Diverse functional responses drive ecosystem drought impact and recovery - insights from an ecosystem-scale drought experiment

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The increase in frequency and severity of droughts endangers ecosystem functioning worldwide, however, the mechanisms determining ecosystem susceptibility to drought and legacy effects during recovery remain poorly understood. To disentangle complex ecosystem dynamics we imposed a 9.5-week drought on the Biosphere 2 tropical rainforest, a thirty-year old enclosed forest. To trace ecosystem scale interactions, we implemented a whole-ecosystem labelling approach in the world's largest controlled growth facility: the Biosphere 2 Tropical Rainforest, the B2 Water, Atmosphere, and Life Dynamics (B2WALD) experiment. We measured the dynamics and processes across scales analyzing total ecosystem exchange, soil, trunk and leaf fluxes of H\textsubscript{2}O, CO\textsubscript{2} and volatile organic compounds (VOCs), and their stable isotopes over five months. To trace changes in soil-plant-atmosphere interactions we labelled the entire ecosystem with a \(^{13}\text{CO}_2\)-isotope pulse during pre-drought and drought and traced the carbon flow from the leaves to stems, roots, and soil. Subsequently, we introduced \(^2\text{H}\)-labelled deep-water label during severe drought, providing a unique opportunity to evaluate the importance of deep-water reserves, transit times and legacy effects during the recovery of ecosystem functioning.

The tropical rainforest displayed highly dynamic, non-linear responses during dry-down and rewetting. Drought sequentially propagated through the vertical forest strata, with a rapid increase in vapor pressure deficit, the driving force of tree water loss, in the top canopy layer and early dry-down of the upper soil layer but delayed depletion of deep soil moisture. This induced a two-phase response of ecosystem fluxes: gross primary production (GPP), ecosystem respiration (Reco), and evapotranspiration (ET) declined rapidly during early drought and moderately under severe drought. Atmospheric VOC composition was highly dynamic, with peak emissions of isoprene during early drought followed by monoterpenes and hexanal during severe drought. Thus, the dynamics of different VOCs in the atmosphere closely mirrored different drought stages, and point to distinct physiological processes underlying stages of the total ecosystem response.

Ecosystem \(^{13}\text{CO}_2\)-pulse-labeling showed that drought enhanced the mean residence times of
freshly assimilated carbon—indicating down-regulation of carbon cycling velocity and delayed transport from leaves to trunk and roots. During the recovery significant legacy effects were observed. Interestingly, the majority of the deep-rooted canopy trees tapped into deep-water reserves, but exhibited large differences in transit times until maximum d²H-labelled water was transpired. Drought-sensitive canopy trees, which dominated the ecosystem water flux, responded swiftly reaching ²H-enriched transpiration within 1-21 days and maximum values 14-days after the ²H-pulse. In contrast, drought tolerant canopy trees transpired maximum ²H-labeled deep-water with a delay of 4-weeks. Understory trees and shrubs showed no or minimal ²H₂O uptake, indicating limited access to deep water.

We found highly diverse responses of carbon and water fluxes, driven by the interplay two key factors: species-specific drought adaptations and heterogeneity in microclimate conditions within the mixed forest. These data highlight the importance of quantifying drought impacts on forest functioning beyond the intensity of (meteorological) drought, but also taking the structural and functional composition of the forest into account, as interactive effects between biotic and abiotic factors determine how drought cascades through the system.