the foliage was still substantial at 47°C; and the regression line for those trees suggests that their mean rate of foliage net photosynthesis likely would not have declined to zero until leaf temperature reached 54°C, which is approximately 7°C above the upper-limiting temperature for positive net photosynthesis in the trees that were grown in ambient air.



*Leaf net photosynthetic rate vs. leaf temperature for the foliage of sour orange trees growing in air of either 400 or 700 ppm CO<sub>2</sub>. Adapted from Idso et al. (1995).*

In light of these findings, it can be appreciated that if earth's air temperature continues to rise significantly in the future - for *whatever* reason - we can only hope that the air's CO<sub>2</sub> content rises right along with it; because elevated concentrations of atmospheric CO<sub>2</sub> are a *powerful antidote* for the ill - and sometimes even *deadly* - effects that might otherwise be experienced by much of earth's vegetation.

In a study that reaches somewhat similar conclusions, [Lewis et al. \(2001\)](#)<sup>18</sup> grew Douglas fir (*Psuedotsuga menziesii* (Mirb.) Franco) seedlings in sunlit chambers programmed to track either ambient atmospheric CO<sub>2</sub> concentration or ambient + 200 ppm CO<sub>2</sub>, as well as either ambient air temperature or ambient + 4°C, over a 21-month period, while they measured light-saturated rates of net photosynthesis at approximately monthly intervals. This work revealed that the extra CO<sub>2</sub> they supplied to the seedlings "increased net photosynthetic rates by an average of 21% across temperature treatments during both the 1996 hydrologic year, the third year of exposure, and the 1997 hydrologic year," while "elevated mean annual temperature increased

<sup>18</sup> <http://www.co2science.org/articles/V11/N14/B1.php>.

net photosynthetic rates by an average of 33% across CO<sub>2</sub> treatments during both years." In addition, they found that "between February and August 1996, the short-term temperature optima for photosynthesis shifted by approximately 10°C higher in both CO<sub>2</sub> treatments," and that the elevated CO<sub>2</sub> treatment "increased the short-term (minutes to hours) temperature optima for photosynthesis, as has been observed in other tree species (Idso and Idso, 1994; Eamus *et al.*, 1995)." And as a result of these observations, the four researchers concluded that "an increase of 200 ppm above current atmospheric CO<sub>2</sub> concentrations may shift temperature optima upward 3-4°C, paralleling the increase in mean annual temperatures predicted to occur during the next century," and that "by shifting temperature optima upward, elevated CO<sub>2</sub> may 'acclimate' photosynthetic processes to future temperature regimes."

More recently, [Huang \*et al.\* \(2007\)](#)<sup>19</sup> compared, synthesized and evaluated the scientific literature to that point in time, describing (1) atmospheric CO<sub>2</sub> enrichment experiments conducted on trees and (2) empirical tree-ring studies designed to determine if the growth-promoting effects of rising atmospheric CO<sub>2</sub> concentrations occur in natural forests. And as a result of their analyses, they were able to report that numerous CO<sub>2</sub>-enrichment experiments have "demonstrated significantly positive physiological and growth responses of trees to CO<sub>2</sub>, providing strong evidence to support the direct CO<sub>2</sub> fertilization effect (increased photosynthesis, water use efficiency, above- and below-ground growth) and thus allowing prediction of which ecosystems might be most responsive to CO<sub>2</sub>," with their thoughts in this regard being "warm, moderately drought-stressed ecosystems with an ample nitrogen supply," because, as they continue, "drought-stressed trees could benefit from increased water use efficiency to enhance growth." They note, however, that tree-ring studies on the cold and arid Tibetan Plateau *also* "showed significant growth enhancements as well as increased water use efficiency (24.7% and 33.6% for each species, respectively) in Qilian juniper and Qinghai spruce since the 1850s," citing as evidence for this statement the studies of Zhang *et al.* (2003), Shao *et al.* (2005), Liang *et al.* (2006), Huang and Zhang (2007) and Zhang and Qiu (2007).

One year later, [Hickler \*et al.\* \(2008\)](#)<sup>20</sup> evaluated the process-based LPJ-GUESS model of vegetation dynamics and biogeochemistry (Smith *et al.*, 2001; Hickler *et al.*, 2004) via a site-by-site comparison with the results of four *temperate* forest FACE experiments (Norby *et al.*, 2005). Then, after demonstrating that the model simulations adequately reproduced the magnitude of the FACE site measurements - a mean model-derived net primary productivity (NPP) increase of 25.9% for CO<sub>2</sub> raised to a value of 550 ppm vs. a mean measured NPP increase of 27.8% for the same CO<sub>2</sub> increase - they conducted what they called a "global forest FACE experiment" to see what the successfully-reality-tested model suggested about CO<sub>2</sub> enrichment effects on the NPP of earth's *boreal* and *tropical* forests, as well as its *temperate* forests. For the world as a whole, the model suggested that raising the air's CO<sub>2</sub> concentration to 550 ppm would increase the NPP of its temperate forests by an average of 25.7%, but that its boreal forests would only have their NPP raised by 15.1%, while its tropical forests would experience an NPP increase of 35.1%. However, Hickler *et al.* note that warming "is likely to increase NPP more in cold northern regions than close to the equator because of a greater proportional growing season extension in temperature-limited environments." Consequently, in

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<sup>19</sup> <http://www.co2science.org/articles/V11/N10/B2.php>.

<sup>20</sup> <http://www.co2science.org/articles/V11/N35/B1.php>.

the case of concomitant CO<sub>2</sub> enrichment *and* warming - the latter of which is typically greater at higher latitudes - *all* of earth's forests might well be *equally* hugely benefited.

Publishing in the same year, [Martinez-Vilalta et al. \(2008\)](http://www.co2science.org/articles/V12/N5/B2.php)<sup>21</sup> described how they used tree-ring data from the Catalan Ecological and Forest Inventory "to study the temporal variability of Scots pine stem radial growth (period 1901-1997) across a relatively large region (Catalonia, NE Spain) situated close to the southern limit of the distribution of the species." This inventory, in their words, "included a total of 10,664 plots randomly distributed throughout the forested area of Catalonia," where Scots pine was present in 30.2% of the plots and dominant in 18.4% of them. The results of this laborious undertaking, as they describe it, "showed an overall increase of 84% in Scots pine BAI [basal area increment] during the 20th century, consistent with most previous studies for temperate forests" and in harmony with the *greening of the earth* phenomenon that has accompanied the historical increase in the air's CO<sub>2</sub> content. And in this regard, they make a point of stating that "this trend was associated with increased atmospheric CO<sub>2</sub> concentration," which they interpret to be "a fertilization effect." Over the same time period, however, the five researchers note that "there was also a marked increase in temperature across the study region (0.19°C per decade on average)," and they note that "this warming had a negative impact on radial growth, particularly at the drier sites." But they determined that "its magnitude was not enough to counteract the fertilization effect."

Jumping ahead a couple of years, [Darbah et al. \(2010\)](http://www.co2science.org/articles/V13/N29/B2.php)<sup>22</sup> measured the effects of a *natural and prolonged heat wave* on the photosynthetic rates of quaking aspen (*Populus tremuloides* Michx) and paper birch (*Betula papyrifera*) trees that had been grown from the seedling stage for an additional nine years in the Free-Air CO<sub>2</sub>-Enrichment (FACE) facility near Rhinelander, Wisconsin (USA), where from 0700 to 1900 hours each day throughout the growing season, half of the trees were exposed to an extra ~190 ppm of CO<sub>2</sub>. The results of the study of the heat wave event indicated that the aspen trees "showed no visible symptoms of stress," but that the birch trees exhibited "leaf curling and then yellowing of leaves and finally leaf shedding," with trees in the control treatment dropping 33% of their leaves, while trees in the CO<sub>2</sub>-enriched treatment dropped only 20%. Also, in terms of rates of photosynthesis at saturating light intensities, they found that aspen clone 42E exhibited a 30% CO<sub>2</sub>-induced increase in the 32-35°C temperature range, but a whopping 218% in the 36-39°C range. Similarly, aspen clone 271 exhibited a 38% CO<sub>2</sub>-induced increase in the 32-35°C range, but a 199% increase in the 36-39°C range. Contemporaneously, the birch trees exhibited a 95% CO<sub>2</sub>-induced increase in photosynthetic rates in the 32-35°C range, but a 297% increase in the 36-39°C range.

In discussing their findings further, the four researchers state that they are in agreement with those of Idso and Kimball (1992), who reported that elevated CO<sub>2</sub> (ambient + 300 ppm) increased net photosynthetic rates in sour orange tree (*Citrus aurantium* L.) leaves exposed to full sunlight by 75, 100 and 200% compared to leaves in ambient CO<sub>2</sub> air at temperatures of 31, 35 and 42°C, respectively, suggesting that "elevated CO<sub>2</sub> ameliorates heat stress in tree leaves." They also note that their observations "agree with Veteli *et al.* (2007), who reported that elevated CO<sub>2</sub> ameliorated the negative effects of high temperature in three deciduous tree

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<sup>21</sup> <http://www.co2science.org/articles/V12/N5/B2.php>.

<sup>22</sup> <http://www.co2science.org/articles/V13/N29/B2.php>.

species," and that "Wayne *et al.* (1998) reported that elevated CO<sub>2</sub> ameliorated high temperature stress in yellow birch trees (*Betula alleghaniensis*)." Hence, they conclude that "in the face of rising atmospheric CO<sub>2</sub> and temperature (global warming), trees will benefit from elevated CO<sub>2</sub> through increased thermotolerance."

Contemporaneously, [Ghannoum, et al. \(2010b\)](#)<sup>23</sup> grew individual well watered and fertilized plants of two species of Australian eucalypts - faster-growing *Eucalyptus saligna* and slower-growing *E. sideroxylon* - from seed in 10-L pots filled with 9 kg of loamy-sand in naturally-lit glasshouse compartments maintained at either ambient or ambient + 4°C air temperature and three different CO<sub>2</sub> concentrations (280, 400 or 650 ppm) for a period of 140 days, while measuring various plant responses throughout the course of the experiment. Among other things, this protocol revealed that light-saturated net photosynthesis (Asat) increased by ~50% with each step-increase in the air's CO<sub>2</sub> concentration - i.e., going from 280 to 400 ppm, and going from 400 to 650 ppm - and that in the *higher* of the two temperature treatments, the optimal temperature for Asat increased by 2-7°C across the three CO<sub>2</sub> treatments. And they note, in this regard, that these results "partly explain the strong growth responses to elevated CO<sub>2</sub> and temperature observed in a previous study with the same eucalypt seedlings," citing the study of Ghannoum *et al.* (2010a).

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In introducing their study of the nature of future forests and their inhabitants, [Keenan \*et al.\* \(2011\)](#)<sup>24</sup> indicate that climate models consistently project significant *increases in temperature* and *decreases in precipitation* in the Mediterranean basin; and they say that these changes may have a large impact on current Mediterranean forests and the related ecosystem services they provide. More particularly, they state that *niche-based models* - also known as bioclimatic envelope models or habitat models - are by far the most commonly used method for predicting potential species distribution responses to future climatic changes; and they say that these models typically predict significant *negative* consequences for terrestrial plants and animals in the face of increasing atmospheric CO<sub>2</sub> concentration.

They, however, prefer *process-based models*, which describe eco-physiological processes ranging from purely empirical relationships to mechanistic descriptions based on physical laws. And they write that *these* models - supported by experiments and growth and yield surveys - "suggest that global warming will have a positive impact on forest productivity (van der Meer *et al.*, 2002; Nigh *et al.*, 2004; Norby and Luo, 2004; Briceño-Elizondo *et al.*, 2006; Gaucharel *et al.*,

<sup>23</sup> <http://www.co2science.org/articles/V14/N2/B3.php>.

<sup>24</sup> <http://www.co2science.org/articles/V14/N8/B1.php>.

2008), due to the direct fertilization effect of increased CO<sub>2</sub> and indirect effects such as lengthening of the growing period." Thus, to elucidate the difference in results obtained by employing these two approaches to divining the future, the five researchers assessed and compared the projections of each of them when applied to stands of three forest species (*Quercus ilex*, *Pinus halepensis* and *Pinus sylvestris*) that have widely contrasting distributions in continental Spain.

In pursuing this course of action, Keenan *et al.* found that CO<sub>2</sub> fertilization through projected increased atmospheric CO<sub>2</sub> concentrations tends to *increase* forest productivity in mechanistic process-based models (despite increased drought and presumed temperature stress) by up to three times that of the non-CO<sub>2</sub> fertilization scenario by the period 2050-2080, in stark contrast to projections of *reduced* habitat suitability based on niche-based models for the same period. Thus, they write that their results show that "previous reports of species decline in continental Spain (e.g. Benito-Garzon *et al.*, 2008) may be overestimated due to two reasons." One of these is the use of only one predictive niche-based model, and the other is the failure to account for positive effects of CO<sub>2</sub> fertilization in a warming world. And they add that similar studies in other regions that do not consider these two aspects, are also potentially overestimating species decline due to climate change, noting that "niche-based model results also likely overestimate the decline in [habitat] suitability," and they therefore conclude that "an organism's niche must be modeled mechanistically if we are to fully explain distribution limits," additionally citing the work of Kearney (2006) in this regard.

In the contemporary study of [Osorio et al. \(2011\)](http://www.co2science.org/articles/V14/N27/B3.php)<sup>25</sup>, impacts of drought and high-temperature stresses on photosynthesis, energy partitioning and membrane lipids - as well as the potential ability of Carob or St. John's (*Ceratonia siliqua*) trees to attenuate oxidative damage - were investigated in seedlings growing within controlled-environment chambers, where they were rooted in 3-dm<sup>3</sup> pots filled with a 2:1 mixture of a fertilized substrate and natural soil, and where they were maintained under two thermal regimes - low and high temperature (LT: 25/18°C; HT: 32/21°C) - and three soil water conditions (control, water stress and rewetting), while numerous physiological and biochemical plant properties and processes were repeatedly monitored. This work revealed that the decrease in net photosynthesis (*P<sub>N</sub>*) caused by drought was 33% in the LT chamber and 84% in the HT chamber. *However*, they found that "the negative effects of soil drying on *P<sub>N</sub>* and stomatal conductance of HT plants were no longer detected 36 hours following rewatering." And they add that "although *C. siliqua* seedlings exhibit clear signs of oxidative stress under drought and high temperature, they retain a remarkable ability to quickly restore normal physiological activity upon rehydration," so much so, in fact, that the five Portuguese scientists say they "can state that although *C. siliqua* seedlings exhibit clear signs of oxidative stress under drought and high temperature, they retain a remarkable ability to quickly restore normal physiological activity upon rehydration, which let us believe that they can satisfactorily deal with predicted climate warming and increased soil drying in the Mediterranean area."

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<sup>25</sup> <http://www.co2science.org/articles/V14/N27/B3.php>.

Inching ever closer to the present, [Wertin et al. \(2012\)](#)<sup>26</sup> examined the influence of elevated temperature (ambient + 2°C) and atmospheric CO<sub>2</sub> concentration (700 ppm), applied singly and in combination, on biomass accumulation and the temperature response of net photosynthesis (Anet) and leaf respiration (Rd) of loblolly pine (*Pinus taeda* L.) seedlings grown simultaneously at a northern and a southern site within the species' range, where the long-term mean growing season temperature (from February through October) at the *cool* site was 15.2°C and at the *warm* site was 21.5°C, and where the well watered and fertilized seedlings were grown over the course of two consecutive years in half-cylindrical polyfilm-enclosed chambers located in open fields. And as a result of this effort, they determined, as they describe it, that (1) "biomass accumulation was substantially greater at the warmer site compared with the cooler site regardless of treatment," that (2) "at each site, biomass accumulation was greater in the elevated temperature treatment compared with the ambient treatment," and that (3) "elevated CO<sub>2</sub> increased biomass accumulation and Anet at both sites and in both temperature treatments." In concluding their report, therefore, the five University of Georgia (USA) researchers state that their study "provides an indication that future projected increases in CO<sub>2</sub> and air temperature of 700 ppm and +2°C, respectively, are likely to increase loblolly pine growth in most, if not all, of its current range." And they state that "the large number of studies that have reported an increase in tree growth in elevated growth temperatures compared with current ambient temperature (Way and Oren, 2010) suggest that other species may respond similarly."

Publishing close to the same time on this subject were [Ameys et al. \(2012\)](#)<sup>27</sup>, who wrote as background for their work that in studies where the air's CO<sub>2</sub> content has been *doubled*, "increases in net photosynthesis were reported ranging from 43% to 192% in *Pinus taeda* (Teskey, 1997; Tissue et al., 1997; Ellsworth, 1999; Wertin et al., 2010; Frenck et al., 2011) and from 30% to 256% in *Quercus rubra* (Kubiske and Pregitzer, 1996; Anderson and Tomlinson, 1998; Cavender-Bares et al., 2000)." Likewise, they say that "generally, an increase in air temperature also has a positive effect on net photosynthesis and growth," citing Sage and Kubien (2007) and Way and Oren (2010). But how might loblolly pine and northern red oak trees respond to the *extreme heat waves* that are often predicted to occur in a future CO<sub>2</sub>-enriched world?

In their desire to answer this question, and working with the most recent fully-developed leaves of well watered and fertilized seedlings of *Pinus taeda* and *Quercus rubra* grown in 7.6-L pots out-of-doors at Athens, Georgia (USA) within polyethylene chambers maintained at ambient and elevated air temperatures (Tamb and Tamb + 3°C), as well as seven-day heat waves consisting of a biweekly +6°C heat wave or a monthly +12°C heat wave - which treatments were maintained throughout the growing season - Ameys et al. measured rates of net photosynthesis before, during and after the many mid-summer heat waves they created. In doing so, they found that "an immediate and significant decline in net photosynthesis was observed in seedlings that were subjected to a +12°C heat wave, but not in seedlings subjected to a +6°C heat wave." They also found that "after the third day of the +12°C heat wave, net photosynthesis values stabilized at positive values and did not show signs of further reduction,

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<sup>26</sup> <http://www.co2science.org/articles/V15/N50/B2.php>.

<sup>27</sup> <http://www.co2science.org/articles/V16/N11/B2.php>.

indicating that the photosynthetic apparatus did not accrue additional stress or damage as the heat wave continued." In light of these findings, therefore, they concluded that "if soil moisture is adequate, trees will experience negative effects in photosynthetic performance only with the occurrence of extreme heat waves." And in light of the fact that "elevated CO<sub>2</sub> diminished these negative effects," they opine that "the future climate may not be as detrimental to plant communities as previously assumed."

In concluding this literature review, it is instructive to consider the case of the Paleocene-Eocene Thermal Maximum or PETM of some 56 million years ago, which according to [Jaramillo et al. \(2010\)](#)<sup>28</sup>, "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 presumed driven, as they describe it, by "a massive release of <sup>13</sup>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 planetary warming, they say it was thought 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? 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."

*It is becoming ever more clear that greater warmth and atmospheric CO<sub>2</sub> concentrations are not the "twin evils" that the world's climate alarmists typically make them out to be. Quite to the contrary, they are just what earth's ecosystems need, in order to make them both more stable and more productive.*

<sup>28</sup> <http://www.co2science.org/articles/V14/N4/EDIT.php>.

In discussing their findings, Jaramillo *et al.* write that "today, most tropical rainforests are found at mean annual temperatures below 27.5°C," and they say that several scientists have argued that "higher temperatures could be deleterious to the health of tropical ecosystems," citing Stoskopf (1981), Bassow *et al.* (1994), Lewis *et al.* (2004), Huber (2008, 2009) and Tewksbury *et al.* (2008) in this regard. In fact, they report that tropical warming during the PETM is actually believed to have produced *intolerable* conditions for tropical ecosystems, citing the writings of Huber (2008, 2009). Nevertheless, they reiterate that at the sites that they studied, "tropical forests were maintained during the warmth of the PETM (~31° to 34°C)," and they thus conclude that "it is possible that higher Paleocene CO<sub>2</sub> levels (Royer, 2010) contributed to their success."

In regard to this hypothesis, such would indeed appear to be the case, in light of what is now the well-established *fact* that most woody plants tend to exhibit their greatest photosynthetic rates at increasingly warmer temperatures as the air's CO<sub>2</sub> content continues to rise, as is confirmed by the many studies of this phenomenon discussed above. And in light of Jaramillo *et al.*'s findings, it is becoming ever more clear that greater warmth and atmospheric CO<sub>2</sub> concentrations are not the "twin evils" that the world's climate alarmists typically make them out to be. Quite to the contrary, they are just what earth's ecosystems *need*, in order to make them both more *stable* and more *productive*, which characteristics are absolutely essential for sustaining the still-increasing human population of the planet, as well as preserving what yet remains of what one could call *wild nature*.

In conclusion, the scientific literature of the past few decades continues to indicate that as the air's CO<sub>2</sub> content rises, trees will likely exhibit enhanced rates of photosynthesis and biomass production that will not be negated by any global warming that might occur concurrently. In fact, if the ambient air temperature rises, the growth-promoting effects of atmospheric CO<sub>2</sub> enrichment will likely rise right along with it. Thus, the future ability of earth's trees to produce greater amounts of biomass and, therefore, more timber products to meet the increasing needs of earth's expanding human population, looks promising indeed, just as long as the atmosphere's CO<sub>2</sub> concentration continues to rise.

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