

An investigation of the effect that new leaf respiration has on net ecosystem exchange models

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Abstract Understanding the role that tropical rain forests play in the global carbon cycle is important for understanding both the terrestrial ecosystems role in the carbon balance and the global warming trend in general. In this study, measurements of leaf respiration and soil respiration were taken in a tropical rainforest near Santarem, Brazil. These measurements were scaled up to the canopy level using parts of the De Pury model and compared to nearby eddy flux measurements. The model predicted 5 to 8 micromoles carbon per sq. m s while the eddy flux towers measured 20 to 30 micromoles carbon per sq. m s. The source of this difference is still not understood. Some species of leaves less than a month old were found to respire carbon dioxide, although this factor is generally not included in carbon models. When included in the model, new leaf respiration did not greatly change the net ecosystem exchange outcome, but it potentially could make a small change if more accurate models are used.

Introduction

Anthropogenic carbon inputs into the atmosphere in the form of burnt fossil fuels are now at the center of a debate over the potential climate changing effects of these gasses (Schimel 1994). Emissions of carbon dioxide from fossil fuel sources averaged 5.5 Gt. of carbon per year in the 1980's and tropical deforestation added an additional 1.6 Gt. of carbon per year, but the atmosphere only gained 3.2 Gt. of carbon per year. The oceans were believed to have taken up 2.0 Gt. of carbon per year and regrowth of forests in the Northern hemisphere might absorb an additional .5 Gt. of carbon per year. A sum of 1.4 Gt. of carbon per year is therefore unaccounted for and is often referred to as "the missing sink" (Schimel 1994). This missing sink might be attributed to several terrestrial processes such as CO₂ fertilization of plant growth (Idso and Idso 1994), forest regrowth (Melillo et al. 1988), or N deposition (Peterson and Melillo 1985). Since there is still a great deal unknown about these terrestrial ecosystem sinks, it is important to further quantify them in order to understand their effect on global warming.

Several tools have emerged to study these terrestrial processes such as chamber systems, which are portable machines to measure carbon flux, eddy flux systems, which are instruments above the canopy that measure net ecosystem exchange, and a variety of models that model the overall carbon balance of terrestrial ecosystems. A comparison of direct measurements of CO₂ fluxes of soils and leaves using chamber systems to the eddy covariance method has established that eddy flux measurements can provide an accurate long-term measurement of carbon sequestration in a forest (Goulden et al 1996). Several models of canopy carbon flux have been developed that use these eddy flux towers to verify their accuracy (Chen et al 1999). Many of these models and measurements have come to focus on the Amazon Basin in Brazil because of its importance to the terrestrial carbon cycle. Brazil contains 10% of the world's forest area and 49×10^{15} grams of carbon in forest vegetation, which is 23% of the total tropical vegetation C pool (Dixon 1994).

Previous studies of the Amazon basin indicate that photosynthesis provides a net sink for atmospheric CO₂ during the day but respiration and decay are a net source at night. The daytime uptake was estimated at $9(+4)$ kg C/ ha hr, whereas soils emitted CO₂ at a rate of $1.8(+-.2)$ kg C/ ha hr (Wofsy 1988). These measurements were done by measuring vertical gas profiles of CO₂ in the canopy and direct measurements of CO₂ emissions from the soil. Summing up the day and night carbon flux over a long period of time will give an indication if the forests are a

net source or sink.

New measurements using the eddy covariance technique in the Amazon basin have provided an opportunity to study carbon sequestration of the Amazon. Estimates of carbon flux from the eddy towers can now be used to study the accuracy of models predicting overall carbon balance in tropical rain forests. In this study both photosynthesis and soil respiration measurements were taken and will be compared, through the use of a model, to the eddy flux data from the same area. Daytime leaf respiration of new leaves (less than a month old) was also measured to determine if it is a significant source of daytime CO₂ even though it is generally not considered in models.

Certain types of leaf respiration are in fact accounted for in most models. Leaves continually respire both at night and day, and this form of leaf respiration comprises 50-70% of above ground (autotrophic) respiration and may consume 9-22% gross primary production (Linder 1985; Malhi et al. 1999; Yoda 1983). However, this respiration considers mainly nighttime leaf respiration and does not include respiration from new leaves. In this study, respiration from new leaves will be quantified and along with soil respiration measurements and leaf photosynthesis measurements will be put into a simple model and compared with overall carbon flux of the forest, that will be determined through comparison to nearby eddy flux data.

Methods

This study was conducted near the city of Santarem (55W; 4S) in the state of Para, Brazil, in the Tapajos national forest (approximately 70 km south of Santarem). The vegetation consisted of a closed tropical rainforest with canopy emergent on flat uphill terrain (Hernandez Filho 1993) with a wet season (December to June) and a dry season (July to November). Measurements were taken from June to August 2001 and thus spanned the end of the wet season and the start of the dry season. Leaf Area Index, which is the amount of leaf area to ground area, averaged 4.5 at the end of the wet season and was measured by both direct litterfall and measurements of the extinction of photosynthetic photon flux density by the forest canopy (Goulden, personal communication).

Soil Respiration Measurements were taken with a Licor 6200 (Licor), which is a machine that measures the carbon dioxide flux from either soil or leaves. Soil respiration, which is the amount of carbon dioxide emitted from the ground through such processes as microbial activity,

root respiration, and decaying material, was quantified by weekly visits to 50 sites that ranged from 25 to 50 meters from each other in the shape of a grid (see figure 1). In early June a collar composed of 10 cm diameter PVC pipe was placed at each site so that approximately 10 cm remained above ground while 10 cm was below ground. These collars ensured that each week the same spot was visited. Three measurements were taken over a period of two to five minutes for each collar each week and then averaged.

Leaf Photosynthesis At the site was a large scaffolding walk up tower (45 meters tall) which provided access to the top of the canopy. Using the same Licor 6200 with a different instrument head for photosynthesis, measurements of photosynthesis at three distinct heights in the canopy were also taken on a weekly basis. At heights of 6 meters, 30 meters, and 45 meters, measurements of carbon dioxide flux were taken on several leaves including both new and old leaves. New leaves are defined as those less than a month old and of a lighter or at times reddish or clear color depending on the species. The same leaf was marked so that I could return to measure the same leaf so as to avoid carbon flux differences between leaves. These measurements were taken more sporadically than the soil respiration ones with some weeks having more than one measurement and other weeks not having any. They were taken over a span of seven weeks.

The model Leaf photosynthesis measurements and soil respiration measurements were scaled up to the canopy level using parts of a model formulated by De Pury and Farquhar (1997) in order to get a rough estimate of canopy photosynthesis. Models of this sort do not generally use sampled data because they are trying to predict carbon flux without having to take measurements. Thus, the sample data taken in this study is used in place of many of the components normally calculated for the model. However, many components of the model were still used, such as solar elevation angle and percentage irradiance absorbed by the leaves. These components will detail the percentage of direct beam light absorbed by the leaves (the actual calculation is shown in the results section) on any given day or time of day. This percentage will give the amount of leaves photosynthesizing at the highest level. The remaining leaves will photosynthesize at a lower level using diffuse light. The amount that the leaves photosynthesize at certain light levels will be determined using the data collected from different heights in the canopy. This will give a rough estimate of how much carbon the forest is taking in through photosynthesis. If soil respiration is subtracted from this number, an idea of how much carbon

this mature tropical forest takes in during daylight hours which is also called net ecosystem exchange, can be determined.

There are many potential sources of error in predicting the overall carbon flux of the forest in this manner. First of all, bole respiration, which is the respiration from the trunks and stems of trees is not taken into account, although this is traditionally only a small percentage of the overall carbon balance. Secondly, as is the case with any model, small errors in leaf measurements could be compounded when scaled up to the canopy level. However, at this same site is an eddy covariance flux tower that measures the overall carbon flux of the area. This tower works by measuring instantaneous wind speed with a three dimensional sonic anemometer and an infrared gas analyzer to measure water vapor and CO₂ concentrations. This method has been verified by comparison to other measurements to give accurate daytime predictions of carbon flux (Goulden 1996). In this study, measurements from this eddy flux tower will be used to estimate the accuracy of the model previously described.

New Leaf Respiration Leaves respire both at nighttime and daytime, but nighttime measurements are not included in this model and daytime respiration is generally masked by photosynthesis because more carbon dioxide is entering the leaf for photosynthesis than leaving through respiration. Models generally include these forms of leaf respiration, however no models could be found that accounted for respiration that was seen in certain new leaves measured in this study. At three levels of the canopy, 6m, 30m and 45m newly formed leaves, less than a month old, were measured for photosynthesis. These leaves measured were often at the same height and under the same light conditions as the older leaves measured at the same height. Unlike previous models, leaves were separated into two types: new leaves and old leaves. The data given in the results section suggest that certain new leaves tend to respire versus photosynthesize. This could be significant for two reasons. First of all, if true that new leaves represent a net output of carbon instead of taking in carbon, then including this parameter into a net ecosystem exchange model should improve its accuracy. Secondly, since new leaves generally will grow above old leaves they have the potential to block the direct beam light received by these old leaves. This could further reduce the net carbon uptake by the forest because the older photosynthesizing leaves will receive less light. However, this second possibility will not be addressed in this study because it was not quantified in the measurements. In this study, two forms of the model will be compared to the eddy flux data, first the form of the

model that does not take into account new leaf respiration and second, a form of this model that does include this new parameter of new leaf respiration. The two models are then compared to see which more accurately corresponds to the eddy flux data.

Results

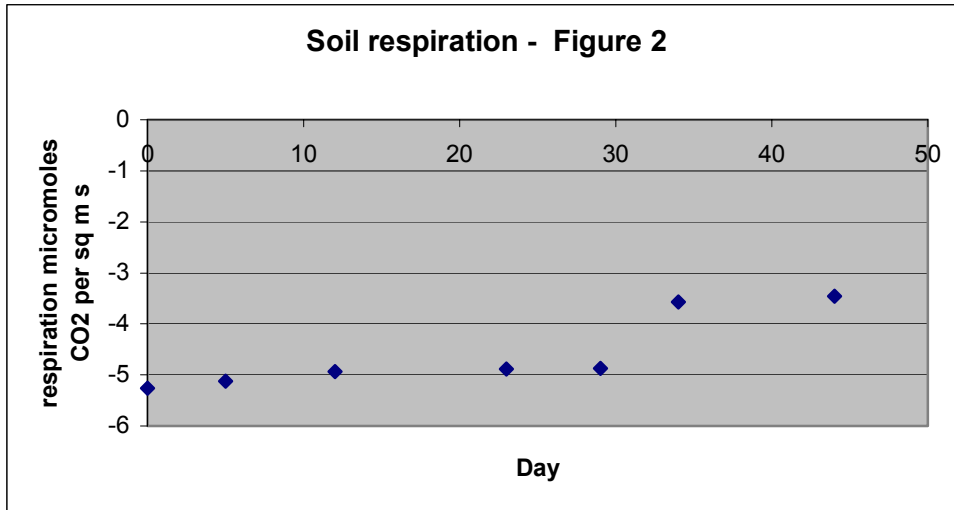
Soil respiration The soil respiration varied a great deal from site to site. When an average of the data was taken over all seven weeks, the means ranged from a high of 14.2 micromoles CO₂ per sq. m sec (SD 7.1) to a low of 1.47 micromoles CO₂ per sq. m sec (SD .29). The averages from all 50 sites are shown in the figure below. The top line shows grid number, the second line shows mean soil respiration, and the third line shows the standard deviation of the mean. The measurements were taken over a seven week period.

Figure 1 - Soil respiration in micromoles CO₂ per sq m s

K12 -3.2 SD1.6		I12 -4.15 SD1.4		G12 -3.6 SD1.0		E12 -5.7 SD1.3		C12 -3.1 SD.5
		I11 -3.0 SD.98	H11 -4.7 SD.46	G11 -3.4 SD.65	F11 -4.6 SD1.3	E11 -3.1 SD.7		
K10 -2.77 SD1.8		I10 -4.0 SD1.6	H10 -5.0 SD1.6	G10 -4.7 SD1.8	F10 -5.4 SD1.1	E10 -7.5 SD3.4		C10 -4.2 SD.72
		I9 -4.2 SD.96	H9 -3.1 SD.64	G9 -5.2 SD.88	F9 -3.9 SD2.3	E9 -3.1 SD.56		
K8 -3.3 SD1.1		I8 -6.1 SD1.8	H8 -5.9 SD.86	G8 -3.7 SD.65	F8 -2.7 SD.52	E8 -4.6 SD.68		C8 -3.2 SD.95
		I7 -3.02 SD.31	H7 -5.9 SD.52	G7 -1.6 SD.27	F7 -4.1 SD1.3	E7 -5.5 SD1.4		
K6 -7.9 SD4.2		I6 -6.3 SD1.4	H6 -4.97 SD1.0	G6 -5.2 SD1.9	F6 -6.2 SD1.8	E6 -2.9 SD1.0	D6 -10.0 SD7.7	
		I5 -3.63 SD.63	H5 -3.87 SD1.7		F5 -2.9 SD.42	E5 -1.47 SD.29		
K4 -9.2 SD1.3		I4 -8.4 SD1.0		G4 -5.8 SD1.4		E4 -14.2 SD7.1		C4 -3.76 SD1.0

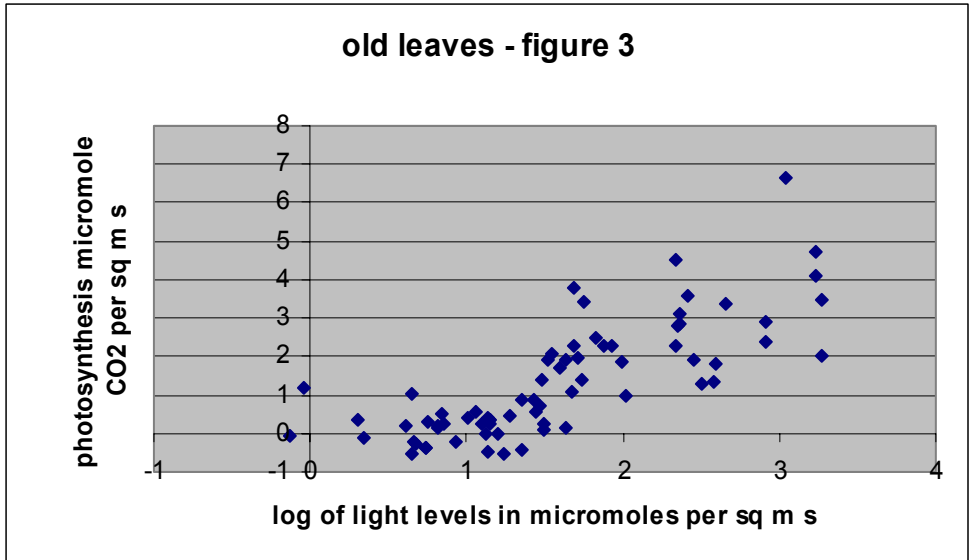
25 by
25 m

Each square has sides of 25 meters. Soil respiration varied quite a bit among different sites on the grid but remain relatively stable from week to week at each individual site as is demonstrated by the fairly low standard deviation at most sites. For example, E8 has a mean of -4.6 and a standard deviation of .68 so over the seven weeks, when data was collected, it always stayed near -4.6 and did not vary much. However, between sites such as E4 and E5, the mean varied drastically. If an average of all 50 sites is taken (meaning all of the numbers on the grid shown in Figure 1 are averaged each week), each week a gradual decline in the average release of carbon dioxide can be seen (Figure 2). The numbers are negative to reflect the fact that carbon dioxide is being given off from the soil.

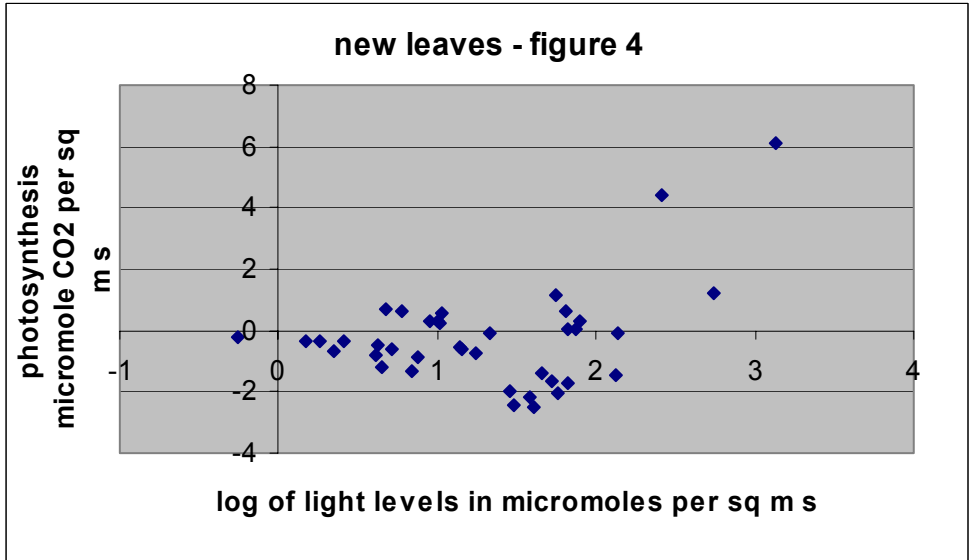


The soil respiration above gives a rough idea of how much the soil was respiring for the overall region on any given day. This average number from all fifty sites is later used in the model. All carbon fluxes are in micromoles CO₂ per sq. m sec and day one is considered to be the first day soil respiration measurements were taken, June 27, 2001.

Leaf photosynthesis and respiration Photosynthesis measurements were much less stable than soil respiration measurements and varied a great deal over days or even minutes. For this reason photosynthesis is presented not by day or week but according to photon flux density (light) which was measured automatically on the Licor whenever photosynthesis measurements were taken. Leaves were divided up into two categories, new leaves and old leaves and then photosynthesis was compared to the log of the light flux. The photosynthesis appears flat up until a little more than 1 (\log_{10} of 10 = 1) which corresponds to about 10 micromoles of light per sq. m sec. After this, photosynthesis appears to increase linearly on figure 3 as light levels increase. The overall average of leaf photosynthesis for older leaves is positive at 1.5 micromoles CO₂ per sq. m s.

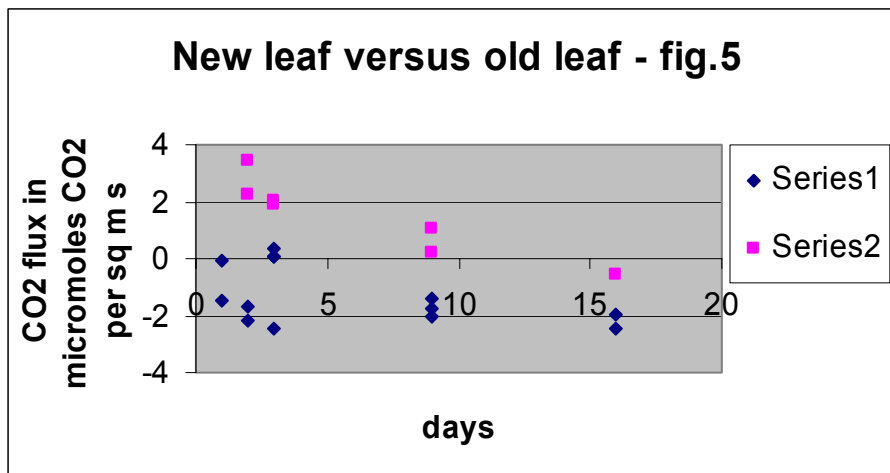


When newer leaves are displayed on a similar graph, their photosynthetic rates do not appear to increase with increasing light levels in the same way as the old leaves. Old leaves showed a clear increase in photosynthetic rate at light levels above 10 micromoles per sq m sec (Figure 3), whereas new leaves showed no such increase until possibly 100 micromoles per sq m sec where only three data points exist (Figure 4). The overall average of the photosynthesis for all the new leaves (-.25 micromoles CO₂ per sq. m s) is a net negative which means they are respiring instead of photosynthesizing.

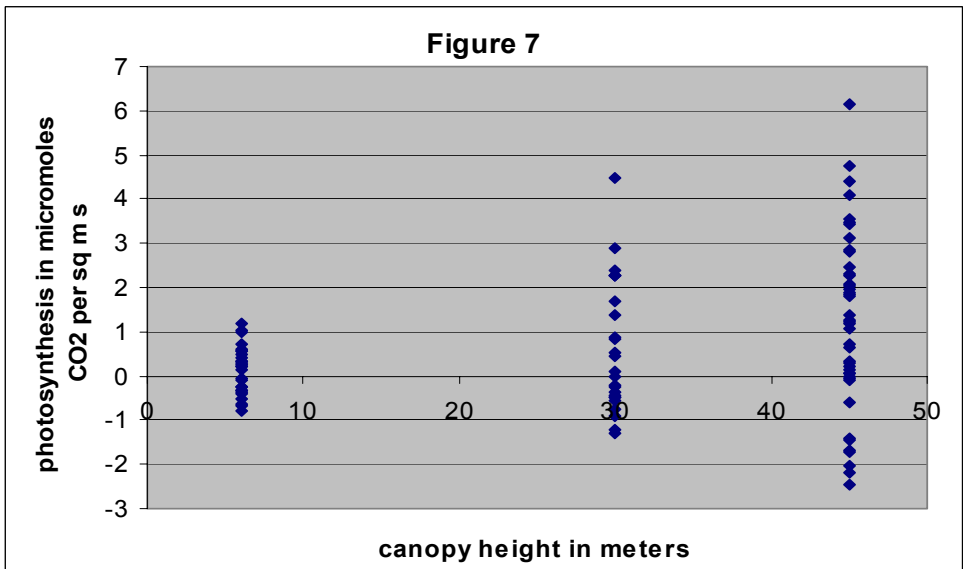
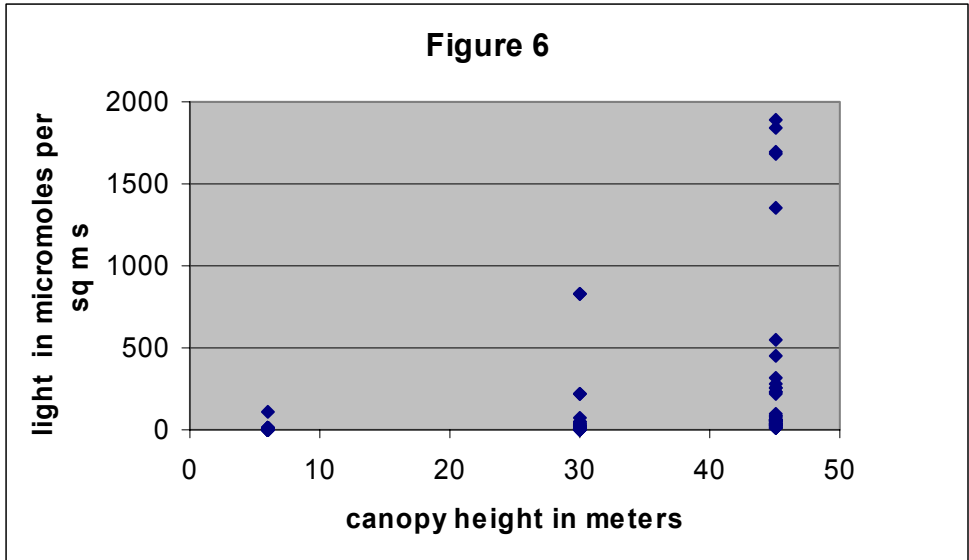


The final three data points suggest that new leaves only photosynthesize past 2 which is 100 micromoles per sq. m. Unfortunately very few measurements were taken above 100 micromoles

per sq. m. sec so it is difficult to say whether those three points are an anomaly or a trend. However, since measurements of these leaves took place over several weeks another possibility is that over time some of the leaves aged sufficiently to begin photosynthesizing. Those last three data points could be either mature leaves or evidence that new leaves need more light to begin photosynthesizing. A comparison between a young (series 1) and old leaf (series 2) on the same tree at the same height (45m) is shown above over a period of two weeks. Light levels on the leaves were roughly the same for both because they were both near each other and at a similar height. This graph demonstrates that in this particular tree species this new leaf can respire up to two weeks. It also shows no indication that respiration of this particular leaf is decreasing.



In order to model canopy photosynthesis a range of how much light the forest receives at different levels is important. The Licor 6200 had a light flux analyzer on it and thus light levels at the three levels of the canopy where measurements were taken are shown in the below diagram. There is a wide range of light levels shown at the top of the canopy in the graph due to clouds occasionally blocking the canopy from receiving direct beam sunlight and instead, diffuse light is received. The bottom of the canopy shows far less variation because it never receives much direct beam sunlight and it is more often in the diffuse form of light. There are occasional sun flecks to the bottom layers but these were not captured in the bottom layers of the canopy because very few reached the bottom of the canopy.



As was seen in previous graphs, light level is a factor that controls photosynthesis. Light levels decrease in the canopy compared to above the canopy and thus, so does photosynthesis. The following graph shows the range of photosynthesis at the three different levels where measurements were taken. Both photosynthesis and leaf respiration tended to be greater at the top of the canopy (45m) than the bottom of the canopy (6m) as can be seen in Figure 7 where both photosynthesis and respiration reach more extreme levels at 45 meters than 6 meters. This can probably be attributed to both increased sunlight and increased growth of new leaves at the top of the canopy. At six meters the average is .13 (SD.54), at 30 meters the average is .62 (SD1.5), and at 45 meters the average is 1.2 (SD 2.0). This data gives an idea of how light and photosynthesis vary within the canopy and this will be used to model canopy photosynthesis.

The Model When an average is taken from the soil respiration data and added to canopy photosynthesis calculated using parts of the de Pury model, a number can be used to compare overall carbon flux against the eddy flux data. In order to calculate overall carbon balance of the forest, it is necessary to use a model. However, most models do not have soil respiration or leaf photosynthesis measurements because their goal is to calculate the overall carbon balance without the work of taking measurements. Since I already have both soil respiration and leaf photosynthesis data I only need to use parts of the models and I can use the data that I took for the rest.

One of the most important things taken from the model was an equation that would determine how much beam light is used by a canopy. The first part of this equation is calculating solar elevation angle. This equation is based on time of day, day of year, position on the globe, and a factor that corrects for time zones. With this information the exact position of the sun can be determined. Since the field site is so close to the equator (4 degrees), the day of year is not important. To determine the hour angle of the sun: $h = \Pi(t-t_0)/12$. t =time of day, t_0 =solar noon (this corrects for differences between time zone time and real time). Solar declination angle = $S = -23.4 * \Pi/180 * \cos[2\Pi(d+10)/365]$. D = day. $\lambda=(90\text{-latitude})/90$. To get solar elevation angle = $\sin B = \sin \lambda \sin S + \cos \lambda \cos S \cos h$. Once $\sin B$ is found, it can be placed in an equation that allows us to determine light penetration through an “ideal canopy”. This equation is based on Beers’s law: $1 - \exp(-(.5/\sin B) * LAI)$. LAI is leaf area index which is how many leaves per area ground and at my field site it averaged 4.5, and .5 is a clumping constant that assumes that leaves are randomly distributed. The LAI was measured according to the procedure in the methods but the clumping constant was figured by looking at the canopy type and was not calculated. The following table shows different percentages of irradiance absorbed at different days of the year, on different times of the day and at different LAI’s at Santarem, Brazil.

Table 1 - % irradiance absorbed

Day of year	Time of day	Leaf area index	% Irradiance absorbed
June 18 = day 169	7:00 AM	4.5	.99
June 18 = day 169	12:00 PM	4.5	.918
Dec. 31 = day 365	7:00 AM	4.5	.99
Dec. 31 = day 365	12:00 PM	4.5	.909
June 18 = day 169	7:00 AM	1.5	.967
June 18 = day 169	12:00 PM	1.5	.565

As can be seen in table 1, day of year does not have a large effect, but both time of day and LAI can affect irradiance absorbed. LAI did not actually change to an average of 1.5, this is just shown to demonstrate how irradiance absorbed can be affected by LAI. “Irradiance absorbed” means that on June 18, at noon, if the leaf area index is 4.5, about 92% of the direct beam sunlight will be captured by leaves. The following procedure is modified from a model (Baldocchi 1986). Thus, to calculate canopy photosynthesis on a clear day at noon, I will assume that 92% of direct beam energy is captured which allows leaves to photosynthesize at their highest level. At lower levels in the canopy, leaves depend on diffuse light (this is light reflected off clouds or in the sky) which will lead to lower photosynthetic levels. So an estimation of canopy photosynthesis on a bright clear day can be made using figure 3 of photosynthesis of old leaves and figure 6 of different light levels in the canopy. If LAI is 4.5 and 92% of irradiance is absorbed .92 LAI is operating at highest photosynthetic levels and 3.58 LAI is using diffuse sunlight. If 100% of irradiance was absorbed then 1 LAI would operate at highest photosynthetic level. More than 1 LAI operating at highest level is not possible because then the leaves would start to shade each other.

Looking at figure 3 or 7, highest photosynthetic rates at the top of the canopy are between 5 and 6 micromoles CO₂ per sq m s. Looking at figure 7 photosynthesis rates seem to decline linearly as you go further down the canopy. From this assumption a very simple linear equation can be used to describe photosynthetic reaction to diffuse light lower in the canopy. Figure 7 has

average rates of about 2 micromoles CO₂ per sq m s. at 30 meters (not including the negative respiration points which will be accounted for later on) and between .5 and 1 micromoles CO₂ per sq m s. at 6 meters. From these points I will make the simplistic assumption that photosynthetic rates from diffuse radiation vary as a low estimate from .5 at the bottom of the canopy to 2.5 at just slightly below the top of the canopy. A high estimate would be between 1 at the bottom to 3 at the top of the canopy. A further simplistic assumption is that this will range between 0 LAI at the bottom and 3.58 LAI at the top. From these assumptions a simple linear equation is formed: Low estimate of photosynthesis = $.5 + ((2.5-.5)/3.58)*LAI$, High estimate of photosynthesis = $1 + ((3-1)/3.58)*LAI$. If we integrate this from 0 to 3.58 we find a photosynthetic capacity of between 5.3 and 7.3 micromoles CO₂ per sq. m s. from diffuse light. This, of course is a very rough estimation with many simplifying assumptions.

If we assume a top photosynthetic ability of between 5 and 6 micromoles CO₂ per sq m s. for direct beam light because in full beam light leaves tend to photosynthesize at their highest levels, then: $6*.92=5.52$ or $5*.92=4.6$. If we then add the photosynthesis from the direct beam light, 4.6 to 5.5 micromoles CO₂ per sq m s. to the photosynthesis from diffuse light, 5.3 to 7.3 micromoles CO₂ per sq m s. we get between 10 and 13 micromoles CO₂ per sq m s. for the entire canopy. Thus, an estimation of canopy photosynthesis on a sunny day at noon is between 10 and 13 micromoles CO₂ per sq. m s.

This will change on cloudy days when there is little beam sunlight and more diffuse sunlight. On cloudy days we can assume that there is essentially no direct beam light and instead it is all diffuse light. However, there will be more diffuse light on cloudy days than on sunny days because the sun energy is about the same (with a small percentage reflected by clouds) but none of it is used in beam light. Thus, to calculate photosynthesis on a cloudy day, one can assume no beam light but an increase in diffuse light that is used by the entire leaf area index. Looking again at figure 7, we might assume that at the top of the canopy, photosynthesis from diffuse light is between 2.5 and 3.5 micromoles CO₂ per sq. m s and at the bottom of the canopy it might be slightly higher than before at between .75 and 1 micromole CO₂ per sq. m s. From this we can form the equation: Photosynthesis for a low estimate = $.75 + ((2.5 - .75)/4.5)LAI$, photosynthesis for a high estimate = $1 + ((3.5-1)/4.5)*LAI$. Integrating this from 0 to 4.5 gives a net canopy photosynthesis of between 7.2 and 10 micromoles CO₂ per sq. m s.

Now it is necessary to include new leaf respiration. Unfortunately it is difficult to find

accurate data for the percentage of new leaf growth because, especially in tropical forests, it widely varies from site to site, but for this model I will assume at any one point 5% of the leaves are new. This assumption is based on observations of the canopy. Looking at figure 4 and 5, I will make an assumption that new leaves respire on average between -.5 and -1 micromoles CO₂ per sq. m s. Thus we can say new leaves respire an average of -.75 micromoles CO₂ per sq. m s 5% of the time: $.75 \times .05 = -.0375$ micromoles CO₂ per sq. m s. Next, we must take an average of the soil respiration data, which was about -5 micromoles CO₂ per sq. m s in June. Now in order to get an overall canopy flux, we must add all these components together: on a sunny day, between 10 and 13 micromoles CO₂ per sq. m s -5 micromoles CO₂ per sq. m s- .0375 micromoles CO₂ per sq. m s = between 5 and 8 micromoles CO₂ per sq. m s. Below is a table showing different possibilities of these combinations.

Table 2 – Net Ecosystem Exchange (all units micromoles CO₂ per sq m s.)

Canopy Photosynthesis	Soil respiration	New leaf respiration	Overall carbon flux
10-13 – sunny day	-5 – in June	.0375	5 – 8
10-13 – sunny day	-3.5 – in Aug.	.0375	6.5 – 9.5
7.2 -10 – cloudy day	-5 – in June	.0375	2.2 – 5
7.2-10 – cloudy day	-3.5 – in Aug.	.0375	2.2 – 5
7.2 -10 – cloudy day	-3.5 – in Aug.	.0375	2.2 – 5
7.2 -10 – cloudy day	-3.5 – in Aug.	0	2.2 – 5

Discussion

Soil respiration Soil respiration in more temperate regions is generally controlled by temperature with an increase in the temperature leading to an increase in soil respiration. However, in tropical regions where the temperature is stable year round, soil respiration appears to be more a function of soil moisture. As was stated at the start of the paper, the wet season ends in mid June and thus the measurements were taken right at the end of the wet season and entering the dry season. This is a possible explanation for the gradual decrease in soil respiration over the weeks. As the dry season was entered, the soil moisture content gradually began to

decrease thus possibly causing a gradual decrease in the amount of soil respiration. There is a large decline in the weekly average values of soil respiration after day 35. This was not accompanied by a major storm or any other apparent climate variable and I have no explanation for this jump except for the possibility that it was due to an error in the machine.

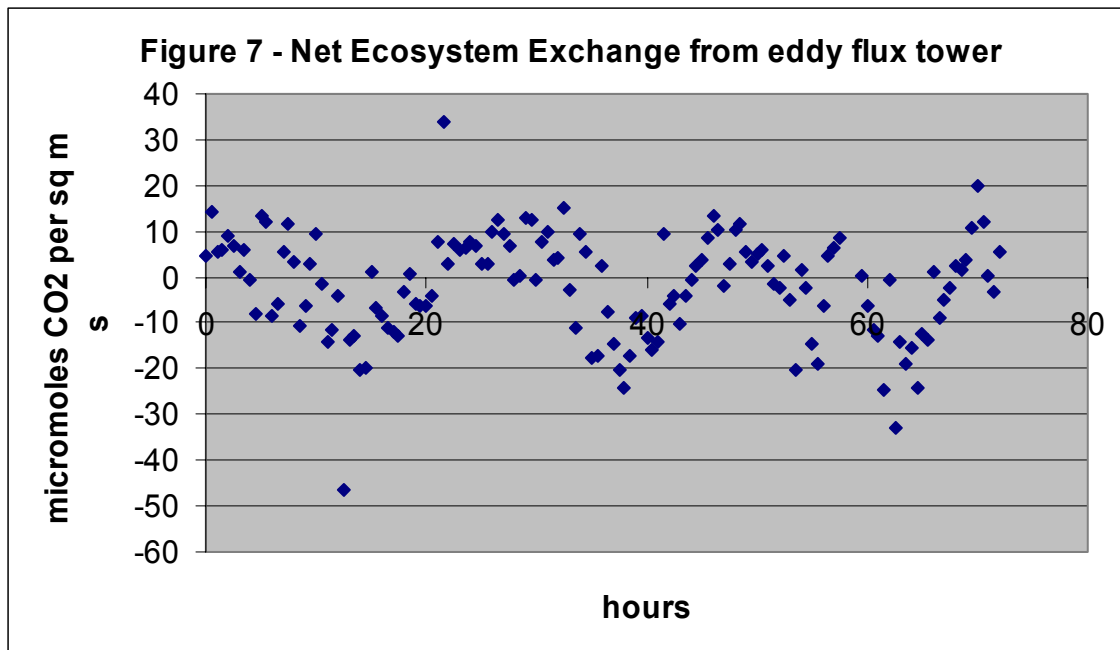
There also was a great deal of variability in carbon flux from site to site on the grid. Within a space of 25 meters, in some places the soil respiration numbers increased by an order of magnitude. If soil respiration is greatly dependent on seasonal wetness and thus soil moisture content as was suggested by Wofsy (1988), then the variability among the different sites could be attributed to different soil drainage characteristics. For instance if one soil was sandy, it would drain more quickly than a clay soil. If soil moisture and soil type do in fact control soil respiration rates, then if soil respiration rates are going to be used in other sites to model overall carbon flux it is important to know soil type and rainfall or soil moisture.

Leaf Photosynthesis The data suggest that certain new leaves from certain tree species respire for some time as they are building their photosynthetic machinery. Overall the photosynthesis levels were lower than photosynthesis levels often found at other sites. Species of plants at other sites can reach maximum photosynthesis levels of 20 micromoles CO₂ per sq. m s in full sunlight and this appears normal in many areas (Bjorkman 1981). This seems to indicate the forest was experiencing some sort of water or nutrient stress, or that the actual measurements were not accurate. Since light levels at the lower regions of the canopy rarely pass 60 micromoles CO₂ per sq. m s with the exception of the presence of a light fleck, then one can conclude that very little photosynthesis takes place in the lower regions of the canopy. There is probably variation in how leaves of different species respond to light and how different species respire when they have new leaves, but because of the constraints of the walkup tower it is difficult to quantify these differences.

There was just one walk up tower in the forest near the site and from it only 4 species of trees were within reach. However because all species within reach had leaves that seemed to respire on a fairly constant basis, one could draw a conclusion that this could be a regular phenomenon. If further studies find that this new leaf respiration is in fact a significant source of carbon dioxide then it is important to include this source into the global models measuring global carbon flux. However the lack of seasonality along with the diversity of trees in the rainforest makes this very difficult to model. Some trees are evergreen but continually grow leaves throughout the

year; some are drought deciduous and shed their leaves at the start of the dry season only to regrow them later in the year. Also, the degree that this form of respiration varies from tree species to tree species has not yet been quantified. If it is in fact species dependent then it will be virtually impossible to quantify in areas of great diversity like the rainforests where hundreds of different species can exist within a square mile, but if it instead just depends on the size and age of the leaf then this will be much easier to quantify over a large scale area and could probably be included in current global carbon models. Looking at table 2 it seems that new leaf respiration is not an important quantity to consider in my model when looking at the overall carbon balance of the forest because it is such a small component compared to the other components. However, it does appear to be a real constant source of carbon dioxide in forests and should probably be included in more accurate models of the carbon balance of the forest that strive to include all real sources of carbon dioxide.

Comparison of model to eddy flux towers Overall, when comparing my numbers of carbon flux in the forest to those from the eddy flux towers, the numbers are different. Below is a sample of three days of eddy flux data. In the following graph, negative uptakes correspond to uptake of CO₂ by the



forest. On a sunny day at noon, the eddy flux tower at the site has carbon fluxes that seem to range between 10 micromoles CO₂ per sq m s. to a high of about 25 micromoles CO₂ per sq. m s (Goulden personal communication). This rate of uptake is similar to those reported

in other tropical forests (Malhi et al. 1998, Grace et al. 1996). At the highest level, this is 2 to 5 times larger than the number that my measurements would predict, however the lowest numbers are within range of my data. The discrepancy between the high results and my data would lead me to the conclusion that there is a problem somewhere within my measurements, within my calculations, or within the eddy flux data. I feel that since the eddy flux system has been demonstrated to be accurate, and that my calculations are based on simple assumptions that if used properly, should not lead to errors of this magnitude, the problem is likely to lie with my measurements or the machine I used to take them. Since my measurements were limited to the leaves that were within reach of the walk up tower, an assumption might be that those leaves were not representative of the forest in general. All of my measurements for the top of the canopy in full light came from just one tree that was within reach. This tree might have an overall lower photosynthesis rate because of some sort of drought or nutrient stress.

Regarding the accuracy of the data from the Licor 6200, maybe for some reason the data might have entirely shifted towards more negative values. Previous studies in the Amazon had found soil respiration to be -1.8 (± 0.2) micromoles CO_2 per sq. m s which is substantially lower than the 5 micromoles CO_2 per sq. m s average that I found (Wofsy 1988). However, even if there was an error that caused the numbers to shift 3 micromoles CO_2 per sq. m s, changing this still would not lead to numbers similar to the eddy flux data. Overall, there must be a reason why my numbers do not match the eddy flux data, but at this moment it is not entirely clear why. Further research that might answer this question would be a complete calibration of the Licor to ensure that its numbers are indeed accurate. If it is found to indeed be accurate, then samples from different trees will be necessary. This could be potentially very difficult because of the great cost and difficulty of constructing a walk up tower. Overall, more measurements should be taken to determine this problem.

This study has found what appears to be new source of respiration in the form of new leaves and recommends that this source be considered a factor in fine scale models of carbon flux in tropical rainforests. This study also found an apparent dichotomy between the highest values for the eddy flux data and the Licor measurements. Since there is no apparent major source of error, it is important to find why the numbers are different when they should be roughly the same. This study has also demonstrated the difficulties of comparing different methods in order to come up with similar results.

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