BIOTROPICA ▮▮(▮▮): 1–10 2010 10.1111/j.1744-7429.2010.00654.x

Assessing Tropical Forests' Climatic Sensitivities with Long-term Data

Deborah A. Clark[1] and **David B. Clark**

Department of Biology, University of Missouri–St. Louis, One University Boulevard, St. Louis, Missouri 63121-4400, U.S.A.

Department of Environmental Sciences, University of Virginia, 291 McCormick Road, Clark Hall, Charlottesville, Virginia 22904-4123, U.S.A.

Estación Biológica La Selva, Puerto Viejo de Sarapiquí, Costa Rica

ABSTRACT

Analyses relating long-term records of tree growth to interannual climatic variation at La Selva, Costa Rica have revealed marked forest sensitivities to both temperature and dry-season intensity (Clark *et al.* 2010). The tropical-forest biome is certain to become warmer, and many areas may become drier. Testing the generality of the La Selva findings with similar analyses of field data from diverse forests across the biome will be a valuable next step. Based on our experiences during the La Selva studies, we propose that such assessments will need to address three issues. One is the number of repeat forest measurements. Short series of re-censuses can be an unreliable basis for assessing climatic sensitivities. For some key climatic factors (*e.g.*, temperature), records consisting of fewer than 10–12 re-censuses can span limited climatic ranges, producing erratic and largely nonsignificant correlations. Multiyear census intervals exacerbate these data limitations. Second, different types of forest-growth data call for different analysis approaches. Cohort and tree-ring records need to be adjusted for ontogenetic growth changes, while stand-level data require taking into account potentially confounding influences from forest compositional changes, as from succession. Third, a reliable meteorological record is critical. Poor-quality or internally inconsistent climatic records can fatally corrupt assessments of forest sensitivities. To be usable in such analyses, the meteorological record requires data quality control, gap filling, and adjustments to maintain the record's internal consistency in the face of commonly occurring methods changes (instruments, siting). We illustrate these issues using analyses of the long-term La Selva records.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: climate change; Costa Rica; global change; meteorology; monitoring; productivity; temperature; tree growth.

QUANTIFYING THE RESPONSES OF TROPICAL-FOREST PRODUCTIVITY to climatic factors such as temperature and rainfall is increasingly recognized as a priority for global change science. The biome's importance for global biodiversity (Kier *et al.* 2005) is one reason. Another is the large role of these highly productive ecosystems in the global carbon cycle (Denman *et al.* 2007, Bonan 2008). Over recent decades, the yearly rates of increase in atmospheric carbon dioxide (CO_2) have been strongly affected by interannual changes in the carbon balance of the terrestrial tropics, with greater tropical CO_2 emissions in warmer and drier years (Clark *et al.* 2003, Adams & Piovesan 2005, Denman *et al.* 2007). Modeling studies have shown that responses of the carbon balance of tropical forests to climbing temperatures and intensified drought could act as a positive feedback to global warming (Berthelot *et al.* 2005, Matthews *et al.* 2007). These projections remain highly uncertain, however, due to the scarcity of field data on tropical forests' climatic sensitivities.

At one exceptional site, the lowland tropical wet forest at La Selva, Costa Rica, two parallel long-term studies (Clark *et al.* 2003, 2010) have been assessing forest climatic responses by relating annual tree growth and dynamics to the interannual variation in climatic conditions during recent decades. Since 1983, annual diameter increments have been measured for large samples of individuals from six focal canopy-tree species, producing the longest such data series for the world tropics (26 re-measurements to date). Since 1997, annual tree dynamics and wood production have been measured at the whole-forest level in eighteen 0.5-ha plots (12 re-measurements to date). These long-term studies have revealed marked sensitivities of annual wood production in this forest to both higher nighttime temperatures and reduced dry-season rainfall, but no detectable influences from the changes in atmospheric [CO_2] or from interannual variation in total rainfall or solar radiation (Clark *et al.* 2010).

The temporal variation in La Selva tree growth (focal species study) closely paralleled the interannual changes in carbon emissions to the atmosphere from the global land tropics during 1984–2000, as inferred from atmospheric gas samples. The hotter the year, both at La Selva and for the tropics as a whole, the greater the reductions in growth by the La Selva trees and the greater the inferred tropical carbon emissions (Clark *et al.* 2003). These correlated findings raise the possibility that the temperature sensitivity shown by trees at La Selva is widespread, presaging declining productivity across the biome as global warming proceeds. Based on other lines of evidence, however, it has been hypothesized (Lloyd & Farquhar 2008, Lewis *et al.* 2009) that physiological benefits from increasing levels of atmospheric CO_2 are dominating and will negate negative temperature effects on tropical forests (but see Körner 2009, Clark *et al.* 2010). Meanwhile, the potential negative impacts on tropical forests from any directional increase in drought severity have become an increasing concern (Malhi *et al.* 2009, Phillips *et al.* 2009, Clark *et al.* 2010).

An urgent research priority is to assess forest climatic sensitivities across the tropical-forest biome (montane forests and dry-to-wet lowland forests, in all major regions of the Asian, African, and American tropics). Diverse research approaches would all contribute to this effort. Although logistically challenging and costly,

Received 6 October 2009; revision accepted 10 March 2010.

[1]Corresponding author; e-mail: deborahanneclark@gmail.com

© 2010 The Author(s)
Journal compilation © 2010 by The Association for Tropical Biology and Conservation

forest-level experiments can be used to test effects of an enhanced level of a particular climatic stressor (*e.g.*, the multiyear droughting of a 1-ha plot at each of two Amazonian sites; Fisher *et al.* 2007, Brando *et al.* 2008). Alternatively, advantage can be taken of the 'natural experiments' provided by current extreme climatic events as possible indicators of the effects of future climates (*cf.* a recent analysis of responses of different Amazonian forests to the 2005 record drought; Phillips *et al.* 2009). When only limited field data are available from a given forest, techniques such as Bayesian analyses can be used to infer underlying response patterns (*cf.* Feeley *et al.* 2007). Ecophysiological observations can increase process-level understanding of forest climatic responses (*cf.* leaf-level and eddy flux observations of strong photosynthetic declines at higher current temperatures in Amazon forest canopies; Tribuzy 2005, Doughty & Goulden 2008). When long-term data exist at a site for both forest performance and local climatic conditions, as in the La Selva studies, the forest's climatic responses over the spanned time period can be directly assessed by examining the relation between these two records.

While all of these types of research will be valuable, this last research approach has particular promise. Over recent decades, long-term forest monitoring has been implemented at many sites around the tropics, including the Center for Tropical Forest Science (CTFS) pantropical plot network (Losos & Leigh 2004) and the RAINFOR Amazonian plot network (Phillips *et al.* 2009). Key climatic factors such as temperature and rainfall show marked interannual variation in the tropics, including recurring extreme events such as strong El Niño's and La Niña's as well as directional change (Malhi & Wright 2004). Long-term records can therefore enable assessment of forest responses over a broad range of a given climatic factor. Analyzing the relation between forest performance and climatic conditions across long observation periods for the many currently monitored tropical forests could greatly enhance current understanding of tropical-forest climatic sensitivities and whether these sensitivities are changing through time. Experiences gained over the course of the two La Selva studies, however, indicate that the accuracy of such assessments will depend on three currently underappreciated factors: (1) the need for long data series (many repeat observations) to detect effects of some of the key climatic factors, (2) the importance of tailoring analyses to the different types of forest-growth data, and (3) the critical importance of having an accurate, internally consistent meteorological record. In this paper, we discuss these three distinct issues, illustrating each with examples from the La Selva data series.

HOW LONG A RECORD IS NEEDED FOR RESPONSE DETECTION?

Even if a study of a given forest spans a very long period, if the actual data series consists of only a handful of re-censuses (*e.g.*, 3–5: Feeley *et al.* 2007, Laurance *et al.* 2009), analyses of the correlation between forest performance and climatic conditions over so few intervals would be questionable. At what point, however, does an accumulating series of successive re-measurements become a reliable basis for assessing forest climatic responses this way?

We used the two La Selva data series to address this question analytically (methods are detailed in Clark *et al.* (2010), with the data provided online in supplemental tables). We extracted from each tree-growth record (focal species: 24 re-measurements; stand-level: 10 re-measurements) all possible included subsequences (segments) of different lengths, starting with series of five successive re-measurements and progressively increasing segment length up to the total number of re-measurements in the record. For each segment, we calculated the Pearson correlation coefficient (r) between annual tree growth and annual means for daily minimum air temperature (henceforth 'temperature'). We then analyzed the relation between the number of re-measurements in a data series and the magnitude and sign of the correlation coefficient.

The analysis results were striking (Fig. 1). The highly significant negative relation between tree growth and temperature that is seen in the long data series (Clark *et al.* 2010) was not detectable from most of the short subsequences. Segments consisting of fewer than ten successive re-measurements produced a wide scatter of

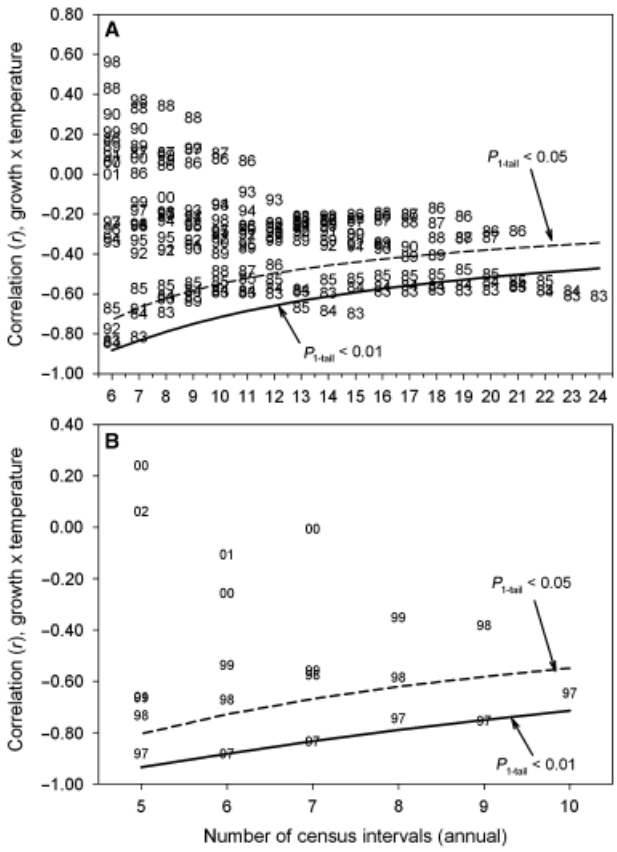

FIGURE 1. Effects of the number of census intervals and the timing of measurement sequences on the correlation between annual tree growth and annual means of daily minimum temperature at La Selva, Costa Rica. In both panels, solid and dashed lines indicate critical r values for 1-tail probabilities of 0.01 and 0.05, respectively. (A) Correlations based on sequences of successive re-measurements from the focal-species study; data-point labels indicate initial year for all possible sequences in the dataset of 6–24 successive census intervals. (B) Correlations based on sequences of successive re-measurements during the first 10 yr of the stand-level study. Data-point labels indicate initial year for all possible sequences in the dataset of 5–10 successive census intervals.

correlation coefficients, few of which were significant. Further, while most correlations from these short segments were negative, some were positive (the opposite direction from the long-term relationship). With progressively longer sequences, however, the growth–temperature correlation coefficients became consistently negative and were more frequently significant.

The explanation is climatic range. In both records, the mean among-year temperature range spanned by segments of a given length steadily increased with segment length. In the focal-species data, the mean across-year temperature range increased from 0.71°C for series of six re-measurements to 1.90°C at 24 re-measurements. Similarly, in the stand-level data, the average interyear temperature range increased from 0.56°C (five re-measurements) to 0.79°C (10 re-measurements). The growth–temperature correlations strengthened as the temperature range spanned by data series increased. For example, among the 19 possible sequences of only six re-measurements from the focal-species record (Fig. 1A), the three producing a significant ($P < 0.05$) negative correlation spanned larger among-year temperature ranges (0.85–1.48°C), than for all but one of the other sequences (0.29–0.77°C). All 26 highly significant ($P < 0.01$) negative correlations shown by any-length segments from the focal-species record (Fig. 1A) were based on the largest interyear temperature ranges (1.48–1.90°C). Conversely, all 66 segments of any length that spanned < 0.80°C produced nonsignificant correlations. Similarly, in the stand-level data (Fig. 1B), the three highly significant ($P < 0.01$) correlations were based on data sequences spanning the greatest among-year temperature range (0.79°C); all correlations based on smaller temperature ranges (0.39–0.61°C) were nonsignificant.

When multiple climatic sensitivities independently affect forest performance, as found at La Selva (dry-season rainfall and nighttime temperatures, Clark *et al.* 2010), the need for longer data series is reinforced. In bivariate correlation analyses to assess the effect of a single climatic factor on forest performance, variation in the other climatic influences ('noise' from the bivariate viewpoint) can obscure the relationship being assessed. While multivariate techniques enable teasing apart such independent climatic effects, they reduce the degrees of freedom provided by a data series.

In addition to the overall increase in climatic range with longer data series, both La Selva records showed a strong effect on spanned temperature range from the inclusion of an extreme year(s) in a given data series. At each sequence length in the focal-species record, those segments that included one or more of the three coolest years (1983–1985) had the greatest among-year temperature ranges (and the strongest correlations; Fig. 1A). Similarly, in the stand-level record, those segments (of any length) that included 1997, the record-hot mega-Niño year, all spanned the maximum temperature range (and all produced a significant growth–temperature correlation; Fig. 1B).

A related issue illustrated by the La Selva data is that multiyear census intervals strongly reduce the sampled climatic range compared with that seen with annual census intervals. When the annual temperatures over the 24 yr of the focal-species study are averaged over 5(4)-yr intervals to simulate the 5-yr census intervals used in many tropical-forest plots (Losos & Leigh 2004, Feeley *et al.* 2007), the spanned temperature range is halved, from 1.90°C (1-yr intervals) to 0.88°C (5-yr intervals).

The difficulty of obtaining a sufficient climatic range for climatic-response analyses will vary among climatic factors. As illustrated above, reaching an adequate temperature range with the La Selva data required long data series. Dry-season rainfall, in contrast, was characterized by consistently large variation within even relatively short series of years, greatly facilitating response detection. In the stand-level study, for all six sequences of only five forest re-measurements the r values of the growth–rainfall correlations were ≥ 0.80, and four of them were significant ($P < 0.05$); all 15 correlations based on six or more re-measurements were significant ($r = 0.81$–0.96, $P_{2\text{-tail}} = 0.03$–0.001).

These findings provide useful general guidance for studying forests' climatic sensitivities based on parallel records of growth and local climate. First, the strength and even the direction of climatic responses suggested by short data series can be highly misleading. Many measurement intervals can be needed to span sufficient contrasts in a climatic factor for accurate assessment of the forest's sensitivity to that factor. For a minority of studies, fortuitous timing (*e.g.*, an extreme climatic year early in the study) will increase the spanned climatic range. When the forest is sensitive to multiple independent climatic factors, evaluating the separate effects of these factors will require even longer data series. Compared with multiyear censuses, annual-scale measurements over the same study period greatly increase the observed climatic range and thus the ability to detect climatic responses. They also increase the probability of alternation of climatic conditions through the record. When repeated sequences of climatic ups and downs are tracked by the forest-growth rates, the evidence for a causal relationship is strengthened.

DISENTANGLING ONTOGENY, SUCCESSION, AND CLIMATIC EFFECTS

The long-term tree-growth studies at La Selva have produced multiple kinds of data on forest growth through time. Experiences with five qualitatively distinct types of tree- to forest-level growth data (Table 1) have underlined the need for appropriately tailored analyses of climatic response. The central question in each case is whether detection of the signal (a forest's climatic response) requires first removing the effects of directional 'noise' introduced by nonclimate factors. The approaches needed to do this will differ by data type, as we discuss below.

Tree-ring and cohort-based records.—The first two data categories (Table 1) involve growth histories of individual trees. An issue with such data, well demonstrated for tropical trees (Schulz 1960, Clark & Clark 1999), is that many species show large changes in inherent growth rates as individuals pass through successive size classes. When a tree's growth record spans a size range over which growth rates characteristically change in that species, the ontogenetic component needs to be removed from the growth record before climatic responses can be assessed. This adjustment ('detrending') should be based on independent data for that species,

TABLE 1. *Different data types from long-term studies of tree growth, with their associated analysis requirements for assessing climatic growth responses.*

Data type	Resulting metric	Analysis requirements
1. Tree-ring records Increment history based on a series of growth rings in a core or cross section from an individual tree	*Individual growth histories* Diameter increments through the part of the tree's life represented in the increment series	To discern climatic influences on the tree's growth history requires removing that species' characteristic ontogenetic changes in growth from the ring record (detrending)
2. Cohort-based records For a given species, growth through time by a sample of trees, all measured over each census interval of the record	*Species-level growth through time* Diameter increments through time of a sample of trees of a given species	To discern climatic influences on the cohort's growth history requires removing from each tree's increments that species' ontogenetic changes in growth (detrending)
3. Stand-level data (old-growth forest) Increments of *all* stems in the plot that are above the minimum diameter and alive through any census interval	*Forest-level growth through time* Plot-level mean diameter increment and estimated aboveground biomass change per hectare, in each census interval	If plot-level floristics and stem size distribution do not change through time, temporal growth variation can be interpreted as climatic (no detrending)
4. Stand-level data (successional forest) Increments of *all* stems in the plot that are above the minimum diameter and alive through any census interval	*Forest-level growth through time* Plot-level mean diameter increment and estimated aboveground biomass production per hectare, in each interval	Effects on stand-level growth of changing floristics and distributions of stem sizes must first be removed from the record, to detect climatic responses of stand-level growth
5. A subgroup of stems in a stand For a selected subgroup (species, size-class), increments of all stems in the plot that are above the minimum diameter and alive through any census interval	*Subgroup growth through time* Mean diameter increment and estimated aboveground biomass production per hectare by the subgroup, in each census interval	If the subgroup's stem size distribution and floristics are unchanged through time, temporal growth variation can be interpreted as climatic (no detrending); otherwise, detrending is required

ideally from other trees at the same site and spanning the same range of climatic variation as in the record being detrended.

For our 16-yr analysis of interannual growth variation at La Selva by cohorts of adults of the six focal tree species (Clark *et al.* 2003), independent data enabled us to identify size-related growth changes. For each species, the long-term study had produced large samples of annual diameter increments from many other individuals of all adult sizes and from 16 climate-years (Clark & Clark 2006). This much larger dataset enabled us to screen and, where necessary, detrend the growth record of each tree in the focal cohorts before assessing each record for relationships with climatic variation (Clark *et al.* 2003).

Unfortunately, datasets are available for few tropical tree species for independently characterizing the species' ontogenetic growth changes. When ontogenetic patterns are instead inferred from the same growth records that are being evaluated for climatic responses, there is a risk of a problem well recognized by dendroclimatologists (Esper *et al.* 2002, Sarris *et al.* 2007). Progressive effects on tree growth from a directional climatic trend, such as growth reductions in response to the recent decadal increases in tropical temperatures (Malhi & Wright 2004), could be erroneously attributed to ontogeny and removed from the record in the detrending operation, thus invalidating any inferences made from the record about the trees' climatic sensitivities.

Growth records based on tree-rings or cohort histories can also be affected by two types of ecological step changes. One is the large jump in growth that typically occurs when a tree moves from shaded conditions to the high crown illumination that comes with reaching the canopy (*i.e.*, 'release'; Brienen & Zuidema 2006). The subsequent increased growth in an individual's record could lead to a mistaken inference of a positive effect of contemporary directional climatic change. One solution is to restrict the analysis to canopy-level trees (Clark *et al.* 2003). Alternatively, each tree's record can be examined for such a step-change increase in growth, and analysis can be limited to the inferred post-release portion of the record (Jump *et al.* 2006). A second possible confounding effect (Lewis *et al.* 2004) is the growth slowdown that can precede tree death (Swaine 1994; D. B. Clark & D. A. Clark, unpubl. data). Such an effect can be ruled out, however, if all the studied trees survive several years beyond the period analyzed.

STAND-LEVEL DATA.—Repeatedly measuring all the live trees in a given plot of forest (data types 3, 4; Table 1) produces a very different type of growth record. Stand-level growth is integrated over all plant species and functional groups and over all stem sizes above the study's minimum size limit. Through time, successive stand-level growth data from a plot are produced by a progressively changing sample of individuals. In each interval, some trees die and new trees

grow into the sample. The stem turnover in tropical-forest stands can be large. In the La Selva stand-level study, for example, 24 percent of the 4400 live stems $\geq$ 10 cm diam in the initial sample (September 1997) had died by the end of year 10, while 25 percent of the 4407 live trees at the end of year 10 (September 2007) had recruited into the sample in years after the initial census.

For assessing climatic influences based on a time series of stand-level growth, a key issue is whether either the floristics or the size distribution of the stems in the plot significantly changes over the study period. If neither does, any temporal variation in the stand growth record can be straightforwardly related to climatic factors. If the sample's composition significantly changes over time, however, such that faster- or slower-growing size-classes or species become a greater fraction of the stems, the temporal patterns in stand-level growth will be the joint result of tree responses to climatic variation and the changes in stand composition.

Distinguishing these two components of the growth record is clearly required for all 'recovering forests' (Chazdon 2003), an increasing fraction of tropical forests. These forests (Chazdon 2008) include secondary stands developing on abandoned cleared land, forests being actively restored through human intervention, and forests recuperating from large natural disturbances. In such stands, the size and species distributions of the stems are directionally changing. If the successional component of the temporal growth changes can be isolated and quantified, that pattern could be used to detrend the record for this 'ontogeny' of stand-level growth, much as is done for the records of individual trees, and then the detrended record could be analyzed for climatic effects.

The question of possible internal change through time also needs to be investigated for stands considered to be old-growth. Although compositional stability is often assumed for such forests, a careful look may prove otherwise. For example, in the 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama (Losos & Leigh 2004), the abundance of 1–2 cm diam stems declined by 21 percent between 1982 and 2000 (Clark 2007). Significant directional floristic changes can also occur (Laurance *et al.* 2004, Chave *et al.* 2008).

Tree subsets within a stand.—The final category of forest-growth data (data type 5; Table 1) is based on a subgroup of trees in a stand-level dataset. When the focus is on a particular species or functional group, if there is little turnover (recruitment, mortality) in the selected group, the growth record will be largely from the same trees followed over a period of time, thus effectively a cohort. If the sample's size distribution shifts substantially over the interval (as the trees grow to progressively larger sizes), the record would need to be detrended for any characteristic ontogenetic effects on growth before it can be assessed for climatic responses. In contrast, if the focal group undergoes substantial stem turnover during the study period and shows no significant net change over time in the stem-size distribution, no detrending is needed. A second type of stand subgroup would be all stems in a particular size range. In this case, the sample needs to be assessed for changes in both size distribution and floristics over the observation period; any detected changes would need to be factored into the interpretation of the temporal growth variation.

Calculating the increments.—For all five types of tree-growth records (Table 1), a consideration is whether to work with absolute diameter increments, or instead to either relativize them to the individual's size (relative growth rate [RGR]; Newbery & Lingenfelder 2004, Feeley *et al.* 2007) or calculate basal-area increments. RGR maximizes growth variation for the smallest trees and reduces it at larger tree sizes; this metric, therefore, leads to a very different species-level growth ontogeny compared with that based on absolute diameter increments. Basal-area increments produce yet a third ontogenetic pattern (Clark & Clark 1999). We recommend basing analyses of tree climatic responses on absolute diameter increments. This metric is the most transparent and it facilitates comparisons of tree growth across studies.

HIGH-QUALITY CLIMATIC DATA: A CRITICAL ELEMENT

Assessing a forest's climatic responses through a study period requires a reliable meteorological record for that period. After recently spending the better part of 2 yr screening and documenting La Selva's records, we now keenly appreciate the need for careful evaluation, and where necessary, improvement of long-term climatic data. Analyses based on off-the-shelf meteorological records can produce highly misleading findings. To be usable for assessing forest climatic responses, the climatic records need to have been screened for many types of errors, gap-filled and, if necessary, corrected for long-term internal consistency.

Data quality.—Many kinds of quality-control issues arise with climatic monitoring, even for the simplest manual data (Aguilar *et al.* 2005). This means that researchers need to investigate whether the quality of an existing climatic record is sufficient for a given type of analysis. Two examples come from the early years of La Selva's weather station. The daily maximum/minimum temperatures were initially read by assorted, unsupervised station personnel, some of whom evidently read the wrong end of the sliding bar in the thermometers; the resulting erratic records had to be discarded and replaced by regression with off-site temperature records. Similarly, the early manual rainfall records include many missed days followed by multiple days' accumulated rainfall, making that part of the record unusable at the daily scale. This problem, also noted in the manual rainfall data from Barro Colorado Island, Panama (Windsor 1990), is likely to affect most manual rainfall records.

The installation of an automated station might be expected to eliminate such problems. Unfortunately, there is *no such thing* as an automatic weather station. Many issues arise with the records they produce. Examples from La Selva include: corrupted or missing data caused by low batteries or temporary system problems during logger re-programming; inaccurate daily summary metrics due to logger malfunction or because calculations were based on incompletely logged days; major data loss when a data storage module failed; and mis-managed data (*e.g.*, lost files or mis-pasting new

records into the master file). Further, as has happened twice at La Selva in recent years, a lightning strike can destroy the automated station; unless complete backup equipment is on site, large data gaps (weeks/months) can result.

The sensors themselves also present challenges. (1) Replicate sensors, even of the same model, can give significantly different readings. Installing a new temperature sensor on the La Selva station in 2007 produced a marked temperature offset (up to 0.7°C higher), requiring back correction of the subsequent record (see 'Internal consistency of the record'). A replacement sensor should first be run in parallel with the existing one, both to check that it is functioning correctly and to produce the necessary cross-sensor regression should there be a significant offset. (2) In the tropics, sensors need frequent maintenance against biotic interference. Wasps build nests in the chamber holding the temperature/humidity sensor. Spiders' webs can internally immobilize tipping-bucket rain gauges. The light sensors need regular cleaning to remove algal build-up and blockage from bird droppings or other detritis. (3) Both types of light sensors (pyranometers, quantum sensors) are far from 'plug and play'. They come with an individualized calibration value. Mis-entering this number into the datalogger program corrupts all data generated by that sensor. Further, quantum sensors progressively degrade under conditions of high temperatures and humidity. At La Selva, a large series of on-site re-calibrations ($N = 14$) showed these sensors can lose 10–20 percent of their sensitivity in the first year. When sensitivity loss is found, the re-calibration data can be used to back correct the sensor's data with a linear interpolation; however, linearity is an assumption, and these corrections are themselves subject to human error.

The quality of meteorological records can be greatly enhanced by real-time quality assurance and on-site measurement redundancy. The shorter the delay before data screening, the smaller the data gap when a sensor fails (*e.g.*, a frozen-up tipping-bucket rain gauge producing periods of null readings, a recurring problem at La Selva). Paralleling the automated data for key climatic factors with daily manual measurements (*e.g.*, rain gauge, high-quality maximum/minimum thermometers) enables error trapping and corrections, detection of significant sensor drift, and gap filling (see below). Similarly, running pairs of quantum sensors or pyranometers that are re-calibrated and replaced on different schedules reduces gaps and uncertainties in the long-term radiation record.

Filling the data gaps.—Unfilled data gaps can produce inaccurate summary climatic data. Given the episodic nature of both heavy rainfalls and droughts, a record with data gaps could mis-represent all rainfall metrics, which are based on totals over given periods. For other climatic factors, the potential impact of data gaps on summary metrics will be greatest for factors with substantial within-year variation (seasonality or extreme events).

Virtually all meteorological records contain data gaps. Even for well-maintained automated stations, corrupted data and data loss can result from sensor replacements, program changes, low batteries, and human error when downloading or managing data. Manual-gauge records, which depend on a person making the measurement every day of the year, are clearly subject to gaps from the human side. When both types of climatic records are screened for data quality, removing questionable data creates more gaps.

Gap filling is therefore a general need for climatic records. On-site redundancy of sensors is the best solution. When only one of a pair of parallel sensors fails, data gaps can be filled based on cross-sensor regressions. A second weather station running elsewhere at the study site provides added benefits (protection against major data loss from total failure of a station; information on how climatic conditions vary spatially within the study site). When no such cross-regression solution exists, however, gaps can be filled by 'bracket-averaging' (filling the data gap with the average of prior and succeeding good data) or using a seasonal model for that climatic factor based on long-term local weather data. When all cases of gap filling and the method used in each case are specified in the climatic record's documentation, subsequent data users have the option to reconstruct the record differently based on the original data.

Internal consistency of the record.—A fundamental concern is that changes over time in measurement methods can seriously corrupt long-term climatic records. Artifactual temporal variation in climatic data can be caused by sensor/gauge replacements, by relocating the weather station, by moving sensors, by major vegetation/structural changes around an existing station (Pielke *et al.* 2007), or by changing how climatic metrics are derived (see below). At La Selva, for example, daily maximum air temperatures reported from the automated sensor are *ca* 0.6°C higher than the manual thermometer readings; likely causes are the thermometer's greater temporal inertia and higher temperatures in the automated sensor's small metal enclosure. Another example is the consistent difference between rainfall measured with a tipping-bucket rain gauge at the top of an above-canopy tower during many periods of the last several years (data provided by S. F. Oberbauer) and that measured by manual gauge at the (ground-based) La Selva met station *ca* 2 km away. The data for daily rainfall from the southwest-trail tower during the year 2000, for example, while highly correlated with those of the La Selva met station ($r^2 = 0.94$, $N = 203$ d), were 15 percent lower.

Any long-term climatic record is highly likely to include one or more significant methods changes, such as the switch from manual to automated temperature measurements, or a sensor replacement producing a data offset. The record's long-term internal consistency therefore depends on explicit adjustment of the data from either before or after such changes, to remove the effect of the methods change on the long-term record. To make such adjustments requires parallel data series from the two instruments/locations/heights over a sufficient period to obtain a good regression between them, and replacement of the actual prior (or succeeding) data with values based on this cross regression.

A researcher unaware of these issues and in need of climatic data for their study site might be tempted to splice together disparate climatic datasets that cover different parts of their study period. Such a patched-together record is unfortunately likely to produce an erroneous climate history. Even when an apparently continuous record is available, its internal consistency should be investigated.

INSIGHTS FROM THE LA SELVA RECORDS.—At La Selva, duplicated sensors and parallel weather stations on site, along with correlated off-site temperature records, have made it possible to construct internally consistent, complete records for daily maximum and minimum temperatures and daily rainfall over the last 27 yr and for monthly rainfall since 1957 (http://www.ots.ac.cr/meteoro/). Although the principal weather station was re-located in 1982, rainfall gauges were run in parallel at the old and new sites for 10 yr, enabling adjustment of the earlier rainfall record by regression. Since early 1992, parallel manual and automated measurements have provided on-site benchmarking for daily maximum/minimum temperatures and daily rainfall. Additional help for gap filling and quality checks for the climatic data have also come from the meteorological arrays run on one or two above-canopy towers during many periods since 1997 (data provided by J. O'Brien, H. W. Loescher, and S. F. Oberbauer). Two insights provided by the resulting long-term records merit discussion.

MEAN TEMPERATURE.—One discovery based on the La Selva records is a dramatic illustration of how internal inconsistency can corrupt a climatic record, in this case for the metric mean temperature, a key climatic parameter for study sites. Daily mean temperature is straightforwardly produced by programming an automated station to average all readings from a temperature sensor over each 24-hr period. But how is/was this metric derived at sites lacking an automated station? Aguilar *et al.* (2003) list four distinct ways mean temperature has been estimated from manual data. A study of Brazilian temperature records, for example, found the mean temperature data to be based on three different estimation methods involving combining and differentially weighting manual-thermometer readings taken at two, three, or four different times in a 24-hr period (Victoria *et al.* 1998). One often-used formula has been to average the readings of each day's maximum and minimum temperatures as read from maximum/minimum thermometers.

This last method underlies the still standard citation (Sanford *et al.* 1994) for La Selva's 'average monthly air temperature' being 25.8°C. With the automated station paralleled by daily maximum/minimum thermometer readings at La Selva since 1992, it is now possible to compare the values for mean temperature derived these two ways. Figure 2A gives the annual values based on complete (gap filled) records of both versions of this metric over the 14-yr period 1993–2006 at La Selva. While both versions indicate increasing mean temperatures over this period, the actual (automated) values are *ca* 1°C lower than the manual-based estimates, and the latter indicate much stronger increases in mean temperature over this period (+0.61°C per decade) than are shown by the actual logged values (+0.25°C per decade).

Further, had the two records been simply spliced together at a hypothetical time of switching from the manual measurements to an automated station (Fig. 2B), the spliced record would have spuriously indicated strong cooling over this period (−0.77°C per decade). Had the La Selva record for mean temperature been produced by simply extending the prior series of manual data-based

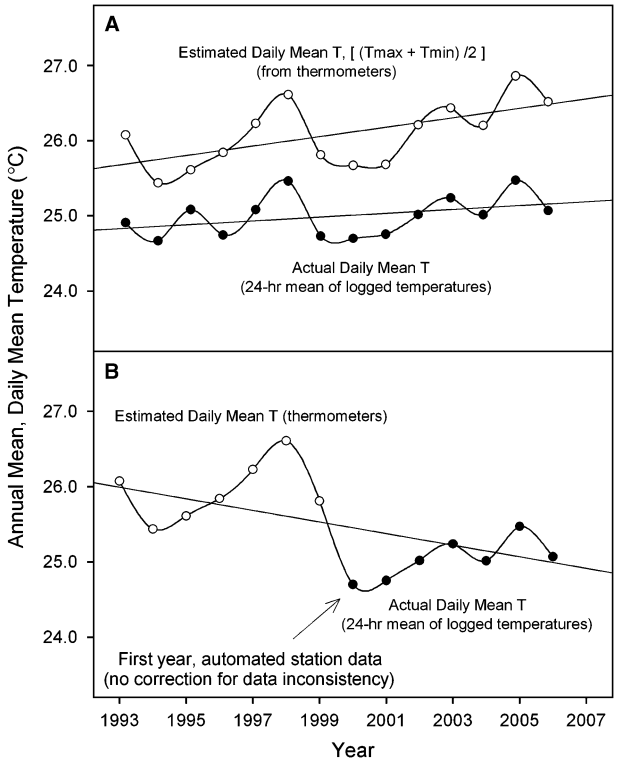

FIGURE 2. Effects of methods differences on the metric mean temperature at La Selva, Costa Rica for the period 1993–2006. (A) Annual means of daily mean temperature as estimated from manual-thermometer data (upper line; mean temperature = −95.94+0.06year, $r = +0.60$, $P_{2\text{-tail}} = 0.02$) are substantially higher and indicate a stronger directional increase than shown by annual values based on 24-h averages of logged temperatures from an automated weather station (lower line: mean temperature = −24.68+0.02year, $r = +0.39$, $P_{2\text{-tail}} = 0.17$). (B) An illustration of how joining data series that were generated by different methods can strongly corrupt a long-term record: a spurious cooling trend is indicated (mean temperature = 179.13 − 0.08year, $r = -0.56$, $P_{2\text{-tail}} = 0.04$) when data from before and after a hypothetical switch from manual to automated measurements are joined with no adjustment for long-term consistency.

estimates with the automated data that began in 1992, the resulting internally inconsistent record would have indicated a spurious cooling on the scale of the long-term interyear range in minimum temperatures over which we found large effects on La Selva tree growth.

It is generally recognized (Victoria *et al.* 1998, New *et al.* 2002) that methods changes through time and among-station methods differences could be affecting the trends inferred from available records of mean temperature from most countries. In the world climatic data bases, some tropical sites' records for mean temperature (Malhi & Wright 2004) have been variously estimated from manual data. The longer records may include shifts between methods of estimating mean temperatures from such data; such a shift in Brazilian temperature records was found by Victoria *et al.* (1998) to strongly affect temperature trends from records initiated before 1938. Tropical records initiated in recent decades may come

exclusively from an automated weather station. Still others, perhaps many, have spanned the switch from manual to automated temperature measurements.

Clearly, for any given site, internal inconsistency produced by a switch in estimation methods, or by the change from manual to automated data, can seriously corrupt a long-term climatic record. As illustrated by the example based on different methods for deriving mean temperature at La Selva (Fig. 2), it will be key to first investigate the methods underlying existing climatic records (studying the available documentation, consulting with the site manager) before considering using them in climatic-response and climatic-trend studies. Especially when datasets are not well documented, useful precautions are to inspect the total graphed record for large step changes and to compare the record with others from nearby areas and to a global tropical index like the tropical Goddard Institute for Space Studies Annual mean Land-Ocean Temperature Index (http://data.giss.nasa.gov/gistemp/tabledata/ZonAnn.Ts+dSST.txt). The La Selva long-term records of annual mean temperature (16 yr) and of annual means of daily minimum temperature (26 yr) are both highly significantly correlated ($P < 0.0001$) with this independent global index ($r^2 = 0.80$ and 0.76, respectively).

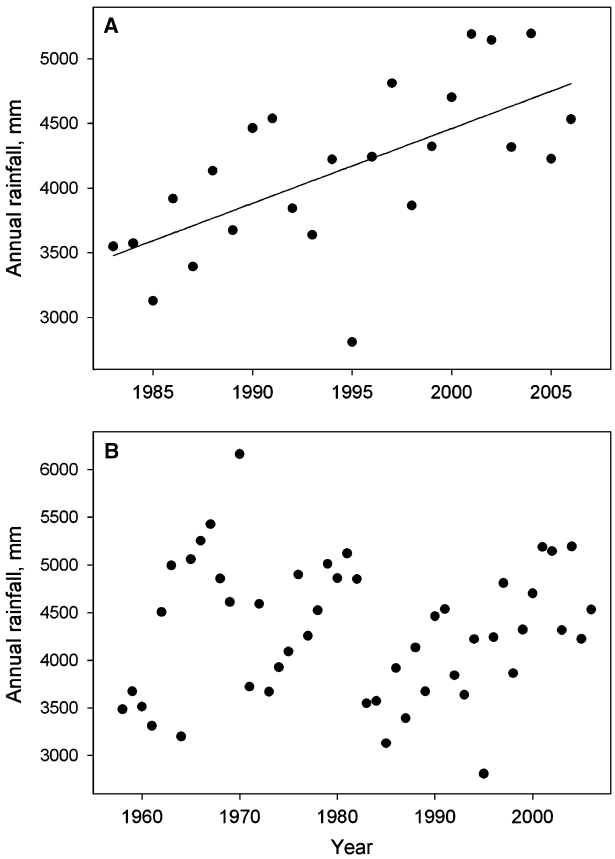

FIGURE 3. The value of long climatic records as context for interpreting short-term patterns. While a significant rainfall increase is seen in recent data (A: 1983–2006) from La Selva, Costa Rica (see text), the total La Selva record (B: 1958–2006) in fact indicates no long-term change.

THE IMPORTANCE OF A LONG VIEW.—A second insight gained from working with the La Selva climatic data is the value of long-term records as context for interpreting shorter-term climatic patterns. During the 24-yr period of the focal-species study, there was a highly significant increase in annual rainfall at La Selva (Fig. 3A; $r^2 = 0.42$, $P < 0.001$). Had the available information been limited to this record, a reasonable expectation might have been that La Selva was headed for further increases in rainfall, an apparent effect of global climatic change. The total 49-yr La Selva rain record, however (Fig. 3B), shows there has been no significant directional change in annual rainfall ($r^2 = 0.002$). Before drawing conclusions from a local climatic record, particularly if it is limited to a few decades, it will be valuable to compare it with longer data series from neighboring locales (Aguilar *et al.* 2003).

CONCLUSIONS

Relating long time series of repeat measurements of the performance of representative tropical forests around the world to parallel records of local climatic variation is one promising approach for assessing this biome's current climatic sensitivities. Although such studies cannot provide certainty regarding how forests will respond in future decades (when temperatures will exceed currently observed tropical ranges; Wright *et al.* 2009), they can reveal which climatic factors are already provoking forest responses in different areas of the world tropics. Such information would improve current vegetation process models, producing more realistic projections of likely futures for these ecosystems.

Based on the analyses and observations presented in this paper, three aspects merit particular attention for this research approach. (1) While long-term forest measurements are underway in many tropical forests worldwide, because multiyear census intervals are nearly universally used, the accumulated data series for most forests is still very small (Clark 2007). More broadly implementing annual-scale re-measurements (as is underway in the CTFS plots) will greatly speed progress toward sufficient data series in many tropical forests. (2) Before carrying out analyses for climatic effects on forest performance, investigators need to evaluate the forest-growth data for possible confounding effects of tree ontogeny or stand-level compositional change and then make the appropriate data adjustments. (3) More attention needs to be focused on sites' climatic records. Greater resources need to be dedicated to climatic monitoring for tropical-forest sites. On-site redundancy for monitoring the most critical climate variables (*e.g.*, manual and automated measurements of daily rainfall and temperatures) and real-time quality assurance can greatly improve long-term climatic records. Issues of data quality are particularly important for long-term records of temperature, given the large growth responses found at La Selva over quite small interannual temperature ranges. Investigators should carefully evaluate long-term climate records before using them to assess climatic impacts on forest performance. Given the global implications of findings from such studies, it is critically important to get them right.

ACKNOWLEDGMENTS

We thank subject editor R. Chazdon and two anonymous reviewers for constructive comments on the manuscript. Partial support of the authors during manuscript preparation was provided by National Science Foundation grants EAR-0421178, LTREB DEB-0640206, and LTREB DEB-0841872. The focal-species and forest inventory studies have been made possible by current and past support from NSF's LTREB program and (in 2003–2008) Conservation International's TEAM Initiative. We thank OTS and the La Selva staff for excellent logistic support, for the institutional investments of personnel and resources for on-site climate monitoring, and for protecting the La Selva forest.

LITERATURE CITED

Adams, J. M., and G. Piovesan. 2005. Long series relationships between global interannual CO_2 increment and climate: Evidence for stability and change in role of the tropical and boreal-temperate zones. Chemosphere 59: 1595–1612.

Aguilar, E., I. Auer, M. Brunet, T. C. Peterson, and J. Wieringa. 2003. Guidelines on climate metadata and homogenization. World Meteorological Organization Technical Document No. 1186, World Climate Data and Monitoring Programme (WCDMP) Series. World Meteorological Organization, Geneva, Switzerland.

Aguilar, E., T. C. Peterson, P. Ramírez Obando, R. Frutos, J. A. Retana, M. Solera, J. Soley, I. González García, R. M. Araújo, A. Rosa Santos, V. E. Valle, M. Brunet, L. Aguilar, L. Alvarez, M. Bautista, C. Castañón, L. Herrera, E. Ruano, J. J. Sinay, E. Sánchez, G. I. Hernández Oviedo, F. Obed, J. E. Salgado, J. L. Vázquez, M. Baca, M. Gutiérrez, C. Centella, J. Espinosa, D. Martínez, B. Olmedo, C. E. Ojeda Espinoza, R. Núñez, M. Haylock, H. Benavides, and R. Mayorga. 2005. Changes in precipitation and temperature extremes in Central America and northern South America, 1961–2003. J. Geophys. Res, 110, D23107, doi: 10.1029/12005JD006119.

Berthelot, M., P. Friedlingstein, P. Ciais, J.-L. Dufresne, and P. Monfray. 2005. How uncertainties in future climate change predictions translate into future terrestrial carbon fluxes. Global Change Biol. 11: 959–970.

Bonan, G. B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320: 1444–1449.

Brando, P. M., D. C. Nepstad, E. A. Davidson, S. E. Trumbore, D. Ray, and P. Camargo. 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: Results of a throughfall reduction experiment. Philos. Trans. R. Soc. Lond., Ser. B 363: 1839–1848.

Brienen, R. J. W., and P. A. Zuidema. 2006. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. J. Ecol. 94: 481–493.

Chave, J., R. Condit, H. C. Muller-Landau, S. C. Thomas, P. S. Ashton, S. Bunyavejchewin, L. L. Co, H. S. Dattaraja, S. J. Davies, S. Esufali, C. E. N. Ewango, K. J. Feeley, R. B. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, T. B. Hart, C. Hernández, S. P. Hubbell, A. Itoh, S. Kiratiprayoon, J. V. LaFrankie, S. Loo de Lao, J.-R. Makana, M. N. S. Noor, A. R. Kassim, C. Samper, R. Sukumar, H. S. Suresh, S. Tan, J. Thompson, M. D. C. Tongco, R. Valencia, M. Vallejo, G. Villa, T. Yamakura, J. K. Zimmerman, and E. C. Losos. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. PLoS Biol. 6, e45, doi: 10.1371/journal.pbio.0060045.

Chazdon, R. L. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. Perspect. Plant Ecol. Evol. Syst. 6: 51–71.

Chazdon, R. L. 2008. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science 320: 1458–1460.

Clark, D. A. 2007. Detecting tropical forests' responses to global climatic and atmospheric change: Current challenges and a way forward. Biotropica 39: 4–19.

Clark, D. A., and D. B. Clark. 1999. Assessing the growth of tropical rain forest trees: Issues for forest modeling and management. Ecol. Appl. 9: 981–997.

Clark, D. A., S. C. Piper, C. D. Keeling, and D. B. Clark. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proc. Natl. Acad. Sci. 100: 5852–5857.

Clark, D. B., and D. A. Clark. 2006. Tree growth, mortality, physical condition, and microsite in an old-growth lowland tropical rain forest. Ecology 87: 2132.

Clark, D. B., D. A. Clark, and S. F. Oberbauer. 2010. Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO_2. Global Change Biol. 16: 747–759.

Denman, K. L., G. Brasseur, A. Chidthaisong, P. Ciais, P. M. Cox, R. E. Dickinson, D. Hauglustaine, C. Heinze, E. Holland, D. Jacob, U. Lohmann, S. Ramachandran, P. L. Da Silva Dias, S. C. Wofsy, and X. Zhang. 2007. Couplings between changes in the climate system and biogeochemistry. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller (Eds.). Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change, pp. 499–587. Cambridge University Press, Cambridge, UK.

Doughty, C. E., and M. L. Goulden. 2008. Are tropical forests near a high temperature threshold? J. Geophys. Res. – Biogeosci. 113, G00B07, doi: 10.1029/2007JG000632.

Esper, J., E. R. Cook, and F. H. Schweingruber. 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. Science 295: 2250–2253.

Feeley, K. J., S. J. Wright, M. N. N. Supardi, A. R. Kassim, and S. J. Davies. 2007. Decelerating growth in tropical forest trees. Ecol. Lett. 10: 1–9.

Fisher, R. A., M. Williams, A. Lola da Costa, Y. Malhi, R. F. Da Costa, S. Almeida, and P. Meir. 2007. The response of an Eastern Amazonian rain forest to drought stress: Results and modelling analyses from a throughfall exclusion experiment. Global Change Biol. 13: 2361–2378.

Jump, A. S., J. M. Hunt, and J. P. Peñuelas. 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Global Change Biol. 12: 2163–2174.

Kier, G., J. Mutke, E. Dinerstein, T. H. Ricketts, W. Küper, H. Kreft, and W. Barthlott. 2005. Global patterns of plant diversity and floristic knowledge. J. Biogeogr. 32: 1107–1116.

Körner, C. 2009. Responses of humid tropical trees to rising CO_2. Annu. Rev. Ecol. Syst. 40: 61–79.

Laurance, S. G. W., W. F. Laurance, H. E. M. Nascimento, A. Andrade, P. M. Fearnside, E. R. G. Rebello, and R. Condit. 2009. Long-term variation in Amazon forest dynamics. J. Veg. Sci. 20: 323–333.

Laurance, W. F., A. A. Oliveira, S. G. Laurance, R. Condit, H. E. M. Nascimento, A. C. Sanchez-Thorin, T. E. Lovejoy, A. Andrade, S. D'Angelo, J. E. Ribeiro, and C. W. Dick. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. Nature 428: 171–175.

Lewis, S. L., J. Lloyd, S. Sitch, E. T. A. Mitchard, and W. F. Laurance. 2009. Changing ecology of tropical forests: Evidence and drivers. Annu. Rev. Ecol. Syst. 40: 529–549.

Lewis, S. L., Y. Malhi, and O. L. Phillips. 2004. Fingerprinting the impacts of global change on tropical forests. Philos. Trans. R. Soc. Lond., Ser. B 359: 437–462.

Lloyd, J., and G. D. Farquhar. 2008. Effects of rising temperatures and [CO_2] on the physiology of tropical forest trees. Philos. Trans. R. Soc. Lond., Ser. B 363: 1811–1817.

Losos, E. C., and E. G. E. Leigh (Eds.). 2004. Tropical forest diversity and dynamism. The University of Chicago Press, Chicago, Illinois.

Malhi, Y., L. E. O. C. Aragão, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, C. McSweeney, and P. Meir. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proc. Natl. Acad. Sci. 106: 20610–20615.

Malhi, Y., and J. Wright. 2004. Spatial patterns and recent trends in the climate of tropical forest regions. Philos. Trans. R. Soc. Lond., Ser. B 359: 311–329.

Matthews, H. D., M. Eby, T. Ewen, P. Friedlingstein, and B. J. Hawkins. 2007. What determines the magnitude of carbon cycle-climate feedbacks?. Global Biogeochem. Cycles 21, GB2012, doi:10.1029/2006GB002733.

New, M., D. Lister, M. Hulme, and I. Makin. 2002. A high-resolution data set of surface climate over global land areas. Clim. Res. 21: 1–25.

Newbery, D. M., and M. Lingenfelder. 2004. Resistance of a lowland rain forest to increasing drought intensity in Sabah, Borneo. J. Trop. Ecol. 20: 613–624.

Phillips, O. L., L. E. O. C. Aragão, S. L. Lewis, J. B. Fisher, J. LLoyd, G. López-González, Y. Malhi, A. Monteagudo, J. Peacock, C. A. Quesada, G. van der Heijden, S. Almeida, I. Amaral, L. Arroyo, G. Aymard, T. R. Baker, O. Bánki, L. Blanc, D. Bonal, P. Brando, J. Chave, A. C. Alves de Oliveira, N. Dávila Cardozo, C. I. Czimczik, T. R. Feldpausch, M. A. Freitas, E. Gloor, N. Higuchi, E. Jiménez, G. Lloyd, P. Meir, C. Mendoza, A. Morel, D. A. Neill, D. Nepstad, S. Patiño, M. C. Peñuela, A. Prieto, F. Ramírez, M. Schwarz, J. Silva, M. Silveira, A. Sota Thomas, H. ter Steege, J. Stropp, R. Vásquez, P. Zelazowski, E. Alvarez Dávila, S. Andelman, A. Andrade, K.-J. Chao, T. Erwin, A. Di Fiore, C. E. Honorio, H. Keeling, T. J. Killeen, W. F. Laurance, A. Peña Cruz, N. C. A. Pitman, P. Núñez Vargas, H. Ramírez-Angulo, A. Rudas, R. Salamão, N. Silva, J. Terborgh, and A. Torres-Lezama. (2009). Drought sensitivity of the Amazon rainforest. Science 323: 1344–1347.

Pielke, R. A. Sr., C. A. Davey, D. Niyogi, F. Souleymane, J. Steinweg-Woods, K. Hubbard, X. Lin, M. Cai, Y.-K. Lim, H. Li, J. Nielsen-Gammon, K. Gallo, R. Hale, R. Mahmood, S. Foster, R. T. McNider, and P. Blanken. 2007. Unresolved issues with the assessment of multidecadal global land surface temperature trends. J. Geophys. Res, 112, D24S08, doi:10.1029/2006JD008229.

Sanford, R. L. Jr., P. Paaby, J. C. Luvall, and E. Phillips. 1994. Climate, geomorphology, and aquatic systems. *In* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). La Selva: Ecology and natural history of a Neotropical rain forest, pp. 19–33. University of Chicago Press, Chicago, Illinois.

Sarris, D., D. Christodoulakis, and C. Körner. 2007. Recent decline in precipitation and tree growth in the eastern Mediterranean. Global Change Biol. 13: 1187–1200.

Schulz, J. P. 1960. Ecological studies on rain forest in northern Suriname. Proc. K. Ned. Akad. Wet. 253: 1–267.

Swaine, M. D. 1994. Long-term studies of tropical forest dynamics. *In* R. A. Leigh and A. E. Johnston (Eds.). Long-term experiments in agricultural and ecological sciences, pp. 305–319. CAB International, Wallingford, UK.

Tribuzy, E. S. 2005. Variacões da temperatura foliar do dossel e o seu efeito na taxa assimilatória de CO_2 na Amazônia Central. PhD dissertation, Universidade de São Paulo, São Paulo, Brazil.

Victoria, R. L., L. A. Martinelli, J. M. Moraes, M. V. Ballester, V. Krusche, G. Pellegrino, R. M. B. Almeida, and J. E. Richey. 1998. Surface air temperature variations in the Amazon Region and its borders during this century. J. Clim. 11: 1105–1110.

Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: Long-term records from Barro Colorado Island, Panamá. Smithsonian contributions to the earth sciences, Vol. 29. Smithsonian Institution Press, Washington, DC.

Wright, S. J., H. C. Muller-Landau, and J. Schipper. 2009. The future of tropical species on a warmer planet. Conserv. Biol. 23: 1418–1426.