# Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models

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*Abstract*

The impacts of climate extremes on terrestrial ecosystems are poorly understood but central for predicting carbon cycle feedbacks to climate change. Coupled climate-carbon cycle models typically assume that vegetation recovery from extreme drought is immediate and complete, which conflicts with basic plant physiological understanding. We examine the recovery of tree stem growth after severe drought at 1,338 forest sites globally comprising 49,339 site-years and compare it to simulated recovery in climate-vegetation models. We find pervasive and substantial "legacy effects" of reduced growth and incomplete recovery for 1-4 years after severe drought, and that legacy effects are most prevalent in dry ecosystems, Pinaceae, and species with low hydraulic safety margins. In contrast, no or limited legacy effects are simulated in current climate-vegetation models after drought. Our results highlight hysteresis in ecosystem carbon cycling and delayed recovery from climate extremes.

*Main text*

Anthropogenic climate change is projected to alter both climate mean and variability, leading to more climate extremes such as heat waves and severe drought (*1*). Increasing variability is likely to profoundly affect ecosystems, as many ecological processes are more sensitive to climate extremes than changes in mean states (*2–4*). In turn, the impacts of these extremes can have major effects on ecosystem carbon cycling, feeding back to accelerate or reduce climate change. The 2003 European heat wave, for example, led to a strong anomalous carbon source, reversing four years of carbon uptake by terrestrial ecosystems on a continental scale (*5*).

Forest ecosystems store nearly half of the carbon found in terrestrial ecosystems (*6*), but the fate of forests under climate change and with increasing climate extremes remains uncertain and controversial. While some studies see large regions of forest as poised on the verge of "collapse" to an alternative state (*7–9*), others suggest forests are relatively "resilient" and likely to experience only modest changes (*10–12*). The sensitivity of forests to climatic extremes has become apparent in global patterns of widespread forest mortality (*13*), which highlight that the forest carbon sink could be weakened or even transition rapidly to a carbon source in some regions (*13–15*). Thus, the response of forests' growth and mortality to extreme drought and heat constitutes a large uncertainty in terrestrial carbon cycle feedback projections (*16*).

Treatment of drought in carbon cycle models is limited by a lack of representation of processes that capture the dynamics of ecosystem response, such as recovery following drought and the potential for legacies or hysteresis, features which are likely critical to predicting future system behavior (*17*, *18*). For example, lags in precipitation, particularly in semi-arid regions, have been shown to be important in the interannual variability of the land carbon sink (*19*). In current climate-carbon cycle models, plant physiological recovery from drought is often assumed to be complete and relatively fast. This is at odds with current understanding of physiological mechanisms in many ecosystems, particularly those with long-lived individual plants. Legacy effects and hysteresis after drought have been documented in stomatal conductance (*20*, *21*), wood anatomy and density (*22*), xylem vulnerability to drought (*23*), drought-induced tree mortality (*24*, *25*), and aboveground primary productivity (*21*, *26*). Dynamics of recovery from severe drought as a biological legacy can have a major influence on vulnerability to subsequent drought events, particularly if the drought return interval is shorter than the recovery time (*17*). The rate of recovery, for example in the re-establishment of hydraulic function following drought, is largely unknown for the vast majority of tree species (*24*).

We test here the occurrence, prevalence, and magnitude of legacy effects after severe drought using tree growth (i.e. tree ring width) stand-level chronologies from 1,338 sites, representing 49,339 site-years, across the globe, primarily in northern hemisphere extra-tropical forest ecosystems. We selected tree-ring master chronologies (typically of 10-20 trees per site) from the International Tree Ring Data Bank (*27*) that contained at least 25 years of data during 1948-2008. We define drought legacy as a departure of observed tree growth (ring-width index) in the period following a drought episode from that expected based on the relationship between growth and climate. Wood growth is ideal to test for drought legacy effects because it provides a long temporal record and has major carbon cycle implications. Wood is a carbon pool with slow turnover that stores immense amounts of ecosystem carbon (*6*), and wood growth is tightly correlated with net primary productivity (*28*). We further examine the extent to which observed legacy effects are simulated in current vegetation models from the Coupled Model Intercomparison Project, Phase 5 (CMIP5). We ask: i) Are legacy effects after extreme droughts pervasive in tree growth? ii) Are legacy effects more prominent in wet or dry environments? iii) Do legacy effects vary among species with different hydraulic safety margins (*29*), a measure of how close a tree approaches catastrophic damage to its xylem during drought (e.g. (*25*)). iv) Are the legacy effects simulated in CMIP5 coupled climate-carbon cycle models similar to those observed in tree rings?

We quantified legacy effects in tree-ring width chronologies using two methods: 1) the departure of observed from predicted growth recovery after drought based on correlations with climate and 2) partial autocorrelation coefficients. We focused primarily on sites where ring width anomaly exhibited significant correlations ($r>0.3$; mean correlation $r=0.51$) with drought (here Climatic Water Deficit; (*30)*) because we seek to quantify the duration of growth suppression or enhancement after a drought. We found significant legacies in radial growth after severe drought (>2 standard deviations) that lasted 2-4 years (Fig 1a; Fig S1). These effects were substantial in magnitude: ~9% decrease in observed vs. predicted growth in year 1 and 5% in year 2 after drought (Fig 1a). Legacy effects were observed regardless of the minimum climate correlation cut-off (Fig S1) or the drought variable used (Fig S2; Fig S3), and also observed in the partial autocorrelation analysis (Fig S4). There did not appear to be a strong link between the magnitude of the legacy effect and the peak intensity of the observed drought ($R^2=0.01$, $p=0.08$) (Fig S5).

Legacy effects were most pronounced in arid ecosystems (Fig 1b). Mean annual precipitation was the only significant predictor of the magnitude of drought legacy effects in tree growth, although with low explained variance ($R^2=0.05$, $p=0.0003$; Fig S6). Correlations with mean annual temperature and potential evapotranspiration both insignificant ($p>0.05$). Strong legacy effects also tended to occur in semi-arid regions in the northern hemisphere (Fig 2a) and where correlations between growth and drought were higher (Fig 2b). Tree-ring chronologies in the southwestern and midwestern United States, as well as parts of northern Europe, exhibited particularly strong legacy effects (Fig 2a). Positive legacy effects – where observed growth was higher than predicted after drought – were most frequent in California and the Mediterranean region (Fig 2a).

Gymnosperms exhibited slight but statistically significantly larger (magnitude and duration) legacy effects than angiosperms (t=2.25, p=0.02) (Fig S7). Among families, Pinaceae (e.g. pines) and Fagaceae (e.g. oaks) were best represented in the dataset, accounting for >90% of chronologies analyzed. Pines exhibited substantially larger legacies than did oaks (Fig 1c). Although pines were on average found at drier locales than oaks (average $\mathrm{MAP}_{\mathrm{pine}}$ = 660 mm/yr; average $\mathrm{MAP}_{\mathrm{oak}}$ = 760), a model allowing for interactions between precipitation and family was highly significant (t=2.55, p=0.01), indicating that the precipitation-family interaction was important. Indeed, both wet and dry pine sites exhibited strong negative legacy effects while wet oak sites exhibited slightly negative legacy effects and dry oak sites had strong positive legacy effects (Fig S8). Pines also had stronger negative legacy effects than the other main gymnosperm family in the database, Cupressaceae (Fig S9). This is consistent with the generally higher drought tolerance in Cupressaceae than in Pinaceae (*31*) and is supportive of a hydraulic damage mechanism underlying legacy effects (see below).

Several physiological mechanisms may underlie the observed legacy effects of reduced growth post-drought. Loss of leaf area and/or stored non-structural carbohydrates during drought may impair growth in subsequent years (*25*). Pest and pathogen impacts may lag drought or accumulate in drought-stressed trees, thereby lowering growth rates (*25*). Finally, stress-induced shifts in xylem anatomy and associated vulnerability to hydraulic dysfunction, or remnants of drought-induced xylem cavitation, could impair water transport and therefore growth (*25*). While data for the first two hypotheses are not available, testing the third hypothesis is possible with an existing global hydraulic trait database (*29*). We found that species with lower hydraulic safety margins, defined as the water potential at which 50% conductivity is lost minus the minimum measured water potential ($\Psi_{50} - \Psi_{min}$), exhibited larger legacy effects ($R^2$=0.33, F=4.95, p=0.04) (Fig 3) (Table S1). This indicates that species most at risk of hydraulic damage are also those that have the slowest growth recovery after drought. Previous studies at individual sites have observed drought-induced shifts in plant hydraulics especially in the first 3-4 years post-drought in oaks and poplars (*22*, *25*), and our results generalize these findings across many taxonomic groups and a broad geographic range.

The CMIP5 models captured little to no detectable legacy effects from severe drought in the same grid cells where the tree-ring chronologies were located (Fig 4). In many cases, interannual variability of wood carbon growth was quite low and more weakly correlated with water limitation or drought (mean correlations of R=0.01-0.09) than the observed tree-rings at the same locations (mean correlation R=0.25). Only the GFDL ESM2G model exhibited significant legacy effects of 1-2 years (Fig 4a), although of lower magnitude than the observed legacies (Fig 1a). Both GFDL ESM2G and CanESM use a dynamic carbon allocation scheme, but different approaches to allocate carbon, particularly under drought conditions. ESM2G's scheme (*32*) is based on the pipe model for the relationship between sapwood area and leaf area (*33*) and allows drought-induced loss of living carbon, including from the sapwood pool, which may allow it to capture legacy effects. Most CMIP5 class models use constant fractional allocation among the vegetation pools, and this appears to be a crucial limitation to capturing legacy effects of drought.

The response of terrestrial ecosystems to drought has been reported to be one of the largest uncertainties in the carbon cycle (*34*) and is not well-represented in current vegetation models, as evidenced by our model-data comparison. Current models lack representation of some basic physiological and structural properties of plants, such as vulnerability of plant xylem transport to hydraulic water stress, that lead to growth suppression, legacy effects and drought-induced mortality (*35*). We note that mortality is generally not measured or reported at these sites, so our analysis does not examine drought-induced mortality, but mortality or canopy dieback of surrounding trees could potentially generate some of the positive legacy effects in surviving trees that we observed due to increased resource availability. While the impacts of climate extremes on plant mortality and species turnover will also influence carbon cycling (*14*), we detect a strong, pervasive, and previously undocumented legacy effect of drought on tree growth, especially in dry regions. That is, even when climatic conditions return to normal, surviving trees do not recover their expected growth rates for an average of 2-4 years. Given that (i) woody plant growth is a central component of carbon storage and often correlated with productivity and (ii) semi-arid regions' prominent role in global carbon cycle variability (*19*), these legacy effects have potential ramifications for interannual variability of ecosystem carbon cycling and long-term carbon storage. For example, a simple estimate based on southwestern United States forests revealed that legacy effects could conservatively lead to 3% lower ecosystem carbon storage in semi-arid ecosystems over a century, equivalent to 1.6 Gt carbon when considering all semi-arid ecosystems across the globe (*30*).

Drought could lead to changes in a tree's carbon allocation, with less being allocated to bole growth and more to roots ore leaves (*36*, *37*), which would imply that growth declines might not immediately reflect decreases in forests' carbon uptake. The fast turnover of leaves and roots, however, would still result in overall decreases in ecosystem-level carbon storage relative to cases without legacy effects (*37*). A major remaining question is how prominent are legacy effects in tropical forests, where tree-ring analyses are challenging. There are some indications of legacy effects in the Amazon in satellite (*38*) and time-series inventory plot analyses (*39*) following the severe 2005 and 2010 droughts. The lack of legacy effects in CMIP5 models implies that drought impacts and their effect on carbon cycling are not accurately captured. These findings reveal the critical roles of contingency and hysteresis in ecosystem response following climate extremes.

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## Figure Legends

Figure 1: Legacy effects are substantial and persist for 3-4 years. Legacy effects are quantified as the difference between observed and predicted growth (unitless index) after two standard deviation anomaly in climatic water deficit. (a) Legacy effects observed across all 1,338 tree ring chronologies (dashed line) and 695 tree ring chronologies at sites that correlate significantly with the climatic water deficit (solid line and red polygon). (b) Legacy effects at a subset of the above 695 sites categorized as arid (mean annual precipitation < 500 mm) and wet (mean annual precipitation > 1000 mm) sites. (c) Legacy effects at a subset of the above 695 sites supporting either of the two main represented families: Pinaceae and Fagaceae. Shaded regions represent the 95% confidence interval around the mean from bootstrapping (n=5000).

Figure 2: Legacy effects are most prevalent in the southwestern and midwestern United States and parts of northern Europe (e.g. integrated legacy effects < -1.5; dark red symbols). Legacy effects are quantified as the difference between observed and predicted growth (unitless index) after two standard deviation anomaly in climatic water deficit across 1,338 sites. (a) Site-level legacy effect summed over the first four years post drought. (b) Average correlation between tree growth (ring width) and the climatic water deficit (soil moisture from 0-100 cm minus potential evapotranspiration).

Figure 3: Higher legacy effects are associated with species with low hydraulic safety margins. Integrated legacy effects are quantified as observed – predicted growth (unitless index) after two standard deviation drought, summed over 1-4 years, averaged across all droughts within a chronology, and averaged across all chronologies for a given species.

Each point represents a species where legacies and hydraulic traits were both available. Error bars represent ± 1 standard error.

Figure 4: Legacy effects after drought are not observed in predicted woody biomass in Earth System Models. (a-f) Legacy effects after a two standard deviation drought in grid cells that correlate significantly with drought and overlapped the locations of the 1,338 tree ring chronologies in the real world. Shaded regions represent the 95% confidence interval around the mean from bootstrapping (n=5000).

Supplementary Materials are available online and include Materials and Methods, Supplemental Tables, and Supplemental Figures (references *40-67*).