

FOREST ECOLOGY

Ecosystem fluxes during drought and recovery in an experimental forest

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Severe droughts endanger ecosystem functioning worldwide. We investigated how drought affects carbon and water fluxes as well as soil-plant-atmosphere interactions by tracing ¹³CO₂ and deep water ²H₂O label pulses and volatile organic compounds (VOCs) in an enclosed experimental rainforest. Ecosystem dynamics were driven by different plant functional group responses to drought. Drought-sensitive canopy trees dominated total fluxes but also exhibited the strongest response to topsoil drying. Although all canopy-forming trees had access to deep water, these reserves were spared until late in the drought. Belowground carbon transport was slowed, yet allocation of fresh carbon to VOCs remained high. Atmospheric VOC composition reflected increasing stress responses and dynamic soil-plant-atmosphere interactions, potentially affecting atmospheric chemistry and climate feedbacks. These interactions and distinct functional group strategies thus modulate drought impacts and ecosystem susceptibility to climate change.

Climate change is increasing the frequency and severity of droughts worldwide, threatening ecosystem functioning (1) with the potential to strongly diminish carbon sequestration (1–3). This is particularly concerning for large tropical forests, which are a major component of the terrestrial carbon sink (4). Much of the sink capacity of tropical forests can be lost after severe droughts (5), and their overall ability to assimilate and retain carbon is projected to decline further under future warming scenarios (6). Moreover, tropical forests represent a major source of atmospheric biogenic volatile organic compounds (VOCs) (7), which may be amplified under heat and drought (8), causing climate feedbacks through ozone, organic aerosol formation (9), and aerosol-radiation interactions (10). Although large-scale changes in carbon and water fluxes through ecosystems can be observed through monitoring networks (11), many of the mechanisms underpinning these drought-induced dynamics remain unclear (12). Specific knowledge gaps include the following: (i) how total ecosystem susceptibility and resilience are shaped by different plant water use strategies (13) and access to deep water (12); (ii) how drought-stressed veg-

etation adjusts carbon investments into maintenance and protection (14), including the production of VOCs (8, 15); and (iii) how interactions and feedbacks between different components modulate ecosystem dynamics (16–18).

The Biosphere 2 Tropical Rainforest (19) (figs. S1 to S3) is an enclosed experimental ecosystem where interactions among individual ecosystem components in response to environmental changes can be mechanistically studied [e.g., (20, 21)]. As part of the Biosphere 2 Water Atmosphere and Life Dynamics (B2WALD) campaign (fig. S4), we imposed a 9.5-week drought on this system (19) to determine the mechanisms responsible for the overall changes in ecosystem-scale water and carbon dynamics in response to drought and recovery. Drought propagated dynamically through different forest strata (Fig. 1). Atmospheric drought [vapor pressure deficit, VPD] increased rapidly in the sunlit canopy, whereas the understory was buffered by canopy shading and did not reach maximum values until late into severe drought (Fig. 1A). The soil dried out sequentially, with the topsoil drying rapidly during early drought and the deepest soil layers maintaining high moisture until late into severe drought.

The largest decline in ecosystem water and carbon fluxes coincided with increasing VPD and drying of topsoil during early drought (Fig. 1, B and C). Evapotranspiration (ET), ecosystem respiration (R_{eco}), and gross primary productivity (GPP) declined relative to pre-drought values by 58, 50, and 47%, respectively. Each of these fluxes decreased further during severe drought, but at lower rates (30, 27, and 32% of pre-drought values, respectively). Net ecosystem exchange of carbon (NEE = GPP – R_{eco}) was buffered by concomitant reductions in GPP and R_{eco} during early drought. The forest remained a carbon sink—albeit a small one—despite the 79% reduction in GPP under severe drought.

Daytime concentrations of atmospheric VOCs also changed dynamically in response to drought (Fig. 1E). These changes were not uniform among compounds, and concentrations of distinct VOCs increased sequentially in response to drought: first isoprene, then monoterpenes, and finally hexanal. These VOCs play important roles in leaf stress tolerance and signaling (22, 23), and hexanal has been associated with drought-induced leaf senescence (24).

Net uptake of isoprene and monoterpenes by the soil (Fig. 1F) was influenced by both overlying atmospheric concentrations and soil moisture. During drought, the concentration-normalized soil uptake capacity of monoterpenes increased relative to isoprene (fig. S5). This indicates greater persistence of monoterpene scavenging by soils under drought when plant monoterpene emissions were highest. Together, interactions between plants and soil led to distinct patterns in the relative abundance of atmospheric VOC concentrations as the drought progressed (Fig. 1E), serving as a diagnostic indicator of ecosystem drought stress (24), with isoprene indicating the onset of ET and GPP reduction and hexanal indicating their final decline under severe drought.

The structured readdition of moisture to the ecosystem—first in groundwater layers and then surface soil—released ecosystem components from drought with different temporal dynamics. The vegetation moderately responded to the addition of deep water, resulting in a slow increase in GPP and ET. Topsoil moisture, soil respiration, and soil VOC dynamics did not respond, indicating that hydraulic lift (25) was not sufficient to relieve the system from drought. By contrast, soil respiration and

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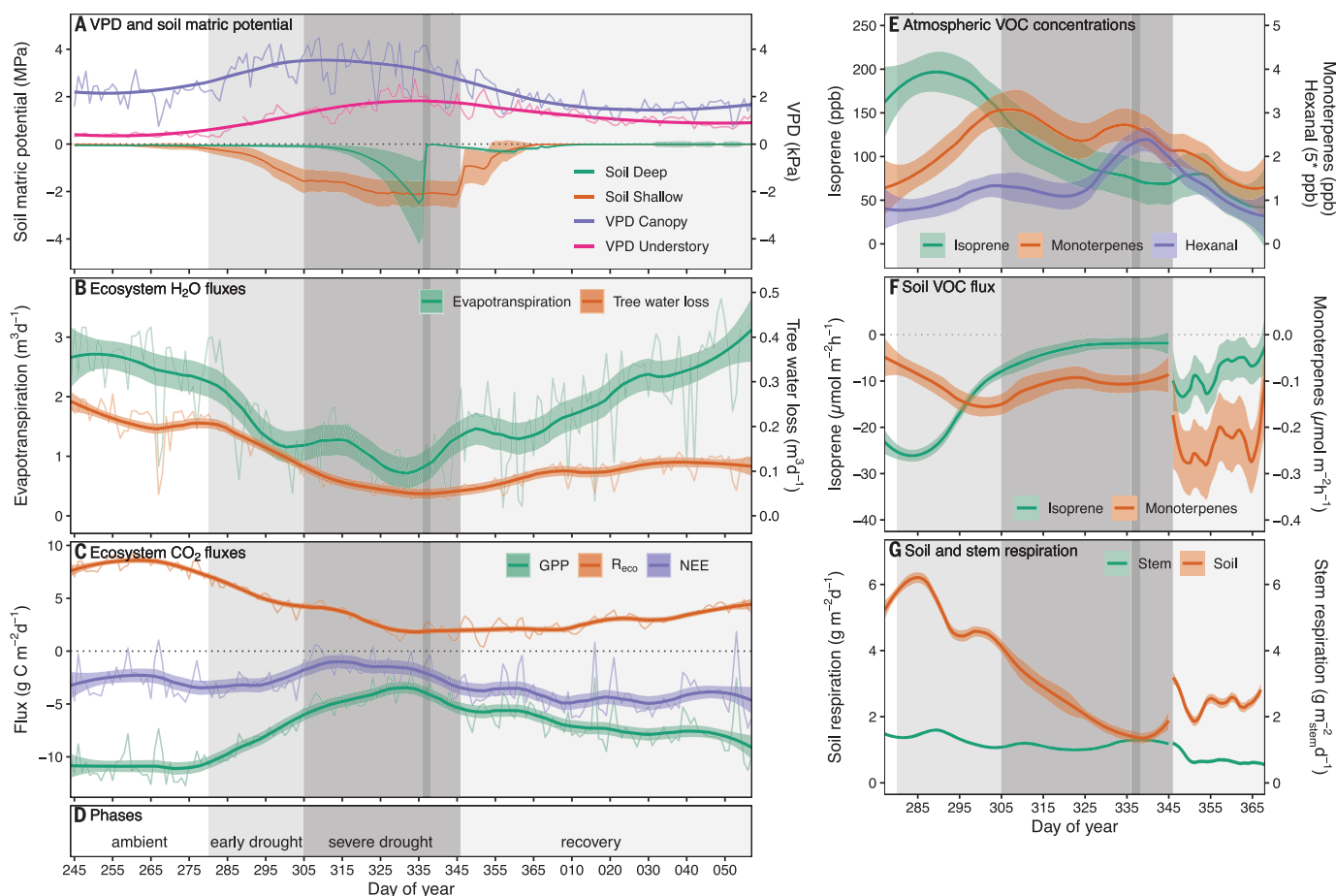


Fig. 1. Ecosystem fluxes of CO₂, H₂O, and VOCs, as well as environmental drivers during drought and recovery. Daily means of (A) vapor pressure deficit (VPD) in the tree canopy and understory in addition to soil matric potential in shallow and deep soil; (B) ecosystem evapotranspiration and tree water loss; (C) ecosystem CO₂ fluxes: gross primary productivity (GPP), ecosystem respiration (R_{eco}), and net ecosystem exchange (NEE); (D) drought phases;

(E) atmospheric VOC concentrations in parts per billion (ppb); (F) daily maximum soil uptake rate of isoprene and monoterpenes ($n = 12$); and (G) daily means of stem ($n = 12$) and soil respiration ($n = 12$). Background shading in all panels matches phases in (D). The vertical dark gray line indicates deep soil rewetting. Thick lines are smoothing splines with 95% confidence intervals, and thin lines in (A) to (C) are daily mean fluxes.

VOC uptake increased immediately upon rain rewetting (Fig. 1). Within 3 months of drought release, ET values had returned to pre-drought levels, but carbon fluxes displayed pronounced legacy effects, with R_{eco} and GPP recovering to 45 and 90% of pre-drought values, respectively.

The vegetation displayed highly diverse drought responses among and within species, driven by the interplay of species-specific drought adaptations and differences in microclimate conditions. We identified four major functional response types: drought-tolerant and drought-sensitive canopy-forming trees and drought-tolerant and drought-sensitive understory plants (table S1).

Drought-sensitive canopy trees dominated total ecosystem water fluxes under pre-drought conditions but had the largest reductions in sap flow coincident with upper soil drying in early drought (Fig. 2), when leaf senescence and substantial leaf shedding were observed. Leaf aging and shedding occurred in all species

to different degrees, but leaf shedding was higher in drought-sensitive canopy trees, particularly in *Clitoria fairchildiana* (~25% leaf loss). By contrast, drought-tolerant canopy trees had significantly lower water fluxes than their drought-sensitive counterparts under non-stressed conditions ($P < 0.001$); they also had more moderate reductions in sap flow with no visible signs of senescence during early drought.

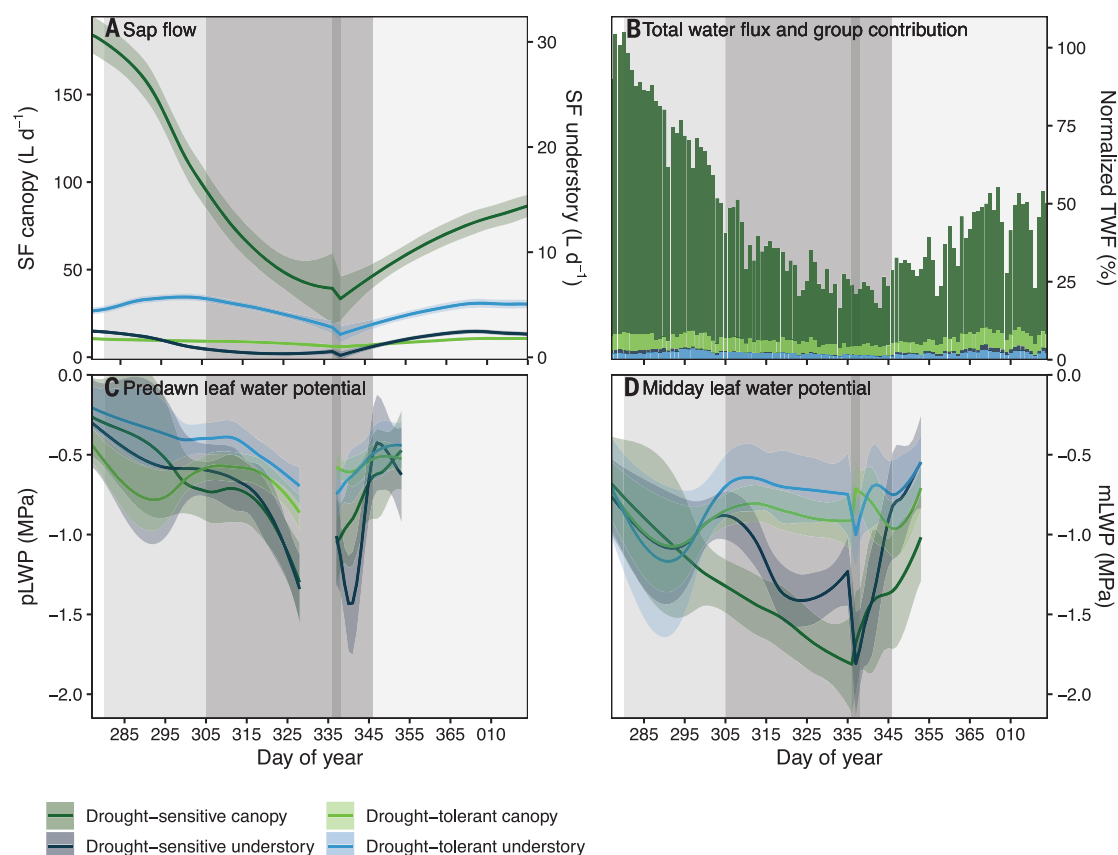
The water fluxes of understory plants were one order of magnitude lower than those of canopy trees (Fig. 2). Drought-sensitive understory plants displayed the strongest decline in pre-dawn and midday leaf water potential, indicating severe stress. Drought-tolerant understory plants showed only modest signs of drought stress. The presence of a robust understory in locations where shading buffered changes in VPD and temperature helped maintain ecosystem functioning at reduced levels during the severe drought. Thus, an intact forest canopy can provide an important beneficial forest

microclimate, with a critical role in buffering the long-term effects of climate warming (26). Overall, total plant water flux from drought-tolerant plants in both strata became more important during the drought, with their combined contribution increasing from 15 (pre-drought) to 35% (severe drought) (Fig. 2B). By contrast, drought-sensitive canopy trees dominated the total water flux (74 and 57% during pre-drought and severe drought, respectively).

The swift reduction in water use by drought-sensitive canopy trees (Fig. 2A) preceded deep soil drying by several weeks (Fig. 1A). Contrary to the expectation that trees would use all accessible water before reducing leaf area and carbon-fueled activities, ²H enrichment of transpiration after addition of a ²H₂O-tracer to the deep soil during severe drought demonstrated that all canopy trees in both the drought-sensitive and drought-tolerant groups had access to deep water (Fig. 3). However, despite accessibility by roots, these deep water

Fig. 2. Physiological responses of different plant functional groups and impact on total water flux. (A) Sap flow (SF) ($n = 3$ to 8 individuals per functional group). (B) Normalized total water flux (normalized TWF) and relative functional group contribution (percent).

(C) Predawn (pLWP) and (D) midday (mLWP) leaf water potential ($n = 3$ to 6). Lines are based on locally estimated scatterplot smoothing. Background shading is as in Fig. 1. For information on plant groupings, see table S1.



reserves were largely spared until severe drought (Fig. 1A). Additionally, despite strong drought stress, there was a pronounced lag between uptake and transpiration of deep water (Fig. 3A). The peak of ^2H -enriched transpiration occurred only after the deep soil had dried after addition of ^2H -labeled water, and when unlabeled precipitation was once again available in the forest. The several-week delay of maximum transpired $\delta^2\text{H}$ values indicates that stem water residence time was unexpectedly long, with the quickest response in drought-sensitive canopy trees and the greatest delay for drought-tolerant canopy trees. This is consistent with low sap flow velocities of drought-tolerant trees (Fig. 2) and with the recovery of tree water content in stems in drought-sensitive species (Fig. 3B).

Although early drought responses by sensitive plants reduced water loss and increased ecosystem drought resistance, these adaptations delayed recovery after the return of rain by slowing the flux of water through the ecosystem. Even after 7 weeks, the total canopy water flux had recovered to only 54% of pre-drought values (Fig. 2B). Drought-sensitive species contributed to a rapid resumption of ecosystem function upon rewetting, but at reduced rates (Fig. 2A). Specifically, legacy effects were caused by persistent struc-

tural changes in drought-sensitive trees (loss of hydraulic conductivity and leaves). By contrast, drought-tolerant species did not exhibit these structural changes and became relatively more important to ecosystem function during drought, contributing to overall ecosystem resistance. However, their generally slower responses limited the contribution of drought-tolerant trees during recovery.

In addition to reducing water and CO_2 fluxes through the ecosystem, the rate at which assimilated carbon moves through ecosystems can decline under drought (14, 27, 28). We traced carbon allocation from leaves to stems and soils with whole-ecosystem $^{13}\text{CO}_2$ pulse-chase experiments (Fig. 4) (19). Reduced carbon assimilation under drought resulted in lower ecosystem ^{13}C uptake (37% of pre-drought values; Fig. 4H) despite addition of twice as much ^{13}C label to the atmosphere under drought (Fig. 4A). Although ecosystem assimilation declined under drought, bulk leaf material became more ^{13}C enriched (Fig. 4, B and C, and table S2), with a greater increase for drought-sensitive plants. Likewise, $\delta^{13}\text{C}$ of leaf respiration was higher after the drought $^{13}\text{CO}_2$ pulse than pre-drought, with greater increases for canopy trees relative to understory plants and for drought-sensitive plants relative to drought-tolerant plants (Fig. 4, B and C, and table S3). Although meta-

bolic activity was reduced, the fresh carbon was preferentially used as respiratory substrate.

Belowground ^{13}C transport was slower under drought, as indicated by $\delta^{13}\text{C}$ values of stem respiration, whereas the ^{13}C residence time in stems increased (Fig. 4, D and I, and tables S3 and S4). ^{13}C enrichment of fine roots was ultimately similar after both label pulses (Fig. 4E). However, soil respiration exhibited less ^{13}C enrichment during the drought, suggesting that ^{13}C was preferentially used for building root biomass rather than for root respiration or exudates.

Despite reduced ecosystem carbon uptake and total VOC emissions, plants continued to allocate a similar proportion of fresh carbon to de novo VOC synthesis, as incorporation of ^{13}C into both isoprene and monoterpenes remained high (Fig. 4, F and G). Maintaining carbon allocation into VOC synthesis demonstrates the fundamental role of these compounds in protecting plants from heat stress and photooxidative damage that can be caused by reduced stomatal conductance and C metabolism under drought (8).

The B2WALD experiment demonstrates the importance of plant functional groups for understanding ecosystem responses to drought (fig. S7) (12, 29–30). Different hydraulic strategies of distinct plant functional groups and

their changing proportional contributions determine the overall magnitude of reduction in ecosystem fluxes as drought progresses (Figs. 2 to 4). Moreover, plant adaptations determine the velocity and residence time of water and carbon in different plant organs such as stems and leaves (Figs. 2 to 4). Therefore, distinct plant hydraulic strategies can increase resistance to drought: The presence of drought-tolerant trees buffered the drought decline in ecosystem fluxes, whereas the rapid restriction of water use in drought-sensitive trees lowered the risk of detrimental depletion of soil water sources, which improves the likelihood of withstanding prolonged droughts. The degree to which ecosystems are able to resist extreme droughts will affect their functioning upon return to more favorable hydrologic regimes. In our study, the drought's legacy was visible as the carbon sink capacity of the forest remained suppressed months after the cessation of drought (Fig. 1), partly as a result of the physiological and structural responses of drought-sensitive canopy trees. This has important implications for coupled climate-vegetation Earth system models, which will miss critical processes if distinct plant hydraulic responses are not considered (12, 31).

Notably, the forest flux dynamics were tightly coupled to shallow soil processes, as the largest decrease in ecosystem fluxes corresponded to early dry-down of topsoil moisture (Fig. 1, S8), despite access to deep water reserves by all canopy trees (Fig. 3). Plants can dynamically adjust their root water uptake depth through active regulation of conductivity in the rooting zone (32); however, most roots are allocated to the upper soil zone, where they mediate important soil-plant interactions in the rhizosphere through carbon and nutrient exchange (18). Drying of this zone induced significant down-regulation of transpiration—particularly in drought-sensitive canopy trees—indicating that changes in critical zones trigger drought responses, rather than changes in the total water accessible to plants. Reductions in transpiration and assimilation were associated with delayed transport of carbon belowground (Fig. 4) and with a likely reduction in fresh carbon allocated to soil respiration (Figs. 1 and 4). Although phloem transport in these trees was delayed by the drought, its magnitude was not reduced (14). Additionally, the rate at which water moved from deep soils to the leaves of drought-stressed, deep-rooted trees was unexpectedly slow (33), with especially long residence times for stem water in drought-tolerant canopy trees (>55 days; Fig. 3). Incorporation of different plant hydraulic strategies and dynamics in response to sequential soil drying in models may be critical for accurately simulating the magnitude and timing of vegetation-driven changes in ecosystem fluxes and land-atmosphere feedbacks under climate change (16, 31).

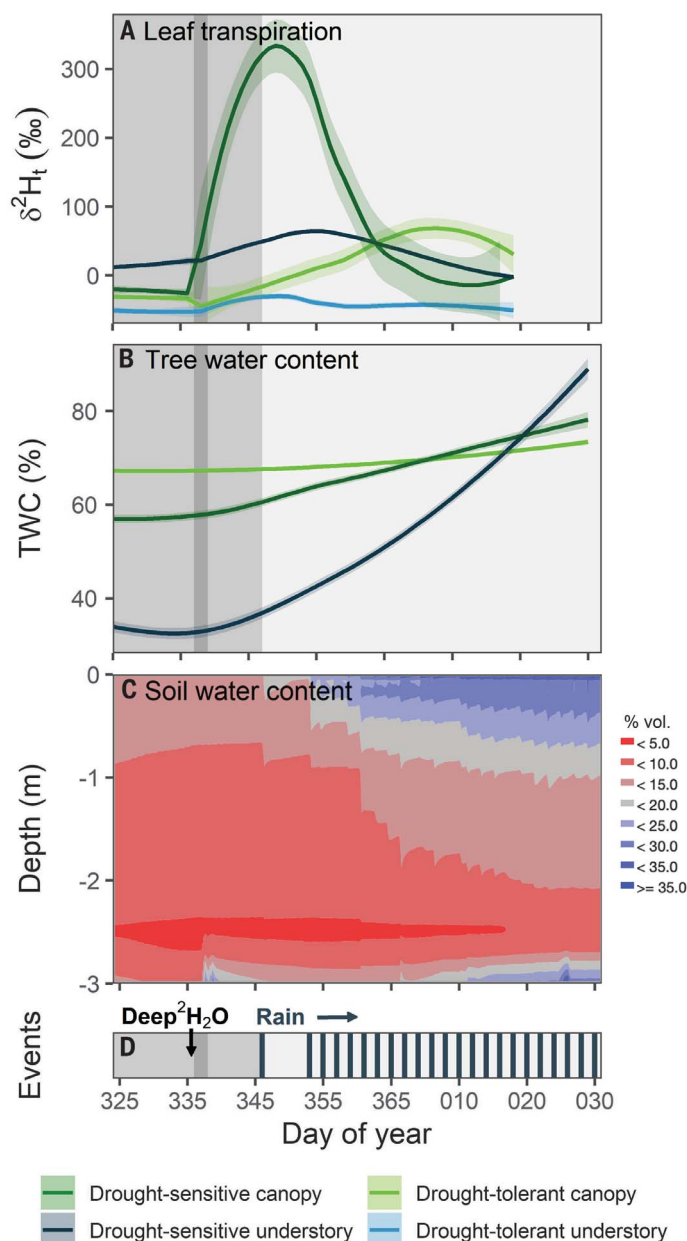


Fig. 3. Deep water uptake and recovery of plant functional groups. A $^2\text{H}_2\text{O}$ -pulse was applied at depth on day 336 (gray line) 10 days before rain. (A) $\delta^2\text{H}$ value of leaf transpiration ($= \delta^2\text{H}_t = (\frac{^2\text{H}}{^1\text{H}})_{\text{transpired water}} / (\frac{^2\text{H}}{^1\text{H}})_{\text{VSMOW}} - 1$, per mil) ($n = 5$ to 10 per functional group), (B) tree water content (TWC) ($n = 2$ to 6; full time series shown in fig. S6), (C) soil water content per depth (percent volume), and (D) rain events after drought. Lines in (A) to (C) are based on locally estimated scatterplot smoothing. No data were available for the TWC of drought-tolerant understory plants. For information on plant groupings, see table S1.

Additionally, Earth system models need to account for coupled plant-soil interactions, which not only change the movement of carbon and water through ecosystems but can also impact atmospheric chemistry. In the B2WALD drought experiment, plant-soil interactions led to a distinct pattern in atmospheric VOC concentrations, which tracked the increase in drought severity (Fig. 1). Moreover, the relative increase in monoterpene

concentrations in early drought can increase atmospheric reactivity, which could potentially promote secondary aerosol formation—including cloud condensation nuclei (34)—representing a feedback that could favor rain and help relieve some of the forest's drought stress (35). Our findings suggest that the goal of understanding and predicting ecosystem function in response to global climate change will be best accomplished by incorporating plant functional

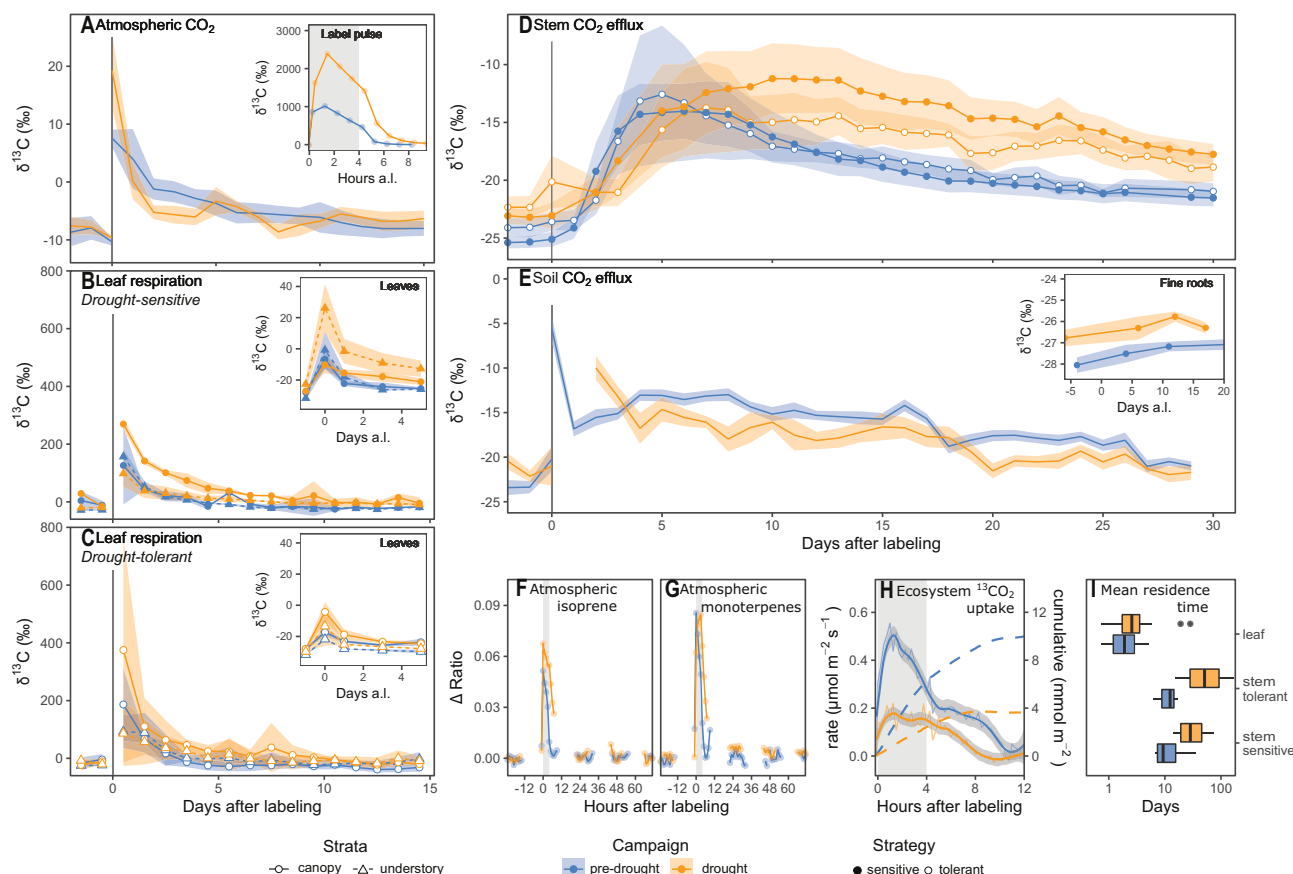


Fig. 4. ^{13}C dynamics in fluxes and pools of ecosystem compartments after pulse labeling. Isotopic composition in (A) atmospheric CO_2 , (B and C) leaf respiration ($n = 3$ to 6 per functional group), (D) stem respiration ($n = 3$ to 6), (E) soil CO_2 -efflux ($n = 12$), and (F and G) atmospheric isoprene and monoterpenes, respectively, relative to the time of $^{13}\text{CO}_2$ -pulse labeling (gray shading) during pre-drought (blue) and drought (orange) conditions. (H) Uptake rate (left axis) and cumulative uptake (right axis) of $^{13}\text{CO}_2$ during and in the initial hours after each labeling pulse (a.l.), derived from ecosystem GPP and $\delta^{13}\text{C}$

of atmospheric CO_2 ($\delta^{13}\text{C} = (^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{VPDB}} - 1$, per mil). (I) Mean residence time of ^{13}C in leaf- and stem-respired CO_2 ($n = 3$ to 6). Open and closed symbols in (B) to (D) denote drought-tolerant and drought-sensitive functional groups, respectively. Circles and triangles indicate canopy and understory, respectively. The ΔRatio in (F) and (G) is the ^{13}C enrichment above the natural abundance of ^{13}C isotopologues. Insets in (A) to (C) and (E) are as follows: (A) strength of atmospheric $^{13}\text{CO}_2$ pulse; (B) and (C) $\delta^{13}\text{C}$ of leaf samples; and (E) $\delta^{13}\text{C}$ of root samples ($n = 2$ to 7). Symbols show mean values \pm standard error.

groups and their interactions with soils and atmosphere into both observational and modeling studies.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abj6789
Materials and Methods
Figs. S1 to S9
Tables S1 to S8
References (37–61)

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An experimental forest ecosystem drought

Drought is affecting many of the world's forested ecosystems, but it has proved challenging to develop an ecosystem-level mechanistic understanding of the ways that drought affects carbon and water fluxes through forest ecosystems. Werner *et al.* used an experimental approach by imposing an artificial drought on an entire enclosed ecosystem: the Biosphere 2 Tropical Rainforest in Arizona (see the Perspective by Eisenhauer and Weigelt). The authors show that ecosystem-scale plant responses to drought depend on distinct plant functional groups, differing in their water-use strategies and their position in the forest canopy. The balance of these plant functional groups drives changes in carbon and water fluxes, as well as the release of volatile organic compounds into the atmosphere. —AMS

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