An investigation of the midday decline in tropical forest photosynthesis

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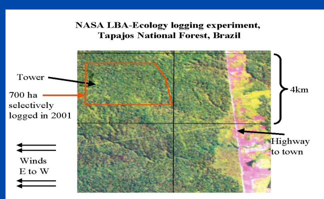
Introduction

The recent use of eddy covariance to measure the net exchange of CO_2 between the atmosphere and a primary tropical forest in Santarem Para, Brazil, has indicated a substantial decline in forest photosynthesis in the afternoon even after taking light differences into account (figure 1, black line is net CO_2 exchange, white line is light, Goulden et al 2002). This effect is also shown in figure 2 where the circles show the mean whole-ecosystem light curve during mornings, the triangles show the light curve during cool afternoons, and the crosses show the light curve during warm afternoons (temp>30C). Afternoon declines in leaf-level gas exchange have been reported for many ecosystems (Larcher 1995), including tropical forests (Koch et al. 1994, Malhi et al. 1998, Williams et al. 1998). Since this decline appears to cost forests a substantial amount of carbon, it is important to understand its cause. Potential causes for this decline include stomatal responses to VPD, low leaf water potential, relative humidity, changes in biochemistry due to elevated temperature, photoinhibition, photorespiration, or intrinsic circadian rhythm. This study attempts to understand this decline by measuring leaf gas exchange while the leaf is kept under constant light, humidity, and temperature conditions for 24 to 36 hours.



Methods

Using the platform towers at km 83 and km 67 of the Tapajos National Forest in order to access the canopy level leaves of several species, a Licor 6400 was used to make continuous photosynthesis measurements every 20 minutes over a 24 hour period. Leaves were exposed to constant light levels ranging between 0, 100, 1000 PAR _mol/m_s, constant temperatures ranging between 26-30 degrees, and constant humidity levels ranging between 60-80%. During some of these photosynthesis measurements water potential measurements were taken from leaves of the same tree every two hours during the daytime. Originally light levels of 1000 PAR _mol/m_s were used on different species, but this was found to be too high for some of the more shade adapted leaves in the lower canopy, so later, light levels of 100 PAR _mol/m_s were used. Light levels of 0 PAR _mol/m_s were also used to test respiratory and stomatal changes in the absence of light. Overall, 11 different species were tested from all different canopy levels. In addition to photosynthesis and water potential measurements, leaf temperature using fine wire leaf thermocouples was also measured from species at all levels of the canopy.

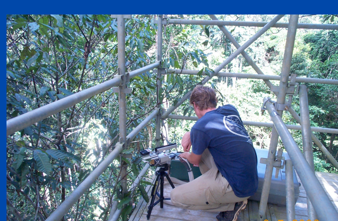


Figure 1

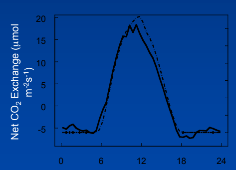
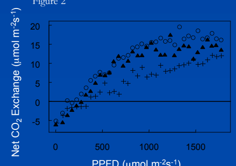


Figure 2



What causes the afternoon decline in photosynthesis?

Leaf Temperature

Tropical leaves exposed to full sunlight can get extremely warm. We measured temperatures of up to 47.5° for plants with large leaves living in gaps (figure 3 and 4). Even understory leaves can reach 40° C when exposed to a light fleck of a few minutes (figure 5). Depending on wind conditions and leaf size canopy level leaves can reach highs of 43°C and sustained averages in the high 30's. Such high temperatures can negatively affect photosynthesis as is seen in figure 6. In this case, a Cecropia, a typical gap species, shows a sharp decline in photosynthesis as temperatures reach 40° C. Leaf temperature measurements show that such a large leafed gap species can reach temperatures beyond 40° C for an extended period, so temperature almost certainly is limiting photosynthesis in gap species. Since canopy leaves also can reach very high temperatures, and tower data shows that canopy level photosynthesis can be substantially decreased on warm days (figure 2), it is likely that high leaf temperature is adversely affecting canopy photosynthesis.

Figure 3

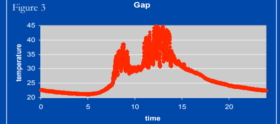


Figure 4

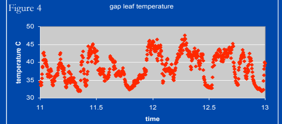


Figure 5

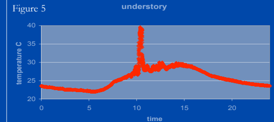


Figure 6

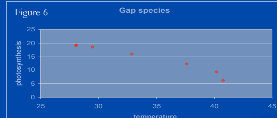
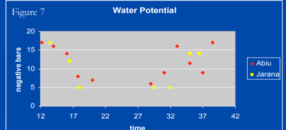


Figure 7



Circadian Rhythm

Even on cool days, photosynthesis is lower during the noontime hours than the morning period (figure 2). Thus, there is another factor besides temperature that is affecting canopy level photosynthesis. At constant light levels of 100 PAR _mol/m_s for a period of 24 to 36 hours, 8 of 11 species tested showed evidence of a circadian rhythm including a decline in photosynthesis that began before noon typically between 10:30- 11:00. (Circadian rhythms are intrinsic biological cycles with a period of approximately 24 hours.) In these species this decline closely matched the decline demonstrated by the eddy flux tower (figure 1), indicating that the noontime decline in photosynthesis is partly due to this circadian rhythm. Six of 11 (figure 10) of the species tested showed a nocturnal decrease in CO_2 uptake that was consistent with a circadian rhythm directly controlling photosynthesis. Two of 11 (figure 11) show showed a nocturnal decrease in CO_2 uptake that was consistent with a decrease in ci that, in turn, was caused by a circadian rhythm. Two species showed no evidence of a circadian rhythm and one species showed a strong decline in photosynthesis at night but no recovery the following day. Certain species responded differently to different light levels with some showing the circadian rhythm at low (100 _mol/m_s) light levels, but not at high (1000 _mol/m_s) light levels, but others showed a circadian rhythm at all light levels (figure 8). At 0 PAR _mol/m_s, the Abiu (figure 8), showed a rhythm in both stomatal conductance and respiration. Circadian rhythms were observed in a wide range of forest groups including liana, gap species, dominant trees and sub-dominant trees. A liana (figure 9) was tested continuously for 2 straight days and showed a slight decline in daytime photosynthesis rates during day hours but surprisingly, the night time levels of photosynthesis increased during the second day.

Water potential measurements (figure 7) demonstrated a great deal of variety between species and time of day. However, dusk and predawn measurements always showed less negative water potential than noontime measurements. There was a peak at the noontime hours but it was not clear as to whether that peak came at 10 AM or 12 PM.

Figure 8

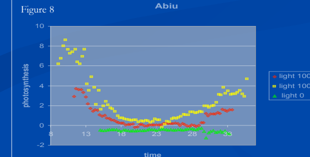


Figure 9

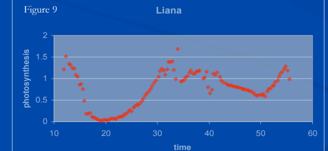


Figure 10

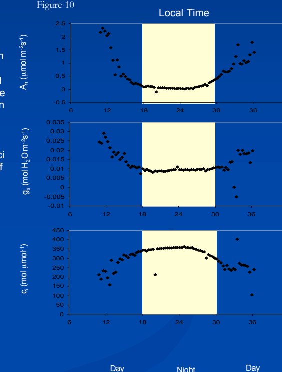
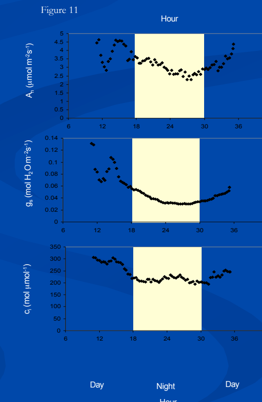


Figure 11



Conclusions

A combination of high leaf temperatures (figures 3-6) and circadian rhythms (figures 10,11) appear to cause the observed afternoon decline in whole-forest photosynthesis (figures 1,2). Circadian rhythms are common in the Tapajos National forest, appearing in 8 of 11 species tested. It is not understood why these trees modulate carbon uptake with a circadian rhthym. It may be that some already dominant trees simply do not need any more carbon for growth, as they are already dominant and an increase in height could possibly increase the risk of a cavitation of the water column. However since this circadian rhythm is also present in species such as liana and cecropia, whose success often depends on their ability to grow quickly, this hypothesis does not seem as likely. It is also not clear why these trees could not use the extra carbon for reproduction purposes. But there must be some advantage to the development of the circadian rhythms since it appears to be present in such a wide variety of species in tropical forests.

The other interesting result found was the very hot temperature that some tropical leaves could reach. Using data from the eddy flux tower, figure 2 (crosses) shows that on warm days (air>30°C) photosynthesis is substantially decreased. With leaf temperatures that can reach 47°C in the gaps and 43°C at the canopy top, this decrease in photosynthesis on warm days may be due to increased photorespiration of leaves caused by high leaf temperature. This indicates that high leaf temperatures also plays a role in limiting photosynthesis in these tropical forests, although more temperature photosynthesis curves will be necessary to determine at what temperature these leaves have their peak. If high leaf temperature already plays a substantial role in decreasing carbon uptake in tropical forests, it seems vital to understand this mechanism more clearly as global warming could cause additional warming of these leaves, thus reducing photosynthesis and creating another potential positive carbon feedback.