DENDROCHRONOLOGY

Pantropical tree rings show small effects of drought on stem growth

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Increasing drought pressure under anthropogenic climate change may jeopardize the potential of tropical forests to capture carbon in woody biomass and act as a long-term carbon dioxide sink. To evaluate this risk, we assessed drought impacts in 483 tree-ring chronologies from across the tropics and found an overall modest stem growth decline (2.5% with a 95% confidence interval of 2.2 to 2.7%) during the 10% driest years since 1930. Stem growth declines exceeded 10% in 25% of cases and were larger at hotter and drier sites and for gymnosperms compared with angiosperms. Growth declines generally did not outlast drought years and were partially mitigated by growth stimulation in wet years. Thus, pantropical forest carbon sequestration through stem growth has hitherto shown drought resilience that may, however, diminish under future climate change.

Tropical forests and woodlands are key components of the global carbon cycle. They represent much of the carbon stocks in terrestrial vegetation, contribute strongly to the land carbon sink, and are a key driver of the interannual variation in this sink (*1*, *2*). The long-term capture and storage of carbon in tropical woody biomass has a high potential to contribute to nature-based solutions to climate change by acting as a CO_2 sink (*3*, *4*). However, the increasing incidence and intensity of droughts may fundamentally alter these services (*5*–*8*), temporarily shifting tropical vegetation to a net carbon source (*5*, *7*, *9*) and thus jeopardizing its role in climate change mitigation (*10*). Droughts can be caused by low precipitation (P), high atmospheric water demand (vapor pressure deficit, VPD), or both simultaneously, leading to a strong climatic water deficit (CWD), calculated as water demand minus supply. Each of these drought types may reduce tropical tree growth.

To understand and predict the risks that droughts pose for the long-term capture of carbon in tropical vegetation, a pantropical assessment of drought effects on stem growth is needed. However, studies of drought effects on tree growth are scarce and poorly replicated spatially (*11*–*13*). This situation limits the ability to generalize and contextualize local empirical findings and to validate terrestrial biosphere models, which currently poorly represent the formation (*14*, *15*) and climate sensitivity of tropical woody biomass (*16*). These modeling uncertainties are bound to persist unless they are constrained by extensive empirical studies.

Here, we leveraged the recent expansion of tropical tree-ring studies (*17*, *18*) to assess drought effects on stem growth at an annual resolution and over multidecadal time scales. We assembled the most extensive pantropical tree-ring network to date, extending across all tropical climates, to answer the following questions: (i) To what extent is stem growth reduced during drought years and does this differ across drought types (i.e., low P, high VPD, and high CWD), seasons (i.e., dry versus wet), and major clades (i.e., angiosperms versus gymnosperms)? (ii) Is there evidence for lagged drought effects on stem growth and, if so, how strong or persistent are these effects? (iii) To what extent does growth stimulation during wet extremes compensate for stem growth reduction during droughts? (iv) Does the magnitude of drought impacts depend on local climatic conditions?

On the basis of current knowledge about growth-limiting factors and results from extratropical tree-ring studies, we hypothesize drought effects to be stronger for CWD droughts than for P and VPD droughts and for gymnosperms than for angiosperms [question (i) (*19*, *20*)]; lag effects to exist, especially for gymnosperms [question (ii) (*19*, *21*)]; drought-induced growth declines to be partially compensated for by growth stimulation during wet extremes [question (iii) (*22*, *23*)]; and drought effects to be stronger in more arid regions [question (iv) (*19*, *23*)].

Pantropical tree-ring network

We compiled a network of 483 tree-ring width chronologies from >10,000 trees spanning tropical and subtropical latitudes (30°N to 30°S). This dataset comprises 163 species and 33 plant families, with similar proportions of angiosperm and gymnosperm chronologies (Fig. 1A and fig. S1). Chronologies were redeveloped from >20,000 time series of raw tree-ring width measurements using a single, flexible detrending procedure that retains short-term growth responses to climate extremes. The resulting ring-width index (RWI) chronologies represent a relative, population-level measure of tree-growth variability. For each site, we identified the 10% driest years since 1930 in terms of P (lowest values), VPD (highest values), and CWD (highest values) in either the wet or dry season. CWD was calculated as cumulative abs(P-PET) for months during the season when the potential evapotranspiration (PET) is greater than P. We studied droughts at the seasonal level because the climate sensitivity of tropical tree growth differs among seasons (*17*). We quantified the impacts of droughts (and wet extremes) on RWI using superposed epoch analysis (SEA) (*24*), a technique that compares the mean RWI anomaly in extreme years with that of random draws from all "normal" years in the chronology and tests significant deviations (*21*). We estimated lag effects during the first and second postdrought years. RWI anomalies provide robust, site-level estimates of drought impacts and can be interpreted as proportional reductions in stem diameter growth (fig. S2); therefore, we

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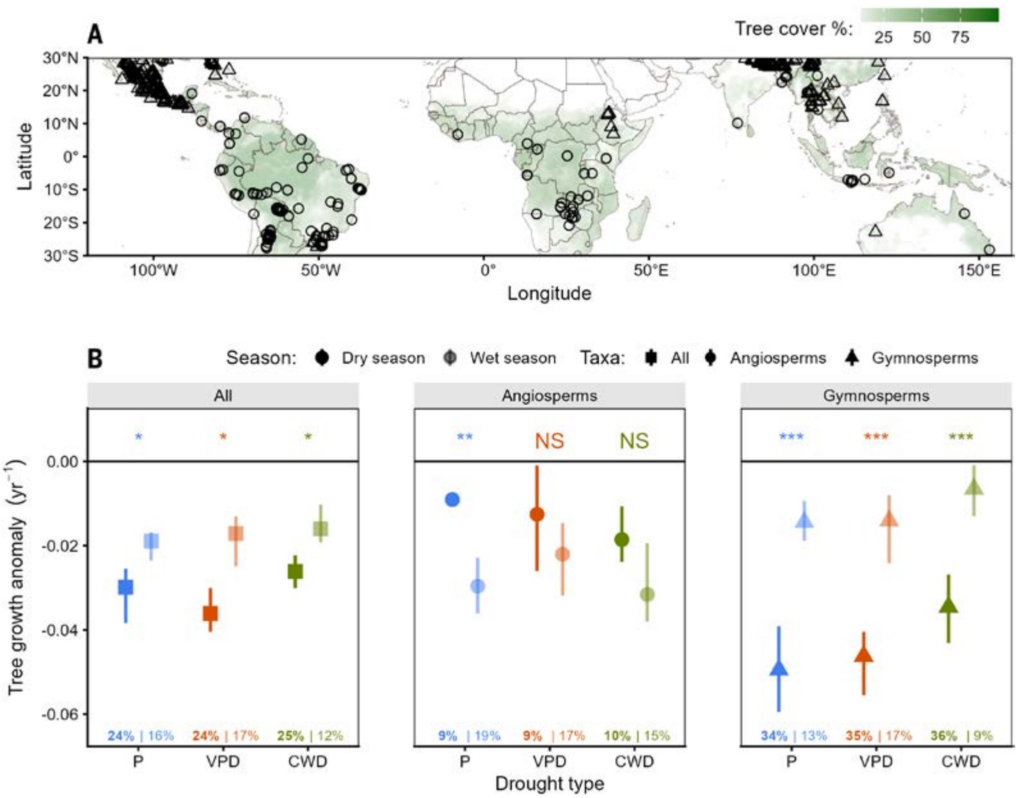

Fig. 1. Pantropical growth anomalies during drought years obtained from a tree-ring network. (**A**) Geographical distribution of 483 tropical tree-ring width chronologies from gymnosperms ($n = 273$, triangles) and angiosperms ($n = 210$, circles). The background color is tree cover percentage (>10%). (**B**) Pantropical median anomalies of annual tree growth (whiskers indicate bootstrapped 95% CIs) during the 10% years with the lowest P, highest VPD, or highest CWD. Results are shown for droughts occurring during the dry season (filled symbols, bold text) and wet season (transparent symbols, normal text) and for angiosperms and gymnosperms combined ("all") or separately. Results of weighted Mann-Whitney U tests between seasons are shown (nonsignificant, NS: $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). No significant differences in growth anomalies were found between drought types for any combination of species groups and season (Kruskal-Wallis tests, $P > 0.05$). Percentage values represent the proportion of significant negative anomalies in SEA analyses ($P < 0.05$). Sample size per symbol is provided in table S1B.

refer to them as "growth anomalies" (or "growth reductions" when negative). To account for the higher abundance of tree-ring studies at high elevations and in arid climates (fig. S3), we present pantropical medians weighted by climatic representativeness.

The drought intensity of the selected 10% driest years (expressed as the number of standard deviations away from the long-term mean) was comparable across the three drought types (fig. S4). Overlap in event years across drought types was small, except for dry-season extremes in P and CWD (fig. S5), suggesting that CWD droughts are more driven by very low P than by very high VPD. Across drought types and seasons, 7% of the droughts occurred during 2 consecutive years, and 0.3% lasted for 3 years. Since 1930, the frequency of droughts has increased for all drought types (fig. S6A), whereas the intensity has increased for some (VPD and CWD) but decreased for others (P) (fig. S6B).

Variable but overall modest drought effects

Growth anomalies during the 10% driest years were predominantly negative (63% of incidences), with strong growth reductions (>10%) occurring in 25% of the chronologies. However, growth anomalies varied across the network from strongly negative to moderately positive (fig. S7A), and growth anomaly variations were stronger for individual drought years (fig. S6C) than for averages across drought years. This wide variety of growth anomalies during individual drought years fully captures previously reported responses of tropical trees to episodic droughts, ranging from stem growth reductions of 20 to 50% (*25*, *26*) to undetectable change (*13*, *27*) or growth increases [for small trees (28)]. The latter may result from reduced cloudiness, enhanced leaf production, and/or competitive release in humid regions (*28*, *29*).

Despite the large variation in site-specific drought responses, bootstrapped 95% confidence intervals (CIs) of the weighted median responses were narrow (Fig. 1B). Overall, the magnitude of growth declines during drought years was modest (Fig. 1B). The pantropical growth reduction for all drought types and seasons was 2.5% (weighted median, 95% CI: 2.2 to 2.7%, with angiosperms and gymnosperms combined). Growth reduction was significantly stronger for dry-season droughts (3.1%; 95% CI: 2.8 to 3.5%) than wet-season droughts (1.8%; 95% CI: 1.6 to 2.1%) (Mann-Whitney U test, $P < 0.001$). Our assessments focus on the pantropical level because continental-level comparisons are hampered by differences in climatic representation (fig. S1D) and local-scale assessments by high local tree diversity (fig. S1E).

One fourth of the growth anomalies during dry-season droughts and 15% during wet-season droughts were significant ($P < 0.05$; Fig. 1B and fig. S7A). SEAs of individual ring-width series revealed smaller proportions of significant growth declines: 10% during the dry season and 7% during the wet season (fig. S8). These lower percentages likely reflect a larger role of nonclimatic factors in inducing growth variation of individual trees (e.g., canopy disturbance and carryover effects) than varation at the population level.

Applying a more stringent selection of drought years (i.e., the 5% driest years) led to a somewhat stronger, but still modest, mean reduction of 3.2% (95% CI: 2.7 to 3.5%). This modest drought response is comparable in magnitude to that from multisite assessments in tropical forests, which reported 6 to 9% reductions in diameter growth or woody biomass productivity (*11*, *30*, *31*). The stronger growth reductions in those studies may be explained by the selection of more extreme droughts.

Drought responses differed markedly between angiosperms and gymnosperms (Fig. 1B). Dry-season droughts induced significantly stronger growth reductions for gymnosperms (4.4%; 95% CI: 4.0 to 5.1%) than for angiosperms (1.1%; 95% CI: 0.5 to 1.9%) (table S1). By contrast, wet-season droughts resulted in stronger growth declines for angiosperms (2.7%; 95% CI: 2.2 to 3.1%) than gymnosperms (1.3%; 95% CI: 0.8 to 1.6%) (table S1). Stronger drought responses of gymnosperms are broadly consistent with the results of extratropical tree-ring studies (*19*, *21*, *22*, *32*). These taxonomic differences cannot be explained by the drought intensity, which was similar for angiosperms and gymnosperms (fig. S4). Possible explanations of stronger drought effects for gymnosperms include a dominant evergreen leaf phenology (89% of gymnosperm chronologies), an inherently stronger growth variability (*21*), a stronger vulnerability to cavitation for *Pinaceae* (80% of our chronologies) (*33*), and lower concentrations of nonstructural carbohydrate (NSC) reserves (*34*). The marked differences in drought responses and hydraulic architecture between angiosperms and gymnosperms call for separate drought analyses of these major clades.

In contrast to our hypothesis about question (i), growth reductions were not larger during CWD droughts compared with P or VPD droughts (Fig. 1B and table S1). This may partially be explained by the high coincidence of CWD and P droughts (fig. S5) resulting in similar effects on tree growth.

Rapid postdrought recovery

Contrary to our hypothesis about question (ii), drought analyses revealed no evidence for strong or long-lasting lag effects for any drought type or season (Fig. 2). Compared with drought years, postdrought years exhibited significantly smaller negative growth anomalies, and anomalies often shifted to positive. Such significant changes were found in 80% of the 36 possible comparisons (of clades, seasons, and drought types) between drought and postdrought years. During postdrought years, the 95% CIs of growth anomalies included 0 or were fully >0 for 70% of the 36 combinations of drought types, seasons, and clades. Postdrought recovery was similar for angiosperms and gymnosperms (Fig. 2) and cannot be explained by postdrought climatic conditions, which were close to normal or only slightly wetter (fig. S4, B and C).

Robustness tests revealed that these drought responses do not shift when applying more rigid detrending methods (fig. S9), alternative climate products (figs. S10 and S11), or more stringent drought selection criteria (fig. S12, A and B) or when selecting 2-year droughts (fig. S12C).

Combined, our results point to a rapid recovery of tree growth to predrought levels and provide no evidence for the existence of strong or long lag effects at the pantropical scale. These results are consistent with the short (<18 months) lag effects in tree growth after droughts observed in tropical dendrometer studies (*11*, *35*) and extratropical tree-ring studies (*22*). However, our results contrast with the strong lagged drought responses for gymnosperms observed in a tree-ring study across extratropical sites (*19*), likely due to differences in site aridity, drought definitions, detrending methods, and species selection (*22*).

Drought effects are partially mitigated by wet extremes

To contextualize drought-induced growth anomalies, we compared the overall effect of the 10% driest years on tree growth with growth changes during the 10% wettest years (SEA analysis). As hypothesized for question (iii), these wettest years caused pantropical tree growth to increase (median 1.8%; 95% CI: 1.5 to 2.0%) (fig. S7B), a magnitude that is comparable to the 2.5% drought-induced growth reduction (Fig. 1B). Similar to drought responses, growth anomalies after wet extreme years were short-lived (fig. S13).

As a result of the growth increases during extreme wet years, net growth anomalies of the 10% driest and wettest years combined were overall very small (–0.4%; 95% CI: –0.2 to –0.5%) and not significantly different from 0 for most drought types (Fig. 3). However, wet extremes mitigated only half (47%; 95% CI: 43 to 52%) of the growth reduction during drought years (across seasons and drought types and for angiosperms and gymnosperms combined; Fig. 3). With increasing frequency or severity of droughts (fig S6, A and B) and in more arid conditions (*23*), this wet-year compensation may be reduced.

Drought impacts increase with aridity

We evaluated the climatic drivers of observed drought effects by interpolating growth anomalies across climate space (mean annual precipitation and temperature). We found that wet-season droughts reduced growth in angiosperms more strongly in hotter and more arid climates (Fig. 4A and figs. S14A and S15A), whereas dry-season droughts had stronger impacts on gymnosperms at more arid sites (Fig. 4A and figs. S14B and S15B). Path analyses yielded consistent results (fig. S16) and also revealed that the expected role of first-order growth autocorrelation in shaping drought effects (*22*) was very small. Our finding of aggravating drought effects with increasing aridity is consistent with those from earlier studies on tropical (*36*) and extratropical (*19*, *20*, *23*, *37*) tree species. Strong local variability in drought responses is common (*35*), likely due to interspecific differences in drought resistance (*38*), spatial variation in soil parameters, rooting depth, access to water (*39*), and variations in the timing, intensity, and duration of droughts (*37*).

We projected the climate-space patterns for growth anomalies during low-precipitation years (i.e., models with highest R^2) into geographic space (Fig. 4B). For angiosperms, this model suggests that the strongest drought-induced growth reductions occur in dry-forest biomes

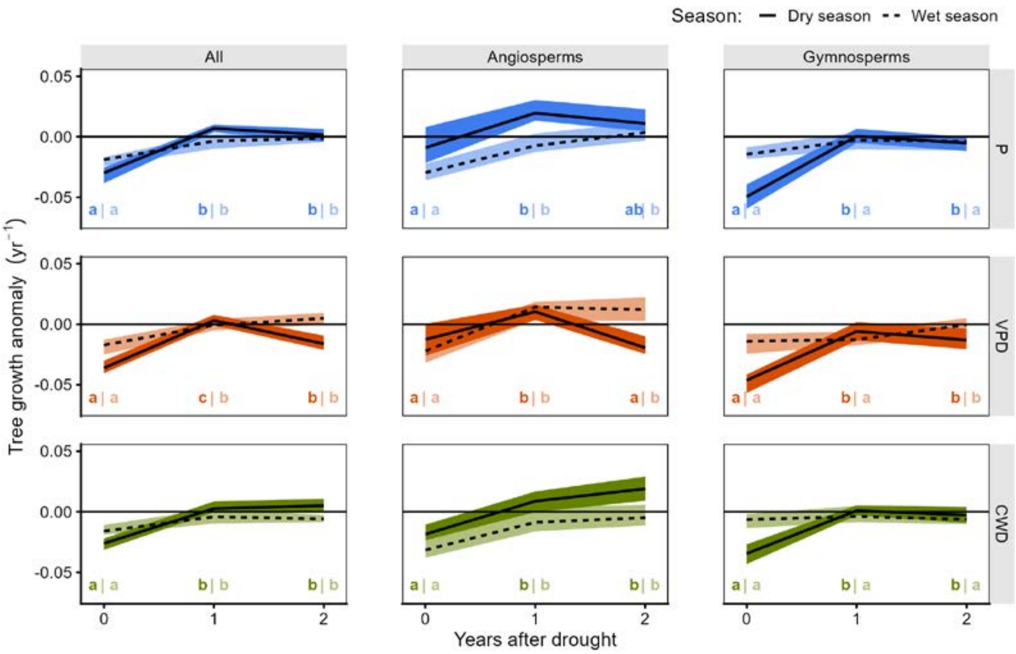

Fig. 2. Drought effects on pantropical tree growth are short-lived. Growth anomalies during and after years with low P, high VPD, or high CWD. Responses are shown for droughts occuring during the dry season and wet season and for angiosperms and gymnosperms combined ("all") or separately. Bands indicate bootstrapped 95% CIs of medians. Different letters indicate a significant difference between years (Mann-Whitney *U* tests; $P < 0.05$) per season (**dry** | wet). Sample size per line is provided in table S1B.

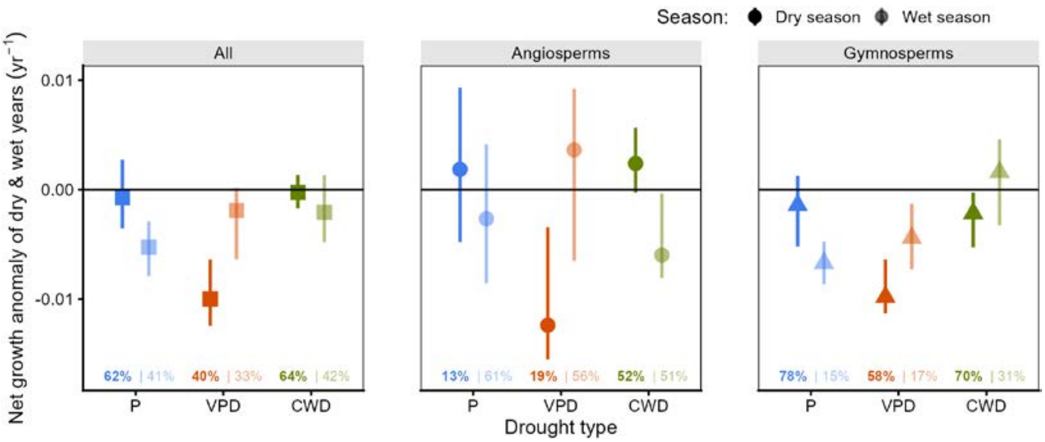

Fig. 3. Wet extremes partially mitigate drought effects on tropical tree growth. Pantropical medians (and bootstrapped 95% CIs) of the net growth anomaly of dry and wet extreme years. Results are shown for extremes occurring in the dry or wet seasons and for angiosperms and gymnosperms combined ("all") or separately. Droughts (and wet extremes) were identified as the 10% years with the lowest (highest) P, highest (lowest) VPD, or highest (lowest) CWD. The net anomaly was calculated as the average of the anomalies of the dry and wet extreme years. Percentages denote the growth loss during drought years that is mitigated during wet extremes per season (**dry** | wet). Sample size per symbol is provided in table S1B.

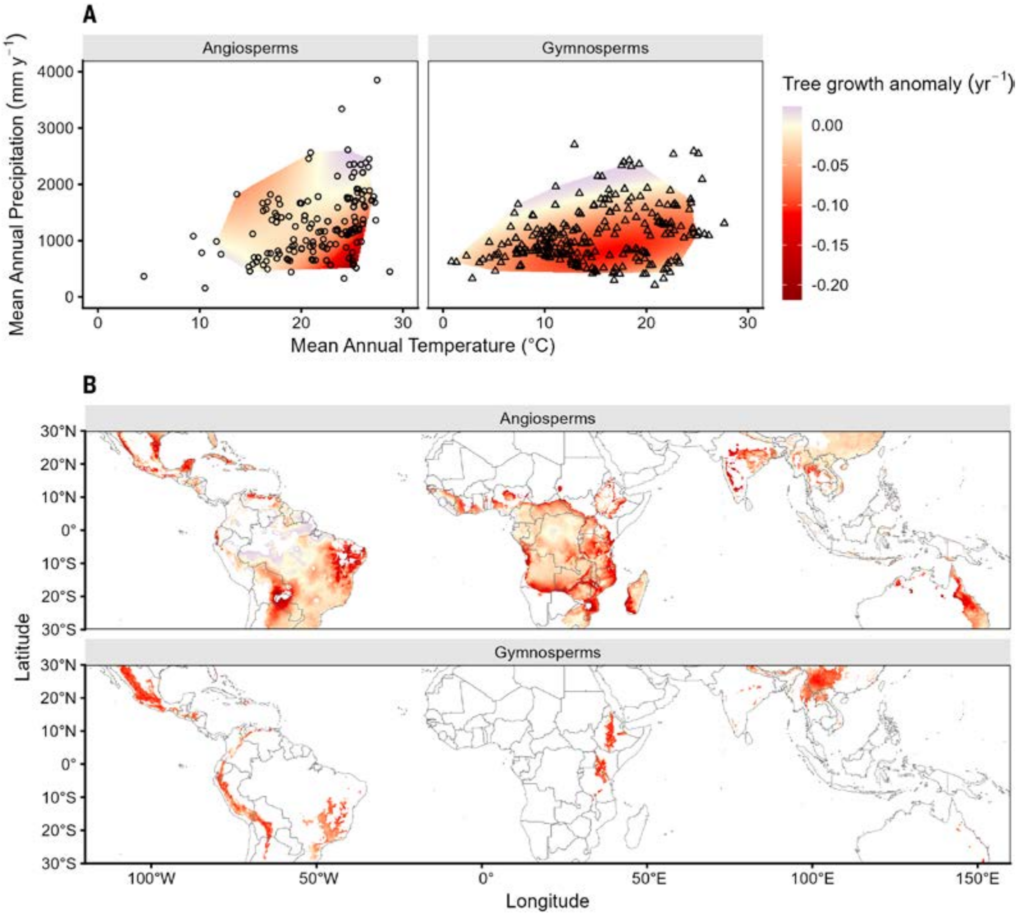

Fig. 4. Climatic and spatial distribution of drought-induced anomalies of tropical tree growth. (**A**) Growth anomalies during years with low precipitation during the wet season (angiosperms, $n = 210$) and dry season (gymnosperms, $n = 273$) interpolated across climate space. The interpolated climate space was restricted to 95% of the climatic ranges of precipitation and temperature. (**B**) Projections of the interpolated values from (A) into geographic space. The geographic distribution of gymnosperms was restricted to elevations >700 m above sea level (i.e., the 10th percentile of their elevational distribution). For Africa, the gymnosperm distribution was further restricted by a species distribution model of the only African gymnosperm in our network (*Juniperus procera*).

in the Americas, Africa, South Asia, and eastern Australia. Modest or positive drought effects on stem growth are estimated in warm, humid zones such as the Amazon region. For gymnosperms, negative growth anomalies due to dry-season droughts are strong throughout high-elevation regions in the Americas, Asia, and eastern Africa. Despite large local variability in drought responses, the bootstrapped uncertainty of these maps is low (fig. S17). Thus, across major climatic gradients at the subcontinental scale, predicted distributions of drought responses likely hold. These results offer opportunities to benchmark and constrain simulated drought responses of woody biomass production in tropical forests using terrestrial biosphere models (*16*, *40*).

Drought responses across components of productivity

The drought effects on stem growth are smaller than those on leaf-level photosynthesis (*31*) and forest-level gross primary productivity (GPP) (*13*) but of comparable magnitude to effects on leaf fall, flushing, and mature leaf area (*35*). In terms of duration, drought impacts on stem growth tend to last somewhat longer (4 to 18 months) (*27*, *35*) than effects on GPP (typically 4 to 6 months) (*41*, *42*). These comparisons suggest more direct and stronger drought effects on carbon uptake through photosynthesis than on its sequestration in woody biomass, consistent with the decoupling of these processes observed in extratropical forests (*43*).

One of the plausible explanations of the observed drought resilience of tropical tree growth is the mobilization of NSCs. Tropical tree species store large amounts of starch and soluble sugars in stems, branches, roots, and leaves (*44*) that are available during dry episodes for osmoregulation, leaf flushing, and stem growth (*13*, *34*, *45*, *46*). NSC mobilization may buffer reductions in stem growth and explain the decoupling of canopy and stem responses to droughts, but this remains poorly quantified. Other mechanisms, including shifts in leaf phenology and stem hydraulics (*47*), may also contribute to drought resilience. Long-term, well-replicated field studies measuring functional and productivity changes are needed.

Limitations, mortality risks, and climate change

We acknowledge several limitations of our study that should be addressed in future studies. First, major sampling gaps exist in Africa and in extreme arid and humid climates (figs. S1 and S3) (*18*). Although we statistically account for biases, data scarcity can only be solved through new studies. Second, our chronologies only include cross-dated RWI series, and our study thus may have excluded individuals that did not cross-date due to extraordinarily strong (e.g., missing rings) or weak drought responses. The latter group of individuals may produce progeny for drought-resilient next generations if weak responses have a genetic basis. Third, our study species represent a small fraction of tropical tree richness, and their drought responses may somewhat deviate from that of the "average" tropical species. Finally, we do not quantify drought responses at the stand level. Upscaling from the tree level to the forest level would require comparing tree-ring–based responses with those from community-wide dendrometer or plot data.

Episodic droughts increase the mortality of tropical trees (*6*, *48*), and drought-induced stem growth reductions may be associated with elevated mortality. To provide a first estimate of the mortality risks associated with the growth reductions reported here for angiosperms, we used significant growth-mortality associations from 10 tropical forest field studies (*49*) (fig. S18, A and B). The resulting estimate is a first indication of the order of magnitude of additional tree mortality. We estimate this to be 0.1% per drought year (95% CI: 0.08 to 0.15%) on top of a 1% year^{-1} baseline (fig. S18C). The resulting carbon loss of this additional mortality may be substantial at the pantropical scale and likely recovers slowly (*50*).

Anthropogenic climate change has intensified drought stress (fig. S6, A and B), resulting in stronger drought-induced growth reductions for all drought types (fig. S6C). Future climate change will further increase the frequency of droughts in tropical forests (*51*, *52*). Our climate space interpolation and path analyses suggest that future warming and amplified climatic variability will cause stronger stem-growth declines during wet-season droughts in angiosperm-dominated tropical lowland forests and woodlands. For gymnosperm-dominated high-elevation forests, the stronger impacts of dry-season droughts are expected in regions where climate change would reduce precipitation. These shifts are unlikely to be mitigated by concurrent CO_2 rise (*9*) because no consistent CO_2-induced growth stimulation has been observed in tree-ring studies (*53*).

Stronger and more extensive droughts occurring under future climate change may shift the modest drought responses observed here for the past decades toward considerably larger and more widespread declines in tropical wood productivity. Such shifts may have implications for the dynamics and residence time of carbon in tropical forests, especially when stronger growth reductions are accompanied by increasing tree mortality.

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SUPPLEMENTARY MATERIALS

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Materials and Methods; Figs. S1 to S18; Table S1; References (*56*–*75*); MDAR Reproducibility Checklist; Data S1

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