IMPORTANCE OF FOREST CARBON DYNAMICS

Understanding of the stocks and flows of carbon in tropical and temperate forests is critically intertwined with many important questions in basic and applied ecology. Because tropical and temperate forests together encompass an estimated 38% of terrestrial carbon pools and 48% of terrestrial net primary production (1), knowledge of their carbon dynamics and of how these dynamics respond to natural and anthropogenic global change is key to understanding the global carbon budget today and in the future – perhaps the most important applied ecology issue of our generation. Given that ecosystem carbon uptake, storage, transfer, and release involve myriad physical, chemical, physiological, and ecological processes including diffusion, enzyme kinetics, photosynthesis, growth, reproduction, herbivory, and decomposition, development of a more complete understanding of carbon dynamics simultaneously demands and facilitates progress on a multitude of fundamental ecological questions. Such progress is sorely needed as we remain tremendously ignorant of tropical forest carbon pools, short- and long-term carbon fluxes, the mechanisms underlying these fluxes, and the likely impacts of global change on carbon dynamics.

A NEW RESEARCH PROGRAM

CTFS has embarked on a new program of research on carbon budgets in tropical and temperate forests, with funding from the HSBC Climate Partnership. This research encompasses collection of new field data at multiple CTFS sites around the globe and related analyses to achieve new insights into forest carbon cycles. We address three broad questions:

First, and most fundamentally, we ask **what are the sizes of carbon pools in tropical and temperate forests, and how do these vary spatially, within and among sites?** The core CTFS tree censuses provide an excellent starting point for estimating above-ground carbon stores in trees and their spatial variation within and among sites. To quantify total carbon stocks within the forest, these estimates of above-ground tree pools will be complemented by assessment of below-ground carbon pools in mineral soil and fine roots, by assessment of aboveground woody coarse woody, and by censuses of lianas – all pools that are large and/or particularly likely to vary greatly among sites or in response to global change. The resulting data will not only provide new information on spatial variation in these pools, but will also determine a baseline for detecting future change in these important carbon pools at these sites.

Second, we ask, **what are the sizes of carbon fluxes in tropical and temperate forests, and how do these vary temporally among years in relation to climate?** Tree growth, tree mortality, litter production, and soil respiration are all dependent upon
temperature, water availability, extreme weather events, and/or other factors. Thus, they vary among years, leading to interannual variation in standing carbon pools in tropical forests and in the fluxes of carbon into or out of forests from the atmosphere (in some years a forest may be carbon sink, in others a carbon source). A better understanding of this variation will provide important insight into the mechanisms underlying the sizes of carbon pools in tropical forests and contribute to better projections of future changes in these carbon pools under different climate change scenarios. We will remeasure a subset of trees on each plot annually in order to characterize interannual variation in tree diameter growth and mortality. We will also census litterfall and soil respiration, which together with tree growth will enable annual estimation of total net primary production and its allocation. We will use repeated censuses of coarse woody debris to quantify fluxes in and out of this pool. Altogether, these data will make it possible to better relate temporal variation in carbon fluxes to temporal variation in climate, as well as establishing a baseline for detecting long-term change.

Third, we ask what mechanisms drive spatial and temporal variation in forest carbon pools and fluxes within and among sites? To establish the correlates of spatial and temporal variation in carbon pools and fluxes, investigate the potential impacts of global change, and test hypotheses regarding the mechanisms underlying variation in carbon dynamics, we need to monitor climatic conditions and characterize soils in a standardized manner at all sites. Such monitoring and characterization also provides an important foundation and context for many other ecological studies. Fundamental soil characterization and nutrient analyses for all sites is a necessary precursor to interpreting site differences in carbon dynamics and ecology more generally, and this one-time effort will be undertaken for all sites at which such data are not yet available. Climatic conditions, including temperature, rainfall, relative humidity, solar insolation, and windspeed will be monitored continuously at all sites using standardized equipment and protocols. The relationship of spatial and temporal variation in climate and soils to variation in carbon pools and fluxes will be analyzed. Plant species functional traits will be measured to test hypotheses relating species performance and climatic responses as well as its consequences for carbon budgets to plant traits. Finally, we will provide grants for related research at CTFS sites that complements the research specifically described here and expands our understanding of forest carbon budgets.

1. **Assessment of Carbon Pools**

The CTFS network sites, with their long-term monitoring commitment, large spatial scale, and pantropical distribution, are uniquely well positioned to detect long-term changes in carbon stocks of old-growth tropical forests due to global change, as well as to capture spatial variation in carbon stocks and changes in these stocks within and among sites. The core CTFS censuses currently make possible estimation of above-ground carbon stored in trees over 1 cm in diameter – which constitute on average about 40-50% of tropical forest carbon stores. HSBC Climate Partnership funds will make it possible to obtain a more complete picture of the largest and most important carbon stocks and their temporal variation on CTFS sites in tropical and new temperate sites, through complementary assessments of carbon pools in soils, roots, coarse woody debris, and lianas. In addition, we will improve estimates of the aboveground woody tree carbon
Assessment of Belowground Carbon Stocks

Belowground carbon stocks in tropical forests are similar in magnitude and variability among sites to aboveground carbon stocks (2), and like aboveground stocks have the potential to be altered significantly by global climate change, nitrogen deposition, and other anthropogenic influences. Indeed, a recent study found a strong decrease in belowground carbon in the United Kingdom, presumably due to climate change (3). Yet belowground carbon has rarely been measured in tropical forests in general, and remains virtually unexamined at CTFS sites in particular. Thus we currently have little knowledge of patterns of among-site variation in belowground carbon and its determinants, and virtually no ability to detect potential changes in this large and important carbon pool.

We will conduct a systematic assessment of belowground carbon in mineral and organic (where present) soil and fine roots at each site to estimate the total size of this pool, characterize current within- and among-site variation, and provide a baseline reference for future studies investigating potential changes in belowground carbon. This assessment will involve digging soil pits outside each plot, taking soil cores in every hectare of each plot (including one extending to the full depth of the soil, except in rocky soils or extremely deep, i.e., >6 m deep, profiles), and processing soil cores for fine root biomass and soil carbon content at various depths. Ben Turner (turnerbl@si.edu), a soils scientist based at the Smithsonian Tropical Research Institute, is heading this research effort.

Coarse roots are also a significant carbon pool (estimated at 5-10% of the total), and one for which extremely little data are available in tropical forests. Because existing methods for assessing biomass and carbon of coarse roots are destructive, no such measurements can be conducted within the CTFS plots. However, we will provide funding for destructive sampling of root biomass in old-growth tropical forests near CTFS sites where opportunities for such sampling exist due to road construction, logging, or other planned tree removal.

Census of Coarse woody debris

Coarse woody debris – fallen or standing dead trees and branches – constitutes a sizeable (5-10% of the total), spatially and temporally variable carbon stock in tropical forests, plays important roles in carbon and nutrient cycles, and provides habitat for many types of organisms (4-6). While the rate of production of coarse woody debris can be estimated from tree mortality and damage rates, standing stocks depend also on decay rates, which vary among sites with climate, soils, and tree species composition, and vary in time with climate and chemical inputs (6). CTFS will measure coarse woody debris stocks and residence times through annual censuses of standing dead trees on subplots and fallen woody debris on line transects (5). The resulting data will provide baseline numbers for an important carbon stock, one that may be especially sensitive to natural and anthropogenic variation in climate and chemistry, as well as context for studies of microbial and animal communities that utilize such debris as a resource.
Censuses of Lianas

While lianas (woody climbers) constitute a relatively small carbon pool in most tropical forests (1-3% of the total pool), they account for a much larger fraction of NPP and have the potential to greatly impact forest carbon dynamics through their negative effects on tree growth, survival, and standing biomass (7). Several studies have found that lianas are currently increasing in abundance in tropical forests (8-10), a change variously hypothesized to be due to lianas disproportionately benefiting from carbon fertilization (11), disturbance (12), and the reduction of vertebrate seed dispersers due to hunting by humans (13, 14). Yet because lianas are infrequently censused, there is still considerable uncertainty about their patterns of abundance and the generality of any increase, and we remain far from an understanding of the underlying mechanisms. Such increase, if present, is of profound importance for forest carbon pools because liana leaf area displaces tree leaf area on a 1-to-1 basis, and because lianas have much lower woody carbon stocks to support each unit of leaf area. To fill this crucial knowledge gap, we will conduct sub-censuses of lianas on plots for which liana data is currently unavailable. These liana censuses will be stratified by size and over space, with larger size classes censused over smaller areas than smaller size classes. We will also make funding available for destructive harvests of lianas to collect data on the allometries of liana biomass, leaf area, and stem diameter in areas outside CTFS plots where forests are being cut for other reasons.

Improving Aboveground Tree Carbon Pools

Our estimates of aboveground tree carbon pools rely on allometric equations relating tree diameter and wood specific gravity to aboveground biomass, as well as on assumptions about the proportion of this biomass that is carbon. The accuracy and precision of the resulting estimates depends crucially on the accuracy of the wood specific gravity data. For many of our tree species, we lack species-level wood specific gravity information, and thus use genus or family means. We will collect additional data on wood specific gravity of tree species at our sites to improve estimates of aboveground tree carbon pools, as well as to build our database of functional traits (discussed further below). Because better estimates of carbon pools can be obtained when tree height allometries are also available, we will also collect tree height data on a subset of trees at sites lacking such measurements. We will further test the assumption that 50% of the dry woody biomass is carbon through measurements of the carbon fraction (including the volatile organic carbon or VOC fraction) in various species. Finally, where cutting of old-growth forests near CTFS sites provides the opportunity, we will provide funding for measuring biomass, diameter, height, and wood specific gravity of whole trees to improve the available datasets on their interrelationship.

2. ASSESSMENT OF CARBON FLUXES

The core CTFS tree censuses provide valuable data on tree growth and mortality rates at different sites and its variation on longer time scales. However, because the censuses are conducted only at 5-year intervals, they shed relatively little light on interannual variation in growth and mortality and its relationship to climate. We will use HSBC Climate Partnership funds to obtain finer temporal resolution data on tree growth, and to collect complementary data on NPP allocated to litter production and below-
ground production. We will also measure fluxes into and out of the coarse woody debris pool.

**Annual Censuses of a Subset of Trees**

Interannual variation in climate, both natural and anthropogenic, drives interannual variation in tree growth and mortality, and carbon dynamics. For example, a study in Costa Rica found that tropical trees grow more slowly in years in which minimum temperatures are higher, presumably because of the higher costs of nighttime respiration. Tree mortality rates vary even more strongly among years in response to droughts, major storms, and other events (e.g., 15). To capture this annual variation, and thereby make it possible to analyze correlations and test hypotheses relating tree growth and mortality with particular climatic and atmospheric signals, such as the El Nino Southern Oscillation (ENSO), we will annually remeasure 2000 trees per plot using dendrometers. The sampled trees will include all of the largest trees on each plot (>80 cm dbh), and spatially stratified subsets of smaller size classes (down to 5 cm diameter).

**Biweekly Litter Censuses**

Though wood provides the longest residence time for carbon of any plant tissues, the majority of net primary production goes into leaves and other more short-lived organs. Production of leaves, fruits, seeds and “litter” in general correlates strongly with coarse woody productivity among sites (16), and responds sensitively to seasonal and interannual variation in climate, as well as to atmospheric carbon dioxide and other anthropogenic influences. For example, fruit and seed production on Barro Colorado, Panama, tracks solar irradiance anomalies associated with ENSO. Leaf, fruit and flower production also directly determines food availability to primary consumers: seasonal rhythms in many animal species correspond with plant phenology (17), years of low fruit production can cause famines and population crashes in frugivores (18), and interannual variation in bee abundance correlates with flower production (S. J. Wright and D. W. Roubik, unpublished data). Thus, we will initiate and maintain biweekly censuses of 100 litter stations per plot, censuses in which we measure the dry mass of leaves, reproductive parts, woody litter (< 2 cm diameter) and other litter entering each station in each census interval. Each station will consist of one above-ground litter trap and one ground litter trap, each 0.5 m² (0.71 x 0.71 m).

**Soil Respiration**

Belowground allocation as a proportion of total NPP varies greatly among sites with climate and soils. Anthropogenic changes in climate and nutrient deposition have the potential to cause changes in this allocation as well. Yet very little is know about belowground processes in tropical forests and associated carbon fluxes. We will measure soil respiration at our study sites in order to estimate belowground allocation and total NPP. We are currently evaluating alternative measurement technologies and sampling designs to determine which are appropriate for our sites.

**Fluxes of Coarse Woody Debris**

Fluxes in and out of the coarse woody debris pool pool are likely to vary strongly among years, and have the potential to change significantly due to anthropogenic
influences. Changes in tree mortality rates and tree stress affect inputs, while changes in temperature, humidity and nutrient deposition affect outputs via decomposition. In order to develop a more mechanistic understanding of the fluxes of carbon into and out of the coarse woody debris pool and their relationship with interannual variation in climate, we will quantify these input and output rates through repeated censuses. Specifically, we will census fallen woody debris and standing dead trees along the same transects and in the same areas twice a year to quantify inputs via mortality and branchfall as well as output rates via decomposition.

3. Investigating the Mechanisms

Fundamentally, a better understanding of carbon cycling in tropical forests requires not only more and better data on carbon pools and fluxes, but also a better understanding of the mechanisms underlying these pools and fluxes. We will use the carbon pool and flux data together with complementary datasets on climate and soils to analyze the relationship of spatiotemporal variation in carbon budgets to variation in potential driving factors, and to test related hypotheses. These efforts will build in particular on meteorological monitoring, soil characterization, and the assessment of plant functional traits, as well as encompassing a broader range of complementary studies initiated by individual investigators.

Meteorological Monitoring

Though the tropics were once thought to be the epitome of stable climates and largely remote from human influences, recent decades have brought increasing awareness of the ubiquity and importance of natural interannual climatic variation as well as of anthropogenic influences on climate and atmospheric chemistry in tropical forests. The carbon dynamics at CTFS sites cannot be understood absent accurate information on the local meteorological context. Temperature, rainfall, wind speed and solar radiation directly affect tree photosynthesis, respiration, growth and mortality, as well as decomposition, nutrient cycling, disease, and herbivores (6, 19). Further, meteorological conditions have important effects on all organisms and ecosystem processes in tropical forests, and thus good meteorological data are a key foundation for ecological research at CTFS sites. Such data are particularly important for documentiong seasonal and interannual cycles such as ENSO, and for detecting long-term climate change. While attention has focused on the larger magnitude temperature changes projected for higher latitudes, tropical regions are expected to warm by 2-4 degrees Celsius by the end of the century (1) – a change that is far from trivial for tropical forest carbon dynamics.

At each site, we will measure temperature, rainfall, humidity, wind speed and direction, and solar insolation at intervals of no more than 10 minutes. The locations of sensors and their calibration schedules will follow standardized protocols to insure comparability of measurements among sites and over time. Many sites already have meteorological monitoring of some kind; equipment and procedures will be added, modified, and/or supplemented as needed to achieve directly comparable data.

Soil Characterization

Soil characteristics have profound influences on plant growth and mortality, microbial activity, nutrient cycles, and ecosystem processes and structure in general.
Soils vary greatly in their structure, water-holding capacity, and nutrient dynamics depending on their parent material, age, and climatic history, as well as on local topography and vegetation. Variation in soil fertility and structure appears to drive much landscape-level variation in floristics (e.g., 20), and may ultimately determine animal community composition as well (21). Soil variation is recognized by soil scientists through elaborate soil taxonomy systems. Soil type thus defined explains considerable variation in coarse wood productivity among neotropical forests – indeed, it has more explanatory power than all climate variables combined (16). Considerable research on soils has been done at a number of CTFS sites, and has resulted in interesting findings (22), but we lack consistent soil characterizations on many plots.

For each site involved in the carbon research effort, we will conduct systematic soil characterization at the same time that soils are sampled for carbon if such characterization has not previously been done. Specifically, soil types on the plot will be mapped and quantitative soil pits will be dug outside the plot in each soil type. Standard soil survey protocols will be followed to describe the soils in the pits, (including color, horizons, etc.) and assign them to taxonomic groups.

**Plant Functional Traits**

Tree species vary greatly in traits such as wood specific gravity, mature height, leaf size, and seed mass – and variation in these so-called “functional” traits often explains variation in plant performance under different conditions. Many such traits have specific explanatory value with respect to the roles of individual species in forest carbon budgets. For example, wood specific gravity relates to tree growth rates (coarse woody productivity), tree mortality rates (inputs into the coarse woody debris pool) and wood decomposition rates (outputs of the coarse woody debris pool). Especially in diverse tropical forests where understanding the role of every individual species based on its performance alone is essentially impossible, plant functional traits offer a valuable framework for generalizing across species. Insofar as they explain performance under different conditions, traits may also explain variation in response to interannual variation in climate and anthropogenic change. Every global change influence is likely to affect different species differently, potentially changing relative competitive abilities and thereby in the longer term forest composition. While the mean effects of a change across all species may be small, shifts in composition towards the species with the most extreme responses could result in much greater effects in the long term. Thus, data on plant functional traits can help us understand the roles of different species in carbon budgets, differential species responses to global change, and the implications of global change for carbon budgets considering trait-related shifts in relative competitive ability.

In parallel with the carbon initiative, CTFS is embarking on a traits initiative to collect consistent data on plant functional traits for tree species and plots around the network. Two of these traits are of particularly direct relevance to carbon budgets – wood specific gravity, and tree height. As part of the carbon research program, we will collect additional data on these traits for species and sites where this information is lacking. In addition, we anticipate that analyses of carbon data will often benefit from consideration of related data on plant traits. Where appropriate trait data are available, we will examine the relationship of functional traits to the roles of individual species in forest carbon budgets, and test related hypotheses.
Complementary Efforts

While the field research program outlined here will provide considerable new information into forest carbon budgets, it is necessarily far from comprehensive – many more studies can provide additional and complementary insights. No research program can do everything or foresee perfectly what data will be most useful. To facilitate a larger carbon research program within the CTFS network, now and in the future, we will offer grants for complementary studies at CTFS sites. These grants may involve any field, lab, remote sensing, and/or modeling studies that provide additional insights into carbon budgets at one or more CTFS sites. We expect that many of these studies will be testing grounds for methods that could potentially be expanded to more CTFS sites in the future. Grant proposals can be submitted as part of the CTFS grants program, or at other times direct to the carbon research program. Interested investigators are encouraged to contact Helene Muller-Landau <mullerh@si.edu> early in the development of their proposals.

IMPLEMENTING THE RESEARCH PROGRAM

Participating Sites

Thanks to a generous grant from the HSBC Climate Partnership, funding is available to advance this research program at all CTFS sites where local PIs and collaborators are interested in performing the research through the end of 2011. In late 2007, field data collection began at four sites: Barro Colorado Island in Panama, Pasoh in Malaysia, and Khao Chong and Huai Kha Khaeng in Thailand. As of July 2008, plans are in development to start the field work at an additional 8 sites in the next 12 months: Lambir Hills in Malaysia, Mudumalai in India, Bukit Timah in Singapore, Fushan in Taiwan, Xishuangbanna in China, and Ituri in Congo, Yasuni in Ecuador, and Manaus in Brazil. In addition to work at the large plots within the CTFS network, data collection is also planned for sets of small plots that span environmental gradients of interest, including rainfall gradients near BCI in central Panama and in Mudumalai in India.

Timeline of Field Research

In planning field work at individual sites, initiation of measurements of carbon fluxes and meteorology is the top priority, as these data are to be collected over multiple years, and their value builds over time. In particular, we recommend first installing dendrometers (as the band dendrometers need to be in place for several months before measurements can begin), then installing or upgrading meteorological monitoring as needed, then initiating the biweekly litter trapping, and next conducting the first of the repeated censuses of coarse woody debris. If the dendrometers have taken up available slack by this time, then it would be advisable to next remeasure these; otherwise the remaining coarse woody debris pool census could be done first. Ongoing measurements would thereafter involve biweekly censuses of the litter traps (requiring 5 days of technician time every 2 weeks), twice-annual remeasurements of the dendrometers, and twice-annual recensuses of coarse woody debris. Soil sampling and subsequent carbon analyses can in principle be done at any time through late 2011; specific scheduling should be coordinated with Ben Turner <turnerbl@si.edu>. Liana censuses can also be done at any time through 2011, and thus scheduled for whatever block of time is locally
convenient. Measurements of wood specific gravity and tree height can be carried out at any time and can be spread out over time, and thus be done by technicians whenever they are not busy with other scheduled tasks. Soil respiration measurement methods are still being evaluated; we anticipate completing this protocol in 2009, with most sites subsequently measuring soil respiration for 1-2 years.

The exact timing of dendrometer remeasurements and coarse woody debris recensuses during the year should ideally be decided for each site based on its seasonality, although practical considerations will also come into play in many cases. For example, in seasonal forests, dendrometer measurements are best made during the wet season, to avoid undue influences of trunk hydration. In such forests, taking measurements at the beginning and end of the wet season allows for partitioning of growth between the wet and dry season. Coarse woody debris censuses could ideally be timed to capture peak input and output rates. For example, in Barro Colorado, treefalls are greatest in the mid wet season, and lowest in the dry season, while decomposition proceeds fastest in the early wet season. Thus, censuses early in the dry season and just before the middle of the wet season would be expected to capture annual highs and lows in coarse woody debris.

Field and Lab Protocols

Detailed protocols for the empirical research program, including sample data sheets have been or are being developed. Protocols for dendrometer measurements, litter trapping, soil carbon assessment, coarse woody debris censuses, and measurement of selected functional traits are currently available by email from Helene Muller-Landau (mullerh@si.edu) and will soon be available on the CTFS web site. We expect to complete protocols for liana censuses and meteorological monitoring by the end of 2008, and a soil respiration protocol in 2009. In addition to the protocols, sample data forms and, where relevant, R code for creating data forms are also available.

Analysis and Publications

We anticipate that this research program will result in numerous site-specific publications in which local investigators report results for their individual sites, as well as integrative studies that take advantage of the directly comparable data collected across the network and involve multiple sites and investigators. The lead scientist and postdoc of the carbon initiative will assist in advancing individual site publications to the degree desired by the local investigators. (Among other things, they will provide computer code in the R language for standard analyses of the carbon data, and answer questions about how to employ this code.) It is expected that individual site data collected with CTFS carbon initiative funds will be available for cross-site comparisons within at most two years after collection, with all participating local investigators included as coauthors on such publications.

LITERATURE CITED


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