

Commentary

Resolving the dynamic impacts of drought on carbon cycling: From mechanism to scale

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Terrestrial carbon sinks are vital for balancing atmospheric carbon and mitigating climate change. While intensifying droughts threaten these sinks, quantifying their effects on carbon balance remains challenging because many mechanisms are poorly understood. This commentary advocates for an integrated, mechanistic framework across scales to resolve uncertainties and improve carbon estimates.

Terrestrial ecosystems absorb ~one-third of anthropogenic carbon (C) emissions each year, serving as vital C sinks that buffer climate change.¹ However, these terrestrial C sinks are highly vulnerable to increasingly frequent and intense droughts. By suppressing plant photosynthesis and accelerating plant mortality,² droughts can drive substantial C losses and flip ecosystems from net C sinks to sources. For example, the 2003 European drought released ~0.5 Pg C, offsetting four years of ecosystem C sequestration.³ Accurately quantifying how drought impacts ecosystem C balances and capturing these sink-to-source transitions is critical, as large C losses could trigger positive climate feedbacks, accelerate global warming, and jeopardize international climate mitigation targets. However, quantifying C sink response to drought remains challenging due to highly uncertain ecosystem responses. A global synthesis of precipitation exclusion experiments indicates that net ecosystem productivity (NEP) decreases by 1.3% per 10 mm reduction in mean annual precipitation, with responses varying widely from -3.5% to 0.86% (95% confidence interval [CI]).⁴ To overcome this uncertainty, we should move beyond viewing drought as a presence-or-absence event. Instead, we need to track its effects through its entire temporal progression, including drought onset, intensification, persistence, rewetting, and post-drought legacies, defined here as the drought impact chain (Figure 1A). The major challenge lies in resolving how C responses dynamically evolve along this chain and vary across

ecosystems. This commentary identifies critical knowledge gaps along the drought impact chain that drive current C budget uncertainties and proposes an integrated framework linking this impact chain with the underlying mechanisms governing C exchange across scales. This framework will help clarify drought-driven, sink-to-source transitions and better constrain global C balance estimates.

Drought onset and progression: The unfolding of the impact chain

To accurately estimate ecosystem C budgets and understand sink-to-source transitions along the drought impact chain, it is critical to resolve how the unfolding of a drought, namely its timing, intensity, duration, and their interactions shapes ecosystem C budgets, as differences in how droughts unfold can trigger distinct ecological pathways and drive divergent C outcomes. For instance, in a semi-arid grassland, early-season drought delayed phenological onset and reduced net C uptake by 34%, whereas peak- and late-season droughts had greater impacts, decreasing net C uptake by 56% and 55%, respectively, due to suppressed photosynthesis and accelerated leaf senescence.⁵ Drought intensity determines irreversible plant damage thresholds, whereas duration governs whether drought stress accumulates or allows adaptation, potentially altering community composition and thus shifting mean C flux and storage.⁶ Crucially, the interaction between intensity and duration drives divergent above-ground net primary productivity (ANPP) responses. Previous

research has shown that across 74 grasslands and shrublands, multi-year droughts caused ANPP changes ranging from near-complete resistance to 97% losses, with mild-to-moderate droughts maintaining reduced ANPP and prolonged extreme drought driving severe losses.⁷

Despite these insights, mechanistic experiments spanning diverse ecosystems and multiple C-cycle processes remain scarce. It remains unclear how these drought characteristics propagate to other C cycle processes, such as below-ground production and ecosystem CO₂ fluxes; which factors dominate which C processes (Figure 1A); and how responses vary spatiotemporally. Explicitly linking these processes to how drought unfolds provides the necessary foundation to accurately evaluate the overall ecosystem C balance.

The active drought phase: Uncovering hidden processes

Beyond tracking how a drought unfolds, accurately assessing ecosystem C budget and predicting sink-to-source transition requires explicitly resolving key ecological processes during the active drought phase. The current lack of quantitative and mechanistic understanding of the processes drives substantial uncertainties in ecosystem C cycle and climate feedback.²

During drought, plant mortality represents a poorly constrained process and is commonly attributed to two main mechanisms (Figure 1B). First, prolonged drought limits C assimilation through stomatal closure, progressively depleting non-structural carbohydrate reserves



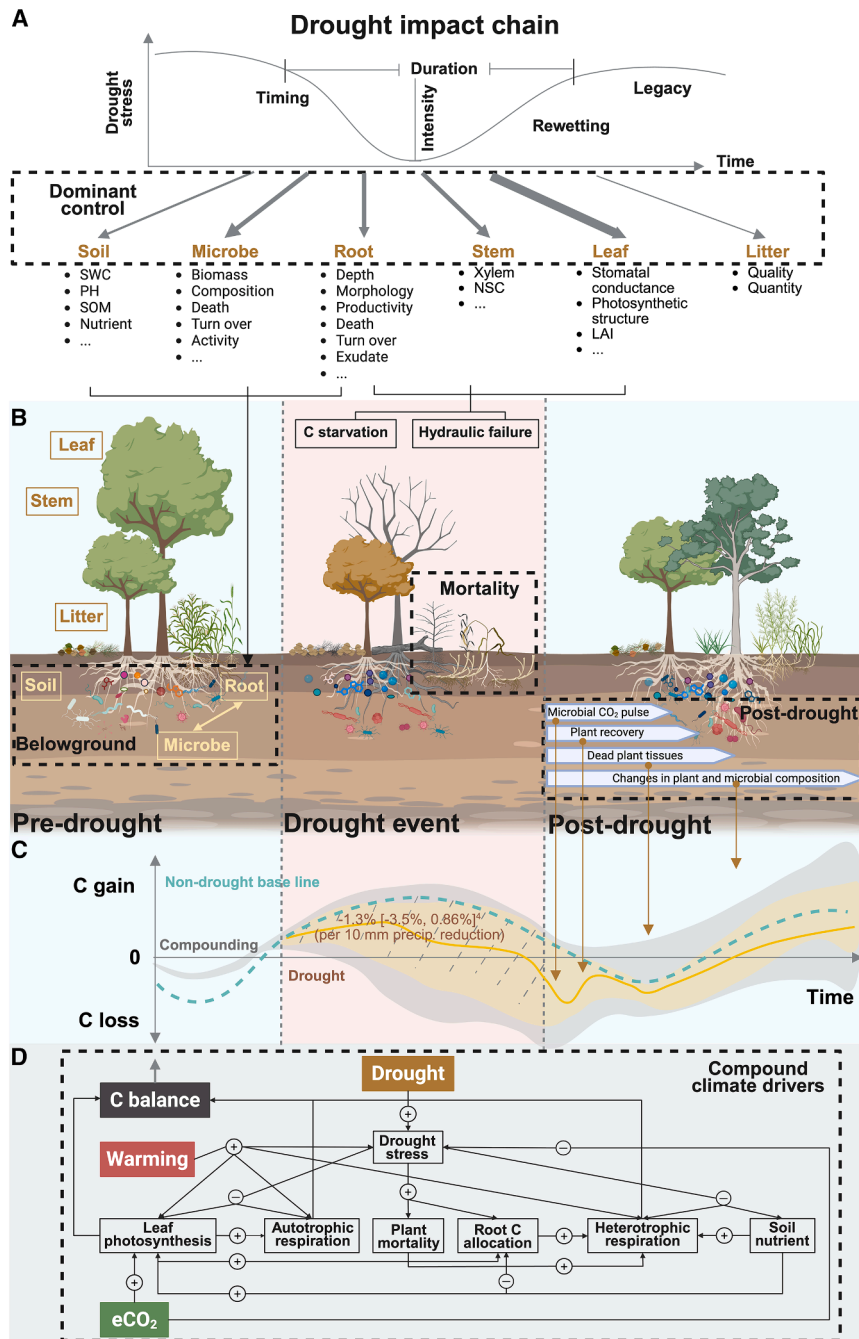


Figure 1. Concept figure showing the mechanistic pathways linking drought impact chain to ecosystem carbon cycling

The black dashed boxes represent the identified key knowledge gaps and challenges.

(A) The drought impact chain is characterized by drought timing, duration, and intensity, as well as the subsequent rewetting and legacy phases. Arrows within the “dominant control” black dashed box represent the influences of the drought impact chain on different ecosystem components and processes. The varying thickness of these arrows is purely illustrative, emphasizing the profound uncertainty in our current understanding, and the actual relative magnitudes of these impacts remain entirely unquantified and represent a critical knowledge gap.

(B) During a drought event, water stress alters hidden belowground carbon (C) dynamics and triggers plant mortality. The post-drought phase is driven by asynchronous recovery dynamics, including rapid microbial CO₂ pulses, delayed plant recovery, the decomposition of dead plant tissues, and the reorganization of plant and microbial communities.

(C) Overall, these processes along the drought impact chain shape the temporal response of ecosystem C balance to drought. The green dashed line represents the non-drought baseline, while the solid yellow line

required for respiration, osmotic regulation, and defense, leading to “C starvation.” Second, intense water stress can trigger xylem embolism, collapse of water transport and irreversible damage to roots and meristematic tissues, causing “hydraulic failure.” Both drive widespread tree mortality and sharply reduce ecosystem C sequestration. For example, the 2015–2016 El Niño drought killed 2.5 ± 0.3 billion stems across 1.2% of the Brazilian Amazon, releasing 495 ± 94 Tg CO₂, of which only 37% was offset by subsequent C uptake over the following three years.⁸

Mortality research predominantly focuses on woody species, leaving herbaceous plants poorly understood. Knapp et al. highlight this as a critical knowledge inequity,² as grasslands cover ~25% of the terrestrial surface⁹ and are highly drought sensitive. Smith et al. showed that a one-year extreme drought reduces grassland ANPP by 38%, well exceeding the 21% reduction in shrublands.¹⁰ However, herbaceous mortality is difficult to detect because aboveground dieback does not guarantee whole-plant death, as many species survive via belowground organs and recover through resprouting or tillering. Therefore, herbaceous mortality is often overlooked and rarely quantified. Resolving this is critical for closing the C budget in herbaceous ecosystems.

Alongside mortality, hidden belowground C processes represent another source of C budget uncertainty and the critical missing link for evaluating ecosystem sink-to-source transition

illustrates the net C balance under drought stress, with the yellow shaded area representing its conceptually hypothesized uncertainty range. An approximate quantitative estimate based on Song et al.⁴ (–1.3% [95% CI: –3.5%, 0.86%] per 10 mm reduction in precipitation) highlights the high uncertainty in NEP responses to precipitation reduction. The broader gray shaded area illustrates the expanded uncertainty range when drought interacts with compound climate drivers (detailed in D). Because these interacting factors can either exacerbate or mitigate drought effects, they introduce substantially greater uncertainty into the overall C balance.

(D) A conceptual model illustrating the complex interactions among warming, elevated CO₂ (eCO₂), and drought and their cascading impacts on net ecosystem C balance. Arrows indicate the direction of influence, with circled plus (+) and minus (–) signs denoting hypothesized positive and negative impacts, respectively.

SWC, soil water content; SOM, soil organic matter; NSC, non-structural carbohydrates; LAI, leaf area index.

during drought (Figure 1B). Most drought studies focus above ground, yet drought increasingly shifts the C cycling below-ground. While drought suppresses above-ground growth through stomatal closure and reduced C assimilation, a global synthesis reveals that plants can reallocate C below ground, increasing root/shoot ratio by 13.5% and altering root morphology to cope with water limitation.¹¹ Plants also divert more fixed C to root exudates, which regulate rhizosphere microbial growth, respiration, and necromass formation, while microbes in turn enhance plant drought resistance and survival.¹² These tightly coupled plant-microbe-soil interactions govern below-ground C dynamics under drought. However, because below-ground processes are spatiotemporally variable and difficult to observe, quantitative evidence for drought-driven changes in C allocation, root and microbial dynamics, and plant-microbe interactions remains limited.

The post-drought phase: Rewetting and legacies

The drought impact chain extends far beyond water stress alleviation (Figures 1B and 1C). Post-drought recovery and legacies can persist for weeks to years, ultimately determining whether ecosystems function as net C sinks or sources.² Capturing this full temporal continuum along the drought impact chain will enhance our ability to mechanistically link short-term drought disturbances to seasonal and interannual ecosystem C dynamics, constraining the C budgets and improving predictions drought-driven sink-to-source transitions over long-term scales.

Upon rewetting, microbes recover within hours to days as dormant cells resume metabolism. Continued root exudation during drought can further stimulate this response, producing pronounced CO₂ pulses that increase emissions by 35.7%.¹³ In contrast, plant recovery is slower, as they must repair hydraulic damage, replace dead roots, and use root exudates to rebuild the liquid bridges needed to reconnect with the soil for water uptake,¹⁴ delaying the recovery of photosynthesis and productivity. This temporal mismatch creates a window of net C loss even after water returns.¹⁵ Furthermore, drought-induced mortality

leaves a substantial C legacy, as dead leaves and roots accumulated during the drought gradually decompose to shape post-drought fluxes (Figure 1B). Drought can also reorganize plant and microbial communities, producing changes in C uptake, decomposition, and rhizosphere processes,¹⁵ driving legacy effects for up to four years or longer.¹⁶ The severe lack of coordinated post-drought observations for these fast and slow C processes creates a major bottleneck in quantifying long-term C balances and predicting persistent sink-to-source transitions.

Multi-factor interactions and spatial scaling challenges

While resolving the drought impact chain is essential for estimating current C budgets and sink-to-source transitions, predicting future dynamics requires contextualizing this chain within concurrent global changes. This is highly complex, as future warming and elevated CO₂ (eCO₂) will interact with drought to shape C cycling (Figure 1D).

A global meta-analysis of manipulative experiments shows that warming generally stimulates plant photosynthesis and growth, with a 1°C warming enhancing aboveground biomass by 9.2% (95% CI: 4.4%–14.1%), root biomass by 19.8% (95% CI: –1.9%–41.4%), and NEP by 78.3% (95% CI: –5.3%–161.8%). Similarly, eCO₂ (+100 ppm) fertilization boosts photosynthesis and belowground C allocation, increasing these components by 8.2% (95% CI: 5.9%–10.6%), 17.9% (95% CI: 10.6%–25.1%), and 4.4% (95% CI: –11.5%–20.4%), respectively.⁴ However, these effects can be profoundly altered by interactions with drought. While eCO₂ can mitigate drought responses by improving water-use efficiency, warming generally amplifies drought-induced C losses. Yet evidence of their combined effects is limited. A large-scale climate manipulation in a northern peatland under a projected 2100 scenario (RCP8.5) showed that future climates more than tripled drought-induced C loss, effectively erasing 9–92 years of ecosystem accumulated C. This exacerbation sharply contrasts with eCO₂'s mitigating effect in uplands.¹⁷ Future drought responses cannot be simply inferred from current observations. Explicitly resolving how interacting climate drivers reshape the impact chain is imperative for accurately

predicting future ecosystem C budgets and sink-to-source transitions.

While satellites offer unprecedented opportunities to monitor terrestrial C fluxes, translating these into robust drought-response estimates for ecosystem C budget across scales remains challenging. For example, even when integrating satellite observations with atmospheric inversions and independent airborne measurements, observations of the 2011 contiguous US drought revealed a net biome productivity anomaly of -0.10 ± 0.16 Gt C. This uncertainty (~160% of the signal) exceeds the anomaly itself, highlighting the difficulty of robustly constraining ecosystem C balance.¹⁸

Furthermore, early drought stress often evades conventional vegetation indices like normalized difference vegetation index or enhanced vegetation index because they primarily track canopy greenness, largely missing early physiological declines such as stomatal closure, which suppress photosynthesis weeks before leaves brown. When greenness eventually declines, attributing it uniquely to drought rather than senescence or disturbance is difficult. Moreover, drought sensitivity varies strongly across ecosystems and even within the same biome or species,¹⁹ reflecting differences in soil properties, plant hydraulic traits, or community composition. Aggregating these heterogeneous landscapes into coarse satellite pixels averages out this variability, obscuring species-level differences and biasing estimates of drought thresholds and C losses. Overcoming these spatiotemporal scaling limitations is critical to accurately constrain large-scale C budgets under drought.

Resolving drought impacts uncertainty across space and time

Accurately evaluating ecosystem C budgets and predicting sink-to-source transitions across time and space involves profound uncertainties. These uncertainties stem not only from unresolved gaps along the drought impact chain—tracking drought unfolding, quantifying hidden processes during drought, and capturing complex post-drought legacies—but are further compounded by interacting climate drivers and coarse spatial scaling limits. These challenges necessitate a mechanism-scale framework connecting the drought impact chain to the mechanistic

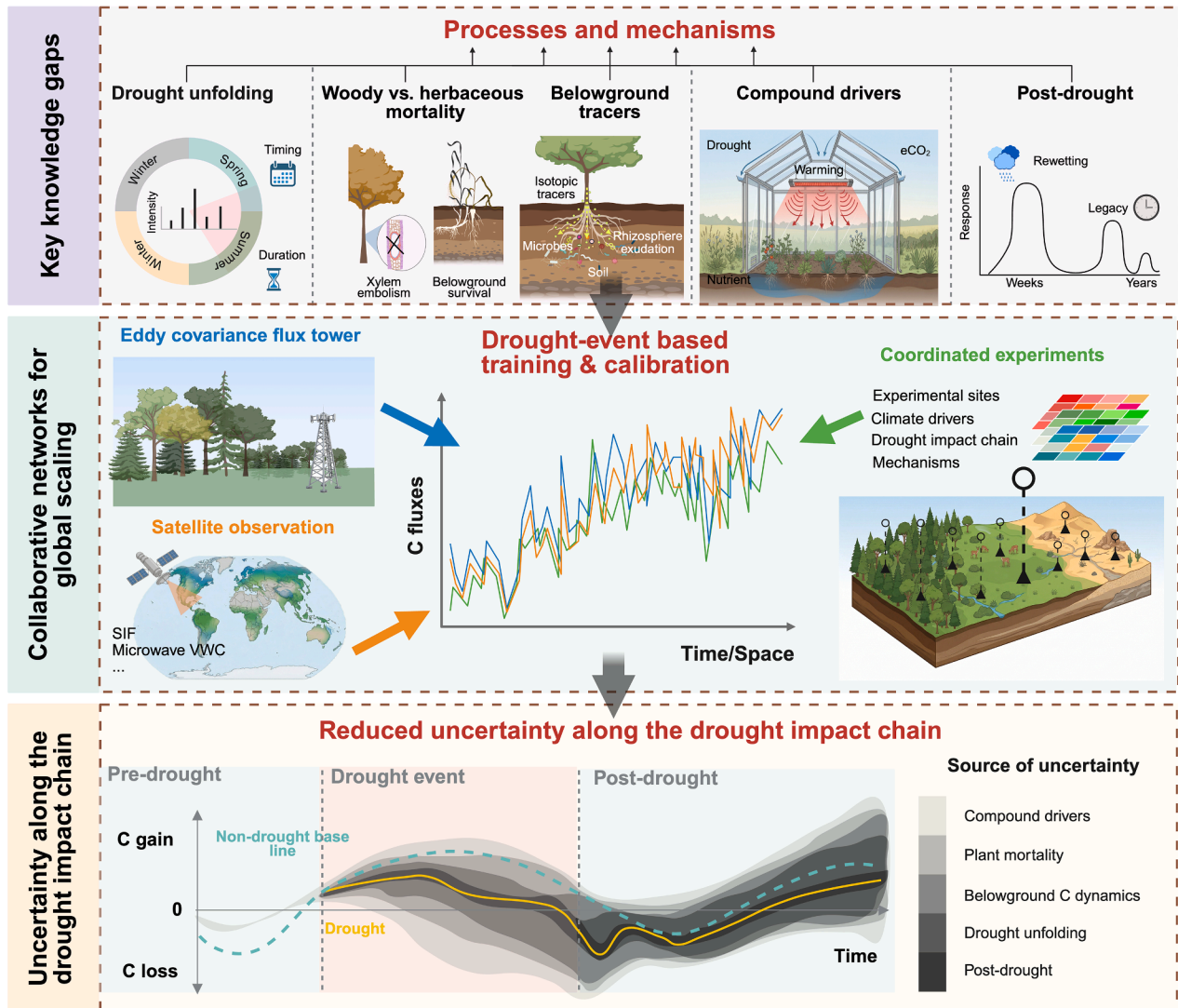


Figure 2. An integrated mechanism-to-scale framework for resolving ecosystem carbon dynamics under drought

The proposed framework addresses critical knowledge gaps by linking process-based field observations and experiments to global-scale remote sensing, ultimately constraining the spatiotemporal uncertainty of terrestrial carbon (C) budget.

Top (key knowledge gaps): targeted field and experimental efforts are required to resolve specific mechanistic processes along the drought impact chain. This includes understanding the unfolding of drought (timing, intensity, and duration), contrasting mortality mechanisms between woody and herbaceous species, deploying isotopic tracers to quantify hidden belowground C fluxes (plant-microbe-soil), utilizing multi-factor manipulation experiments to disentangle the effects of compound drivers, and capturing post-drought rewetting pulses and legacy effects.

Middle (collaborative networks for global scaling): to bridge spatial scaling gaps, coordinated experimental data and eddy covariance flux tower measurements are integrated to generate drought-event-based training datasets. These ground-truth data are essential for calibrating process-relevant satellite observations (e.g., solar-induced chlorophyll fluorescence, SIF; microwave vegetation water content, WWC), enabling the translation of localized mechanisms into regional and global C fluxes.

Bottom (reduced uncertainty along the drought impact chain): a conceptual illustration of how integrating these mechanisms within scaling networks reduces overall C balance uncertainty under drought. The dashed green line represents the non-drought baseline, while the solid yellow line traces the net C flux under drought stress. The shaded bands provide a purely conceptual illustration of the progressive partitioning and reduction of various uncertainty sources, ultimately yielding more robust predictions of drought-driven, sink-to-source transitions over time and across space.

processes driving C-cycle outcomes across scales. A coordinated approach that explicitly traces solutions back to these identified knowledge and data gaps is essential (Figure 2).

To effectively resolve how the drought impact chain drives C cycling and

reduce the uncertainty across time and space, we need to integrate experimental and observational networks across biomes using a standardized, process-relevant drought matrix that captures drought timing relative to phenology, intensity, duration, and re-

wetting magnitude and rate (Figure 2). Such coordinated datasets will allow diagnosis of which C-cycle processes are dominated by specific drought attributes along the impact chain, and how their interactions shape ecosystem C responses.²⁰

Within the drought impact chain, targeted efforts are urgently needed to uncover the hidden ecological mechanisms during the drought phase, specifically plant mortality and below-ground C dynamics (Figure 2). In woody systems, mortality surveys can be linked to biomass loss, deadwood inputs, and subsequent decompositions. In herbaceous systems, field measurements could assess below-ground survival and recovery potential, including bud-bank viability, organ persistence, and resprouting probability. Long-term observations could track mortality of dominant species and functional groups to capture delayed or cumulative drought effects. Concurrently, below-ground C dynamics during drought, including root and microbial growth, mortality, and turnover, can be quantified using targeted isotopic or molecular tracers. Moreover, translating these isotopic and molecular fluxes into robust model parameters (e.g., variable root exudation rates, C allocation partitioning, and microbial C use efficiency and turnover rates) will help parameterize and validate microbially explicit Earth system models, enabling accurate simulations of plant-microbe interactions and long-term soil C pools.

To close the temporal loop of the drought impact chain, post-drought C cycling must be integrated into observational frameworks (Figure 2). High-frequency post-drought C fluxes can be linked to plant mortality and regrowth, microbial turnover, litter inputs, and soil C dynamics to attribute CO₂ pulses and quantify long-term drought legacies. Tracking changes in plant and microbial community will further enable a process-based understanding of subsequent C balances across years.

Furthermore, to ensure these mechanistic insights remain robust and to improve model projections under future climates, the drought impact chain must be evaluated with the context of interacting global change drivers (Figure 2). We urgently need multi-factor experiments combining drought with warming, eCO₂, and altered nutrients. Disentangling these complex, non-linear interactions is vital to empirically constrain future terrestrial C sink projections.

Finally, constraining global C budgets and predicting large-scale sink-to-source transitions require scaling up these fine-

scale observations and mechanistic insights (Figure 2). At larger scales, satellite-detected canopy or biomass loss demands ground calibration of below-ground survival to better incorporate mortality. Advanced tools, such as microwave observations of vegetation water content can help constrain hydraulic mortality thresholds as well as monitor water loss during drought.²¹ Methods like solar induced fluorescence may offer more direct insights into photosynthetic response to drought. Meanwhile, integrating high-resolution satellites with close-range measurements can capture intra- and interspecific variability often lost in coarse pixels. Coupling remote sensing with flux networks using event-based training datasets, spanning drought, rewetting and recovery, can improve the detection of extreme drought amplitude, spatial heterogeneity and post-drought pulses (Figure 2). These advances will strengthen mechanistic understanding and prediction of C cycling under extreme drought.

Drought impacts on ecosystem C balance can be assessed using the impact chain framework linking climatic forcing, ecological processes, and C-cycle outcomes. Closing gaps along this chain aligns with the consensus to resolve the underlying ecological mechanisms across different stress phases.^{2,20} This process-integrated framework links various phases of drought to ecosystem C-cycle responses, grounded in coordinated field observations and flux-calibrated remote sensing, capturing spatiotemporal drought effects (Figure 2). This enables scalable, mechanistic predictions of terrestrial ecosystem C sink-to-source transitions. By integrating these mechanisms into data products and models, we can reduce global C budget uncertainties and informing biologically grounded climate mitigation strategies under drought.

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AUTHOR CONTRIBUTIONS

Conceptualization: M.D.S., Q.Q., Y.L., A.K.K., and A.F.F.; writing – original draft: Q.Q.; visualization:

Q.Q.; writing – review & editing: Y.L., A.F.F., M.D.S., and A.K.K.; all authors read and approved the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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