Drought Sensitivity of the Amazon Rainforest

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Amazon forests are a key but poorly understood component of the global carbon cycle. If, as anticipated, they dry this century, they might accelerate climate change through carbon losses and changed surface energy balances. We used records from multiple long-term monitoring plots across Amazonia to assess forest responses to the intense 2005 drought, a possible analog of future events. Affected forest lost biomass, reversing a large long-term carbon sink, with the greatest impacts observed where the dry season was unusually intense. Relative to pre-2005 conditions, forest subjected to a 100-millimeter increase in water deficit lost 5.3 megagrams of aboveground biomass of carbon per hectare. The drought had a total biomass carbon impact of 1.2 to 1.6 petagrams (1.2×10^{15} to 1.6×10^{15} grams). Amazon forests therefore appear vulnerable to increasing moisture stress, with the potential for large carbon losses to exert feedback on climate change.

Old-growth forests in Amazonia store 120 Pg (1.2×10^{17} g) of carbon in their biomass (*1*), and through photosynthesis and respiration they process 18 Pg C annually (*2*), more than twice the rate of anthropogenic fossil fuel emissions. Relatively small changes in Amazon forest dynamics therefore have the potential to substantially affect the concentration of atmospheric CO_2 and thus the rate of climate change itself. A key parameter in determining the magnitude of this effect is the sensitivity—or resilience—of tropical forests to drought. Increased moisture stress is a dominant feature of some modeled 21st-century climate scenarios for Amazonia, particularly for southern Amazonia (*3*–*5*), and there is some evidence that this has already commenced (*6*). Prolonged tropical droughts can kill trees (*7*–*10*), and some models predict climate-induced Amazon dieback this century (*4*, *11*, *12*). But it has also been suggested that dry conditions may cause Amazon forests to "green up" (*13*, *14*) and that increases in solar radiation during drier periods boost tropical productivity (*15*–*17*). Large-scale on-the-ground assessments of the ecological impacts of tropical droughts are completely lacking, precluding tests of these ideas.

In 2005, large areas of the Amazon Basin experienced one of the most intense droughts of the past 100 years (*18*), providing a unique opportunity to directly evaluate the large-scale sensitivity of tropical forest to water deficits. The 2005 event was driven not by El Niño, as is often the case for Amazonia, but by elevated tropical North Atlantic sea surface temperatures (*18*), which affected the southern two-thirds of Amazonia and especially the southwest through reduced precipitation as well as higher-than-average temperatures (*18*, *19*). Both the anomalous North Atlantic warming and its causal link to Amazon drought are reproduced in some recent modeled scenarios for 21st-century climates (*5*, *12*), and thus the event of 2005 may provide a proxy for future climate conditions. Through a large long-term research network, RAINFOR, we have monitored forest plots across the basin for 25 years. After the drought we conducted an emergency recensus program covering all major Amazon nations, climates, soils, and vegetation types. Here we report the results of this large-scale natural experiment to assess the impact of tropical drought on the ground.

By 2005 the RAINFOR network consisted of 136 permanent plots located in old-growth forest distributed across 44 discrete landscapes ("sites") (*20*). We used tree diameter, wood density, and allometric models to compute biomass at each point in time, as well as rates of biomass gain ("growth") and loss ("mortality") between censuses, correcting for possible sampling effects (*20*). To establish the pre-2005 Amazon baseline, we first determined the long-term biomass changes in our plots. To assess drought impacts, we focused on the 2005 event, evaluating net biomass change, growth, and mortality and the differences in these relative to earlier records, focusing on the 55 plots that were regularly censused both before and after the drought. To

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estimate the moisture stress at each location, we compiled meteorological data sets and determined the maximum dry-season intensity for each year in the 2005 measurement interval and for each year in the entire pre-2005 measurement period. Forest sensitivity to drought was then determined by relating the change in biomass dynamics to the change in mean maximum moisture stress. The results presented below are based on the sampling unit of individual plots; in (*20*) we explore the sensitivity of our findings to varying both the spatial scale of the sampling unit and the method of estimating moisture stress.

Before 2005, plots recorded a long-term net increase in aboveground (dry-weight) biomass, weighted by sampling effort, of 0.89 Mg ha^{-1} year^{-1} (bootstrapped 95% confidence intervals: 0.65, 1.12). This increase occurred through a multidecadal period spanning dry and wet episodes, including several El Niño events. The net biomass gain was widespread and is not a sampling artifact (*20*). These results confirm previous measured and modeled indications of a persistent biomass carbon sink—now based on a much larger data set—and are consistent with Amazon forest productivity increasing with time (*21*–*25*).

By contrast, through the 2005 drought period there was no net biomass increase in monitored plots [net rate of change –0.71 (–1.93, +0.30) Mg ha^{-1} year^{-1}; n = 55, interval mean 1.97 years]. Before 2005, 76% of plots (93 of 123) gained biomass, but during the 2005 interval only 51% did so (28 of 55); this difference is highly significant (P < 0.01, Mann-Whitney U test). To assess whether biomass changes were drought-related, we developed meteorological and soil data sets to estimate evapotranspirational demand and soil moisture stress (*20*). For plots with longer and more intense moisture deficits than normal, there were clear net losses [–1.62 (–3.16, –0.54) Mg ha^{-1} year^{-1}; n = 38, interval mean 1.96 years]. The distribution through time of all measured biomass dynamics (Fig. 1) reveals that the drought coincided with the first substantial decline in measured biomass in Amazonian plots since measurements started. However, fingerprinting the drought impact is complicated by switching among plots being monitored, the nonequilibrium initial conditions, divergent climatologies and soils, and contrasting conditions in 2005 itself. Within-plot analyses help to control for such effects and confirm the drought's impact: Relative to their extended period of earlier biomass gains, plots monitored through 2005 experienced negative change [difference = –1.50 (–3.01, –0.44) Mg ha^{-1} year^{-1}; n = 43]. Among the 28 plots with longer and more severe water deficits than normal during 2005, the rate of aboveground woody biomass accumulation declined by 2.39 (1.12 to 3.97) Mg ha^{-1} year^{-1}, whereas by contrast the 15 nondroughted plots continued to gain [difference = +0.76 (–0.78, +2.00) Mg ha^{-1} year^{-1}].

The Amazon forest spans a large climatic range, from the almost aseasonal high-precipitation northwest to the strongly seasonal southern fringes with frequent prolonged moisture deficits (*26*, *27*). Distributions of neotropical trees reflect their drought sensitivity (*28*), so we hypothesized that any drought impacts will be experienced by plants as a function of relative departure from their long-term environmental conditions. For each site, we therefore estimated the magnitude of the drought experienced during the 2005 interval relative to local, long-term estimates of water balance. We find that relative drought is indeed strongly

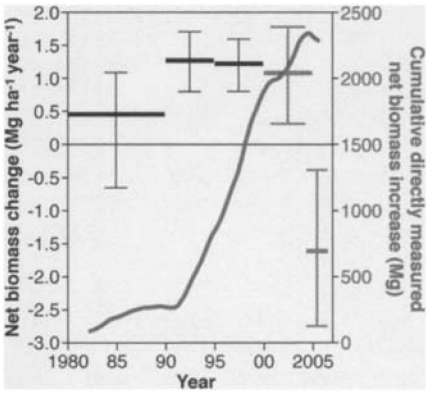

Fig. 1. Interval-by-interval, plot-by-plot net biomass change measured in Amazonia since 1980. The multidecadal carbon sink is evident, strongly reversed in 2005. Long sampling intervals may have obscured earlier fluctuations (see fig. S1). Red line (scale on right) represents the total cumulative biomass increase of Amazon trees ≥10 cm in diameter as actually measured in permanent plots, as a function of the mid-date of each census interval, with a running mean of 50 intervals. Black and blue distributions (scale on left) represent mean and 95% bootstrapped confidence intervals for interval-by-interval biomass change weighted by sampling effort (*20*). Black distributions indicate predefined periods (1980–1989, 1990–1994, 1995–1999) where the chronological span of each bin represents the interval mid-dates that fall within that period. Blue distributions align intervals with the 2005 drought event to reveal its impact, contrasting all 2000–2004 predrought measurements with all droughted plots monitored in 2005.

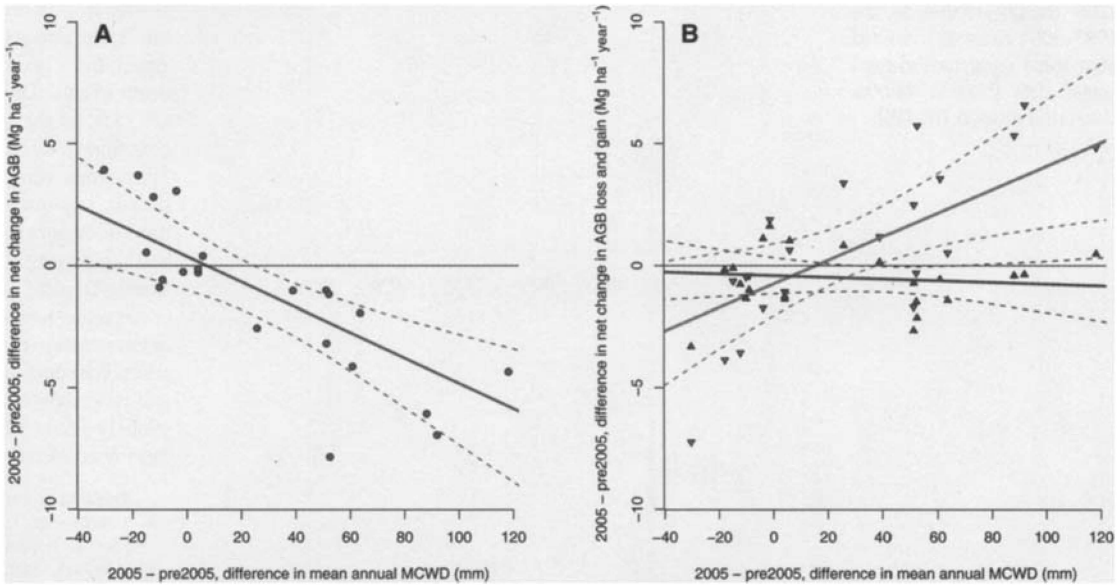

Fig. 2. Biomass dynamics response to the relative intensity of the 2005 drought. Differences in (**A**) plot biomass change (blue) and (**B**) mortality rate (red) and growth rate (green) are shown for trees ≥10 cm in diameter for the drought interval relative to pre-2005 as a linear function of drought relative intensity, weighted by monitoring effort (*20*). Change in drought intensity is measured by change in maximum climatological water deficit (MCWD, accounts only for rainfall). Uncertainty in precipitation is included in the bootstrapped estimates of the relationship of difference in biomass change versus difference in MCWD and confidence intervals (*20*). Plots known to have different 2005 interval MCWD are treated as independent; values are otherwise averaged across contributing plots. Alternative models that account for variation in soil properties, evapotranspiration, and plot definitions give very similar results (*20*). Polynomial or break-point functions do not provide closer fits.

implicated as the driver of the network-wide shift in forest behavior (Fig. 2) but that the absolute intensity of the 2005 dry period was only weakly related to biomass dynamics (fig. S5): Those forests experiencing the most elevated moisture stress relative to their long-term mean tended to lose the most biomass relative to their pre-2005 trend (Fig. 2). These losses were driven by occasionally large mortality increases and by widespread but small declines in growth. Our method may fail to capture growth impacts well because intervals were longer than the period of potential moisture constraint, thereby masking its effects (drought can kill trees but can only temporarily stop growth). Analysis at the site level confirms that the relationship between forest response and droughting is not driven by a few anomalous plots (*20*), and accounting for local soil water-holding capacity, temperature, humidity, and radiation shows this relationship to be robust regardless of how the moisture balance is estimated (*20*). Moreover, just as the earlier net gains were widespread across the basin, the 2005 declines were well distributed spatially (Fig. 3). From Fig. 2, and assuming a proportional impact on smaller trees and lianas (*20*), we estimate that an average forest hectare subject to a 100-mm increase in maximum water deficit lost 5.3 Mg of aboveground biomass carbon over the average 1.97-year drought census interval relative to pre-2005 conditions (bootstrapped confidence intervals 3.0, 8.1).

We also recorded the identity of trees that died. Fast-growing, light-wooded trees may be especially vulnerable to drought by cavitation or carbon starvation (*7*, *29*–*31*), and consistent with this, trees dying during the 2005 period had lower wood densities than those dying before. In 25 drier-than-average plots with dead trees identified, trees recorded as dead in 2006 were 5% lighter than in previous censuses [mean wood density of dead trees fell from 0.60 to 0.57 g cm^{-3} ($P = 0.02$) (*20*)]. Apparently, Amazon drought kills selectively and therefore may also alter species composition, pointing to potential consequences of future drought events on the biodiversity in the Amazon region.

Relative to the predrought sink, we estimate a total impact of –1.21 Pg C (–2.01, –0.57) by simply scaling the per-plot impact by the total droughted area (~3.3×10^8 ha) and assuming that nonmeasured components of biomass were equally affected. Scaling the per-site impact yields slightly greater values (*20*). Alternatively, we can scale the observed relationship between relative biomass change in plots and droughting (Fig. 2) by the moisture deficits across Amazonia estimated from remotely sensed rainfall data (*19*, *20*). This suggests an even greater impact on the biomass carbon balance of the droughted area: –1.60 Pg C (–2.63, –0.83). Site-based scaling-up indicates similar values (*20*). Although better understanding of soils is needed to determine the local effects of meteorological drought, the magnitude and consistency of these estimates demonstrate Amazonia's vulnerability to drought and the potential for changes in tropical climates to have large carbon cycle impacts. Our on-the-ground data reveal that, despite apparent "greening up" during dry periods (*13*, *14*), Amazon drought accelerates mortality over large areas (Fig. 2B) (*20*).

The exceptional growth in atmospheric CO_2 concentrations in 2005, the third greatest in the global record (*32*), may have been partially caused by the Amazon drought effects documented here. However, our findings do not translate simply into instantaneous flux estimates because carbon fluxes from necromass will lag the actual tree death events. Drought can suppress respiration (*17*, *33*), so the system as a whole might even contribute a temporary net sink even though the live biomass was in negative mass balance. Nonetheless, our results constrain the aggregate impacts of drought because trees are by far the largest and longest-lived of the aboveground carbon stores. Tropical droughts may intensify and become more frequent this century as a result of anthropogenic climate change (*1*, *3*–*5*, *11*). In addition to directly affecting Amazonian peoples and biodiversity, such events appear capable of strongly altering the regional carbon balance and thereby accelerating climate change.

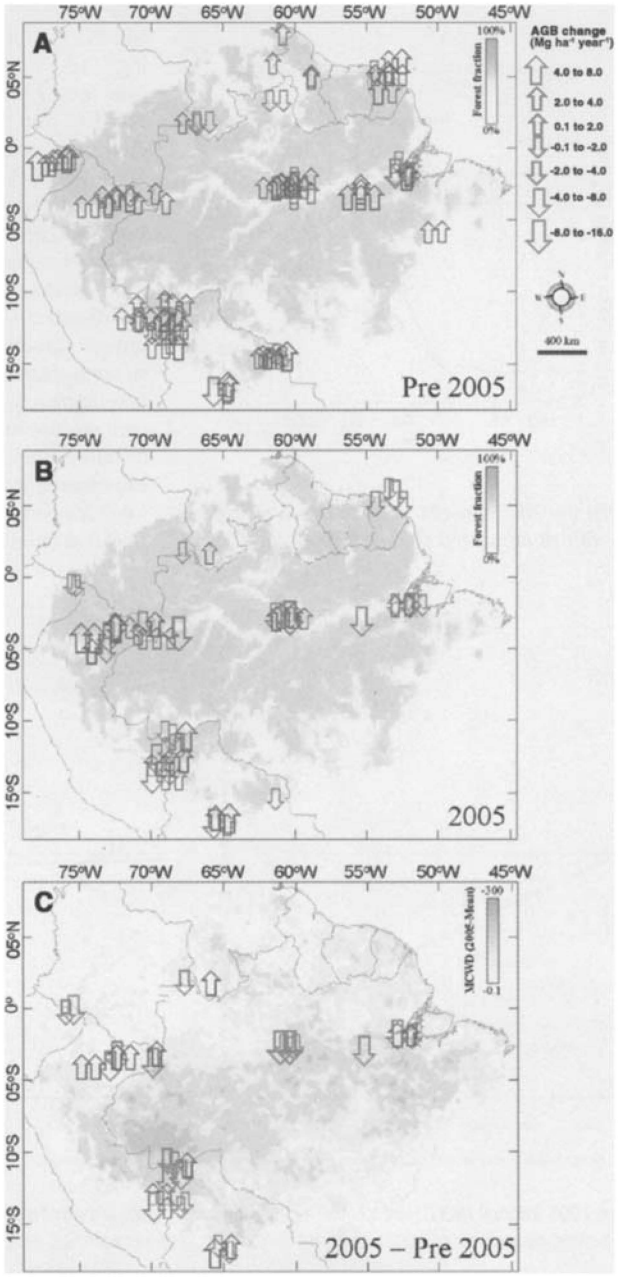

Fig. 3. Aboveground biomass change in the Amazon Basin and contiguous lowland moist forests. The 2005 drought reversed a multidecadal biomass carbon sink across Amazonia. Symbols represent magnitude and direction of measured change and approximate location of each plot. **(A)** Annual aboveground biomass change before 2005. **(B)** Annual aboveground biomass change during the 2005 interval. **(C)** Difference in rates of change in aboveground biomass, 2005 versus pre-2005, for those plots monitored throughout. Grayscale shading in (A) and (B) represents proportion of area covered by forests. Colored shading in (C) indicates the intensity of the 2005 drought relative to the 1998–2004 mean as measured from space using radar-derived rainfall data [Tropical Rainfall Measuring Mission (TRMM)].

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Supporting Online Material

www.sciencemag.org/cgi/content/full/323/5919/1344/DC1
Materials and Methods
SOM Text
Figs. S1 to S8
Tables S1 to S7
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Species Response to Environmental Change: Impacts of Food Web Interactions and Evolution

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How environmental change affects species abundances depends on both the food web within which species interact and their potential to evolve. Using field experiments, we investigated both ecological and evolutionary responses of pea aphids (*Acyrthosiphon pisum*), a common agricultural pest, to increased frequency of episodic heat shocks. One predator species ameliorated the decrease in aphid population growth with increasing heat shocks, whereas a second predator did not, with this contrast caused by behavioral differences between predators. We also compared aphid strains with stably inherited differences in heat tolerance caused by bacterial endosymbionts and showed the potential for rapid evolution for heat-shock tolerance. Our results illustrate how ecological and evolutionary complexities should be incorporated into predictions of the consequences of environmental change for species' populations.

Species throughout the world face many anthropogenic environmental disturbances (*1*). Some disturbances, such as land-use change, occur progressively and predictably. Others take place as increases in the frequency or magnitude of environmental shocks, such as the anticipated increase in tropical storm severity (*2*). Regardless of the mode of disturbance, changes in species abundance will depend on the multigenerational response of their survival and reproduction within ecosystems. Although the response of species' populations depends on the direct effects of environmental disturbances on species physiology, behavior, and life history (*3*, *4*), three additional complexities may play major roles in the long-term change in species' populations (*5*).

First, the change in a species' population growth rate in response to an environmental disturbance depends on how the species interacts ecologically with other species in the ecosystem (*6*). For example, if a competitively dominant species is sensitive to a disturbance, then a competitively subordinate species may benefit indirectly from the disturbance through competitive release (*7*). Although the role of food web interactions is well-known in theoretical work (*8*) and a growing number of empirical studies document these effects (*9*–*11*), most of this work has not considered how the strength of these interactions might change because of density-dependent effects during the environmental change.

A second complexity is the possibility that species may evolve tolerance to the environmental change (*12*). Empirical studies have now documented a growing list of species that have undergone evolutionary responses to environmental changes (*13*, *14*). If genetic variation exists, then environmental disturbances with large impacts on population growth rates may drive rapid evolution of tolerance.

The third complexity is that ecological and evolutionary complexities might interact (*15*). If ecological interactions modify the response of population growth rates to environmental changes, then they might also modify the selective regime for tolerance and, hence, evolution. In turn, evolution may change population growth rates and interactions among species, thereby increasing the complexities of predicting population changes.

Here, we investigate these three complexities for predicting population changes of pea aphids in response to increasing frequency of episodic heat shocks. To show that ecological interactions can modify population responses to environmental disturbances, we subjected field-caged populations of pea aphids and predators to an experimentally increased frequency of heat shocks (*16*). Our goal was to contrast the effects of two similar ladybeetle predators, investigating how species-specific differences in aphid density–dependent attack rates affect the change in aphid population growth rates when subjected to environmental change. To investigate the potential for evolution, we constructed aphid strains that differed in the presence of stably inherited endosymbionts that affect heat-shock tolerance. We

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