**Title:** Tropical tree drought sensitivity is jointly shaped by drought characteristics, species adaptations, and individual microenvironments

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# Abstract (150 words)

Droughts are increasingly impacting forests worldwide, threatening their critical carbon sink. Tree species adaptations to hot and dry conditions – for example, dry season deciduousness in tropical seasonal forests – might confer drought resistance, but such resistance may be variable across microenvironments and drought events. We analysed dendrometer band measurements on 1820 trees across 30 species in a seasonally dry forest in Thailand to assess tree growth responses to two climatically distinct droughts. Species and individuals exhibited a wide range of drought responses within each drought and inconsistent responses across droughts. Deciduous species were more sensitive to early wet-season drought than evergreen species, and this difference was amplified in wetter microclimates. Exposed trees were more sensitive, but presumed greater water access through larger size or wetter topographic positions buffered growth declines. Heterogeneous drought responses of species and individuals indicate potential spatiotemporal insurance effects in diverse forests in the face of increased drought.

# Introduction

Globally, intense drought is becoming more frequent, affecting forest demography, diversity, and carbon (C) cycling (IPCC 2023). However, our ability to predict drought impacts on tree woody growth and resultant ecosystem C sequestration remains limited, particularly for tropical forests, whose critical C sink is threatened by drought (Brando *et al.* 2019) but for which long-term records of annual woody tree growth are rare (Zuidema *et al.* 2022). For forests worldwide, separate studies have shown that drought characteristics, species traits, and microenvironment all affect tree growth responses (e.g., Bennett *et al.* 2015; McGregor *et al.* 2021), but we know little about their combined effects or potential interactions, which could fundamentally alter our understanding of forest responses to drought. Specifically, if drought tolerance is influenced independently by drought characteristics, species traits, and microenvironment, tree drought responses may be conserved, and therefore linearly predictable; i.e., a species with low sensitivity to past droughts would have low sensitivity in any microhabitat and through any drought. In contrast, if these factors interact, the species and individuals that exhibit resistance to one drought may prove much more vulnerable in a different drought. The resultant amplification of the complexity and diversity of drought responses may act as a mechanism for promoting species diversity and stabilizing ecosystem function as drought regimes intensify (Dahinden *et al.* 2017; Luo & Keenan 2022; Naumann *et al.* 2018).

Drought, or hot/dry conditions anomalously departing from climatic means during any time of year, is notoriously hard to define and encompasses a variety of types based on the meteorological variables affected and the severity and duration of the climatic anomalies (Slette *et al.* 2019). While forest drought responses are often considered to follow consistent patterns across droughts (e.g., Bennett *et al.* 2015; **refs?** ), droughts with different characteristics may in fact have very different effects on tree growth (**refs?**). In tropical forests with dry seasons unfavorable to growth, tree drought responses may vary dramatically depending on the timing of drought relative to seasonal cycles of climate, photosynthesis, and woody growth (García-Cervigón *et al.* 2020). Analyses to date have found that tropical tree growth is particularly sensitive to dry season precipitation (Clark *et al.* 2021; Clark *et al.* 2010; Zuidema *et al.* 2022); however, these analyses represent only a very limited set of tropical tree species and climates. It remains unknown how diverse assemblages of tropical tree species respond to different types of droughts, including those occurring at different times relative to regular seasonal cycles.

Tree species adaptations to cope with drought vary widely in type and strength, often leading to classification of species as “drought tolerant” or “drought sensitive” (**refs?**). In tropical seasonal forests in particular, trees have evolved to maximise growth, reproduction, and survival under periodic hot/dry conditions, with strategies ranging along a spectrum from hydraulic safety to efficiency, leading to tolerance or avoidance of dry conditions (González-M. *et al.* 2021). Dry season deciduousness represents an extreme “avoidance” strategy along this continuum, where species lose leaves during the dry season to avoid foliar water loss and have acquisitive strategies during leaf-on periods (De Souza *et al.* 2020). Other strategies include deep roots (hydraulic safety, to access deeper water in the dry season), more negative leaf water potential at turgor loss point (, hydraulic safety, to maintain gas exchange and photosynthesis under hot and dry conditions), and *large vessels (hydraulic efficiency)* (Chitra-Tarak *et al.* 2021; González-M. *et al.* 2021). Under drought conditions, some of these strategies can lend drought resistance while others can amplify drought sensitivity, especially under severe droughts (Chitra-Tarak *et al.* 2021; González-M. *et al.* 2021; Kunert *et al.* 2021). Moreover, besides being constant or adaptively conserved, these strategies can also have developmental or ecophysiological controls. For example, some species regulate negative ’s, leaf deciduousness, and root depth based on environmental cues, leading to intraspecific or interannual variation and potentially resulting in spatiotemporal variation in drought responses [Williams *et al.* (2008); REFS Lasky? Hulshof?].

Finally, the microenvironments that individual trees experience influence growth responses to drought. Across horizontal axes, microenvironments defined by topographic and edaphic variation shape tree drought responses. While habitats with relatively moist soils (e.g., low-lying topographic positions) are clearly more hospitable during drought, trees in these microenvironments may be more vulnerable if less drought-adapted (e.g., less negative , Kunert *et al.* 2021) or acclimatized (**refs?**). Indeed, there are observations of trees near streams undergoing greater growth declines (McGregor *et al.* 2021) and increases in mortality (Zuleta *et al.* 2017) during drought. Across vertical axes, trees of different sizes have their crowns and root systems in sometimes dramatically divergent microenvironments. Aboveground, tree crowns in canopy or emergent positions are exposed to higher evaporative demand and thermal stress driven by higher solar radiation, wind speed, and vapor pressure deficit (Vinod *et al.* 2023), and such exposure makes trees more vulnerable to drought (Ma *et al.* 2023; Scharnweber *et al.* 2019). These aboveground gradients in crown exposure are at least partially offset by the tendency for large trees to have larger and often deeper root systems (**refs?**) and thereby potential to access more reliable water sources (**refs?**). However, trees with deeper roots that rely on regular access to deep water may be more vulnerable during severe droughts when those sources are depleted (Chitra-Tarak *et al.* 2021). While the overall tendency is that larger trees suffer greater growth declines during drought (Bennett *et al.* 2015), it remains unclear whether this is driven primarily by crown exposure, by greater height itself makes trees more vulnerable to drought based on the physics of hydraulic flow through a porous medium (Fernández-de-Uña *et al.* in press; **mcdowell\_darcy\_2015?**), or by trait differences across vertical axis (Vinod *et al.* 2023). Thus, horizontal and vertical microenvironmental gradients modify tree drought responses, likely in interaction with drought characteristics and species traits.

We hypothesize that tree drought sensitivity is jointly and interactively shaped by drought characteristics, species adaptations, and microenvironments, resulting in variable drought responses of species and individuals across droughts, and of species across microhabitats. We test this by examining individual tree growth during two ENSO drought years within a 14-year record of dendrometer band measurements in a seasonally dry forest in Thailand. Specifically, we test predictions that i) both species and individuals respond differently to different droughts. ii) Deciduous species, which rely on wet seasons for growth, are particularly sensitive to wet season drought. iii) Exposed trees are more sensitive to drought, but water availability, either through larger topographic location or tree size (and corresponding rooting volume), can buffer growth declines.

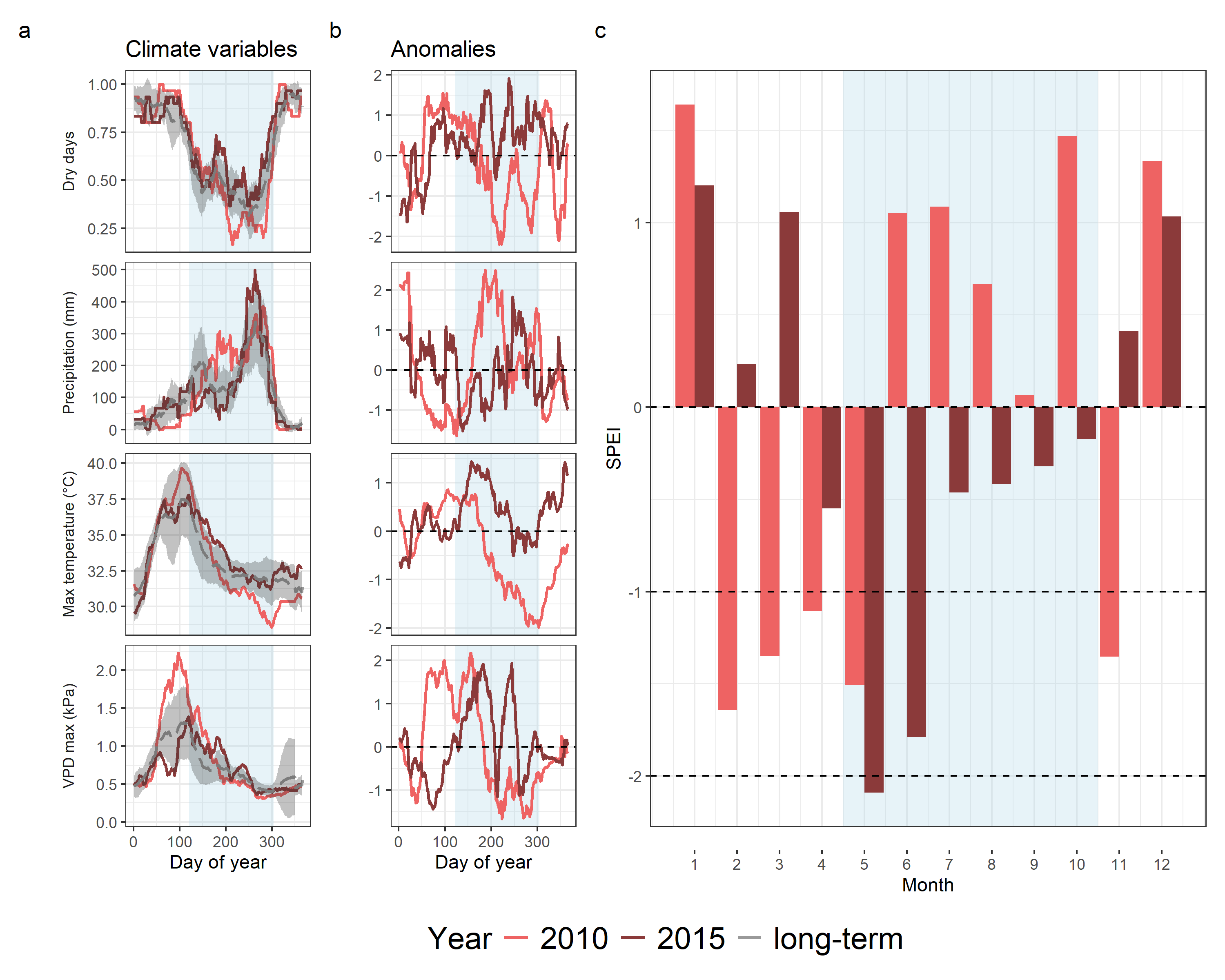
Table 1: Summary table of hypotheses tested, effects of variables on drought sensitivity and corresponding evidence. For each variable x year combination, "+" indicates a positive effect, "-" indicates a negative effect and "n.s." indicates that the effect was not statistically significant.

|  | 2010 | 2015 | evidence |
| --- | --- | --- | --- |
| **Drought characteristics** |  |  |  |
| Timing | dry season | early wet season | Fig 1 |
| min SPEI | -1 | -2 | Fig 1 |
| consecutive months SPEI < -1 | 4 | 2 | Fig 1 |
| max VPD anomaly (SD) | +2 | +2 | Fig 1 |
| max T~max~ anomaly (SD) | +0.8 | +1.5 | Fig 1 |
| **Species effects** |  |  |  |
| Deciduousness | n.s. | - | Fig 3 |
| 2010 sensitivity |  | n.s. | Fig S5 |
| **Microenvironment & individual effects** |  |  |  |
| Topographic Wetness Index (TWI) | - | + | Fig 3, 4 |
| Deciduousness:TWI | n.s. | - | Fig 3 |
| crown exposure | - | - | Fig 4, 5 |
| other size effects | + | - | Fig 4 |
| 2010 sensitivity |  | n.s. | Fig S6 |

# Materials and Methods

***Sites and data***

Our study site was the Huai Kha Khaeng ForestGEO plot (15.6324 N, 99.217 E), hereafter “HKK”, in the Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani, Thailand. This is a 50-hectare plot in mixed deciduous tropical forest, with a mean annual temperature of 1400 mm and a strong dry season from November to April (Anderson-Teixeira *et al.* 2015). The region is periodically affected by droughts associated with the *El Niño* Southern Oscillation (ENSO, **refs\_ENSO?**). The dominant canopy species are *Hopea odorata*, *Vatica harmandiana*, *Dipterocarpus alatus* and *Tetrameles nudiflora* and lower layers of the canopy are dominated by sub-canopy evergreen and deciduous species like *Miliusa horsfieldii* and *Polyalthia viridis*. Long-term analysis of tree-ring data shows that tree growth at Huai Kha Khaeng has been influenced by temperature and rainfall (Vlam *et al.* 2014).



***Figure 1. Climatic characteristics of drought years and average years*** in the Huai Kha Khaeng ForestGEO plot. For four daily climate variables dry days, precipitation, maximum temperature and VPD, panel a) represents rolling means for 30 days around the focal day for that year. Grey line represents the mean of this rolling mean from 2008 to 2019 and ribbons represent standard deviation around this mean. Panel b) represents anomalies of this rolling mean from the values across the timeseries. Values, therefore represents the number of standard deviations from the mean on a given day. c) shows 1-month Standardised Precipitation Evapotranspiration Index (SPEI) values for each month in 2010 and 2015. Across all panels, light blue background represents the average wet season, from May to October. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/10>

In the HKK plot, metal dendrometer bands were installed in 2008 on 2353 trees across 152 species following standard protocol (Muller-Landau 2008). Trees were selected were based on the relative abundance of species in the forest, with more individuals banded from the abundant species (ranging from 230 trees to 1 tree per species), and spanning the size and habitat distribution within the plot. On each tree, the dendrometer band was installed at 1.4 m from the ground, a height of 10 cm above the regular point of measure for the whole plot census (typically 1.3 m), except on irregular trunks or buttresses when they were shifted above. All dendrobands were censused two times a year - in the wet and dry season - typically in June and January. During the census, the size of the window opening along the band was measured using Mitutoyo digital callipers (least count = 0.01 mm) and the diameter of the tree at the dendrometer band was measured using standard DBH tape.

***Calculating annualised growth increments***

Using the late wet/early dry dendrometer band censuses, we calculated annualised growth for each year for each tree. We first removed measurements with likely data entry errors because of misplaced decimals, potential misidentified bands (old band numbers that restarted after stopping) or misidentified individuals (individuals with conflicting metadata across censuses). We used the raw window size measurements combined with the diameter measurement at installation to calculate diameter at each dendroband census using standard equations that uses the chord across the measurement window to estimate the arc, assuming a circular cross section[condit]. We used a direct measurement of at the time of installation if it was available. If the tape measurement at the first window size measurement was not available for any band, we excluded window size measurements until the first available diameter measurement. We then calculated annualised diameter increments for each individual for each year by finding the difference in diameter from the previous year () and adjusting for the number of days between measurements ().

To ensure that the data did not smooth over multiple years, we excluded increment measures with missing values for and then excluded large measurement outliers (> 3 standard deviations from the mean across all observations). Tape measurements themselves are not precise enough for calculating drought sensitivity; error for each tape measure is 1mm, error for growth is at least 2mm. In comparison, median annual growth across trees in HKK is ~1.4 mm and calculating deviation from annual growth needs sub-mm precision. However, tape measurements can be used to check for consistency in trends or identify outliers. We calculated increments from annual tape measurements made on each dendrobanded tree at each census and removed dendroband measurements that had low agreement with these annualised increments calculated from tape measurements. Finally, we excluded trees with negative increments over the whole timeseries, and included only species that had at least 10 individuals, resulting in a final dataset of 1820 individuals across 30 species.



***Figure 2: Growth increment timeseries and drought responses*** across trees and species in the Huai Kha Khaeng ForestGEO plot. a) Median of annualised growth increments across ten dominant species (colours) and all trees (black) from 2009 - 2022. b) Distribution of drought sensitivity of tree growth across all individuals in the two drought years. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/11>

***Drought years and characteristics***

We identified drought years of interest in the dendroband timeseries - 2010 and 2015 - based on two drought indices and corroborated by meteorological data, local expertise, and plot-level growth responses. Within the dendroband timeseries, two ENSO events had occurred; 2010 was a moderate ENSO event while 2015 was a very strong ENSO event (**REF?**). We also calculate Standardised Precipitation-Evapotranspiration Index (SPEI) at the 1-month scale using the SPEIbase dataset (Vicente-Serrano *et al.* 2010). Defining drought as periods with two or more consecutive months with 1-month SPEI < -1 also resulted in identification of 2010 and 2015 as drought events. These years also corresponded with expert knowledge of major droughts that affected the region as well as meteorological records (see next paragraph; Fig. 1) and plot-level growth declines in the timeseries (Fig. 2). We note that although tree growth was unusally low in 2020, this year did not emerge as a drought year either in the examination of drought indicators or from expert knowledge.

To characterise the two focal droughts, we used data from a weather station near the plot and publicly available climate data for the region. We used daily weather data collected from 2001 to 2019 at the Forest Fire Research Station [CHECK WHERE], located ~20 km from the ForestGEO plot. *(SPECIFY WHICH VARIABLES WERE OBTAINED FROM WHICH SOURCE, AND OTHER SOURCES.)* We first calculated daily values of Vapour Pressure Deficit (VPD) using the equation

We then calculated rolling means of precipitation, number of dry days (precipitation = 0), VPD and maximum temperature over 15 day periods across the whole year for each year. Finally, we calculated daily rolling anomalies for each variable for 2010 and 2015 from the long-term daily expectation as

***Variables for analysis***

For the two drought years, 2010 and 2015, we calculated growth sensitivity for each tree to each drought as a growth anomaly from its mean annual increment from calculated from dendrometer band window size.

We first calculated the mean annual increment for each tree as the mean of the annualised increments across the whole timeseries. We then calculated sensitivity for each tree for each drought as

By scaling the difference in increment to the mean annual growth of each tree, this metric allows us to compare across slow and fast growing individuals and species.

*(See* [*issue #28*](https://github.com/forestgeo/growth-precip-thailand/issues/28)*)* To account for potential biases in dendrometer band increments from water-related growth or shrinkage, we also calculated growth occurrence using a zero-growth assumption (Zweifel *et al.* 2016). Timing of measurement and seasonal dynamics in tree hydration and bark dynamics could contribute to negative values in dendrometer band increments, unlike woody growth from tree ring datasets (Chitra-Tarak *et al.* 2015). Using a zero-growth model, we calculated growth occurrence as 1 under positive diameter change and any change <=0 as 0. To account for biases introduced by timing of measurements and seasonal dynamics, we used this simplifying assumption to corroborate the patterns observed with the sensitivity metric.

Across all individuals in the plot, we calculated topographic wetness index for an expectation of the water availability across space based on the concavity/convexity of a location. We used a Digital Elevation Model from a 5 m x 5 m elevation layer collected at plot establishment. We used the *whitebox* package in R (Lindsay 2016; Wu & Brown 2022) to fill and breach this layer, calculate flow accumulation at each cell and then calculate TWI as . We defined tree size as the diameter at breast height (calculated from dendrometer band window measurement) at the previous census. We estimated crown exposure for each tree at each census using crown illumination index, an ordinal categorical variable from 1 to 5 (least to most exposed) measured at each dendroband census.

We calculated deciduousness as a species level trait using data published in Williams *et al.* (2008) for the top 30 species. We defined deciduousness as the mean proportion of crown leaf loss at maximum loss across individuals in the species, with a score ranging from 1 to 4 where 1 is most evergreen and 4 is most deciduous. Data was unavailable for *Alphonsea ventricosa*, an evergreen species, and so we manually assigned it a deciduousness score of 1, in the middle of the evergreen range. An alternate measure of deciduousness is the duration spent at maximum crown loss. This was strongly correlated with the proportion of crown loss; we chose to use the proportion of crown loss because it was available for a larger list of species.

***Statistical methods***

We first modelled sensitivity as a simple random intercept model

We then used the predicted sensitivities from this model and tested their correlations with deciduousness using simple linear models.

To model the interactive effects of deciduousness and wetness on sensitivity, we modelled

We then calculated predictions across all combinations of values from observed maximum to minimum of TWI and deciduousness within this dataset.

To further disentange the microenvironmental drivers of drought sensitivity, we simultaneously modelled:

and

Simultaneously modelling the effect of variables on sensitivity and the effect of DBH on CII in this way allows us to disentangle causual linkages between these processes. We chose to model a species random effect on all slopes here to account for variation across species instead of specific traits which may have different effects with each of the variables. However, we also ran simpler models with species random effects only on the intercept, the results of which are reported in the Supplementary Material. Across all models, we used Gaussian priors for the distribution of the response variable sensitivity, considered CII as an monotonic predictor (ordered factor) and centred and scaled the other predictors. We modelled CII as an ordinal categorical variable with a cumulative logit link function. In the combined form, the model therefore used a multivariate distribution of Gaussian and logit.

All statistical analyses were performed using R version 4.4.0 (R Core Team 2024). Mixed models were fit through Bayesian regressions using MCMC methods using the package *brms* (Bürkner 2017). We ran 4 MCMC chains for 3000 iterations with 1000 of these set as warmup. We extracted draws, calculated distributions and checked convergence using functions from the *posterior* package (Bürkner *et al.* 2023; Vehtari *et al.* 2021).

# Results

## Drought characteristics

The two droughts analysed had distinct temporal climatic characteristics, with 2010 primarily a dry season drought and 2015 a wet-season drought (Table 1, Fig 1). The 2010 drought peaked between February and April (dry season), with drought characteristics including lower precipitation, higher number of dry days, higher maximum temperature, and higher VPD relative to the long-term mean and 1-month SPEI values below -1. In 2015, similar deviations occurred in May and June (early wet season), with 1-month SPEI in May reaching -2, the lowest in the the entire dendroband census time period.

## Growth timeseries and drought responses

The increment timeseries using dendrometer band measurements revealed plot- and species-level patterns in interannual growth variation (Fig 2a). Median annualised growth rate across the years of measurement for the whole plot was 0.02 0.03 mm. Median annual increment differed by species with *Gluta obovata* having the lowest (0.06 0.2 mm) and *Dipterocarpus alatus* the highest (0.36 0.34 mm) among the 30 species analysed. *(See* [*issue #27*](https://github.com/forestgeo/growth-precip-thailand/issues/27)*)*

Drought years were associated with lower growth across the plot. In 2010, the median annual increment was 0.02 mm, 13.33% lower than the median across all years. The drought year 2015 had the lowest median annual increment 0.01 mm, 52.68% lower than the median across all years. While median species responses to the 2010 drought were variable, all species had lower increment than a typical year in 2015. Besides decrease in magnitude of growth, the proportion of trees with negative growth was also higher in the drought years (Fig S4). Across the years, on average, 11.42% of the trees had negative growth, with a minimum of 6.7% in 2011. The drought year 2015 had the maximum proportion of trees with negative growth in the timeseries, 22.57%. *(See* [*issue #28*](https://github.com/forestgeo/growth-precip-thailand/issues/28)*)*

On average, trees had negative drought sensitivities for both droughts, but with considerable variation (Fig 2b). Median drought sensitivity across all trees in 2010 was -0.27 0.92 while in 2015 it was -0.55 0.98. In 2010, species-level sensitivities ranged from -0.09 for *Alphonsea ventricosa* to 0.07 for *Afzelia xylocarpa*. In 2015, these ranged from -0.11 for *Dimocarpus longan* to 0 for *Mitrephora thorelii*.

## Species effects

Species median sensitivities in 2010 and 2015 were not correlated with each other (Pearson’s correlation coefficient r = 0.1, p = 0.6, Fig S5) but on average had lower mean and median sensitivities in 2015 than in 2010 (Fig S5), in alignment with median sensitivities across all trees.

Deciduousness species had lower negative sensitivities in 2015, but not in 2010 (Fig 3a). In 2015, predicted sensitivities from intercept-only models of sensitivity with a species random effect on the intercept showed a significant negative association with deciduousness value (r = -0.41, p = 0.03). On the other hand, in 2010, predicted sensitivities had no significant association with deciduousness (r = -0.05, p = 0.8). Moreover, models of all trees with TWI and deciduousness as predictors showed that the conditional effect of deciduousness on sensitivity (controlling for topographic wetness) was significant and negative in 2015 (-0.08; 90% CI -0.12, -0.04) but not in 2010 (-0.02, 90% CI -0.05, 0.02).



***Figure 3: Variation in sensitivity among species*** in the Huai Kha Khaeng ForestGEO plot during droughts in 2010 and 2015. a) Relationship of the mean species sensitivities from model fits of an intercept-only model, with mean species deciduousness values. Line shown for significant correlation. b) Predicted sensitivity values across the observed range of deciduousness and topographic wetness index from a model with TWI, deciduosness and their interaction across all trees modelled for each drought year separately. For comments: <https://github.com/forestgeo/growth-precip-thailand/issues/12>

## Microenvironment and individual effects

Individual tree responses to drought were not correlated with each other (Fig S6).

TWI had no significant on sensitivity in 2010 but a positive effect in 2015. Specifically, across all trees, the model with TWI and deciduousness showed that TWI had no effect on drought sensitivity in 2010 (median effect =0, 90% CI -0.04, 0.03) but a positive effect in 2015 (median effect =0.05, 90% CI 0.01, 0.08). The interaction between TWI and deciduousness was not significant in 2010 (median effect =0, 90% CI -0.01, 0.02) but was significantly negative in 2015 (median effect =-0.02, 90% CI -0.03, 0). Combined, predicted sensitivities of deciduous trees was more negative than evergreen trees in 2015, with this effect stronger in wetter sites (Fig 3b).

The differing effects of TWI on sensitivity in the two droughts, along with the influence of deciduousness, were confirmed by models that controlled for crown exposure and DBH as well as species variation in intercept and slopes (Fig 4a). These models showed small negative sensitivities in wetter sites in 2010 (median effect =-0.04, 90% CI -0.09, 0.02), but a strong positive effect of TWI in 2015 (median effect =0.05, 90% CI 0, 0.11). The positive effect of TWI in 2015 was, however, mainly due to the response of evergreen species; deciduousness had a significant negative correlation with the slopes of the TWI effect in 2015 (Fig 4b). Predictions across the range of observed variables also showed that deciduous species generally had larger negative sensitivities in 2015, which did not increase with TWI (Fig 4c). On the other hand, neither the mean sensitivities across species nor their response to TWI were associated with deciduousness in 2010.



***Figure 4: Drivers of variation in sensitivity among individuals***. All panels represent model results from models (one for each year) predicting sensitivity with microenvironment conditions with species random effect on all slopes. a) Coefficient plots showing median effects and 90% CI for wetness, exposure and DBH of tree. b) wetness effect across all species and its relationship with deciduousness value. Line represents a significant correlation. c) Predicted relationship of drought sensitivity with topographic wetness index across all species derived from model predictions. Black line represents overall relationship (panel a); coloured lines for each species reflects deciduousness values. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/13>

Crown exposure was associated with stronger negative sensitivities in both droughts. In the same models with species random effects on intercept and slope, the simplex parameter for the ordered factor crown exposure in 2010 was significant and negative (median effect =-0.15, 90% CI -0.32, -0.07), while in 2015 the negative effect was not as strong (median effect =-0.06, 90% CI -0.17, 0.03). Predicted effects of crown exposure on sensitivity decreased monotonically, with a decrease to negative sensitivities in category 4 and 5 in 2010, but all crown exposure categories had negative sensitivities in 2015 (Fig 5b).

DBH was a significant predictor of crown exposure, with larger DBH associated with higher exposure categories in 2010 (median effect =4.02, 90% CI 3.75, 4.29) and 2015 (median effect =4.2, 90% CI 3.92, 4.49) (Fig 5a). Controlling for this direct effect of exposure, the remaining effect of DBH *per se* was significantly positive in 2010, while it was weakly negative in 2015 (Fig 4a, Fig 5a).



***Figure 5: Effects of size, exposure and water availability*** from combined models. Hypothesised relationships between microenvironment variables and drought sensitivity with their modelled effects in the HKK ForestGEO plot in the droughts of a) 2010 and b) 2015. Solid lines represent relationships where 90% credible intervals do not overlap 0, blue and red lines represent positive and negative effects respectively and line thickness is scaled to the effect size. c) Modelled sensitivity across crown exposure classes in 2010 and 2015. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/14>

# Discussion

We show that, at least in one tropical seasonal forest, the drought sensitivity of tree growth is jointly and interactively shaped by drought characteristics, species adaptations, and local environmental conditions (Table 1). Analysing two droughts in a 14-year dendrometer band timeseries, we found lower-than-average growth in drought years, reflecting in lower plot-level growth (Fig 2). Comparing across droughts, there was little consistency in species- or individual-level drought responses, reflecting dissimilar effects of a key species trait (deciduousness) and variables linked to water access (TWI, DBH) under differing drought conditions. Despite lower absolute extremes of temperature, vapor pressure deficit, and number of dry days (Fig. 2a), drought in the early wet season (2015) elicited stronger responses across trees, especially deciduous species that are expected to have stronger seasonality in growth phenology (Fig 3). Interestingly, in 2015 (but not 2010), evergreen and deciduous species had divergent responses along a wetness gradient; evergreen trees fared better and deciduous species suffered worse declines in wetter sites (Fig 3b, Fig 4b). While trees with more exposed crowns were consistently more sensitive to drought, additional effects of DBH – presumably including rooting volume and depth – were dissimilar between the drought events (Fig 4a). In other words, water availability buffered exposure-associated growth declines through different mechanisms in the two different droughts; larger trees (with likely deeper roots) fared better in the dry-season drought while trees in wetter sites suffered smaller growth declines in the wet-season drought (Fig 5). Taken together, these results indicate that joint and interactive effects of drought characteristics, species traits, and individual microenvironments produce enormous heterogeneity in individual and species drought responses of tropical trees. This finding that individual droughts have divergent effects on species and individuals may contribute to the maintenance of species diveristy and ecosystem stability.

While our analysis of 30 species across size classes and habitats spans representative spatial and ecological variation realistically and beyond the scope of previous such analyses, we are limited in quantitatively analysing differences associated with drought characteristics because of low sample size. The two droughts analyzed differed in multiple aspects, including ENSO strength, seasonal timing, and magnitude and duration of meteorological extremes and anomalies (Fig. 1).  
Thus, quantitative analyses parsing out the specific effects of drought characteristics (e.g., timing, degree of anomaly) are currently impossible. While the meteorological data justify our characterization of these droughts as “dry-season” (2010) and “wet-season” (2015), growth records from numerous additional droughts would be necessary to rigorously generalize differences based on the seasonality of drought effects. Given the relative rarity of drought and the lack of multi-decadal records of annual tree growth for diverse tropical forests, there is currently no data set on which such an analysis could be performed. In temperate and boreal forests, where the majority of species form annual growth rings, tree-ring analysis can disentangle species and individual sensitivities to larger numbers of droughts (although sample sizes still remain limited). *(KAT paused editing here.)* Indeed McGregor *et al.* (2021) found that species sensitivities were different across drought events. However, as this accumulating dendrometer data record continues to grow, so does the potential to answer these questions across a wider range of forested ecosystems.

Tropical dry forests represent periodic hot/dry conditions, creating selective pressures for adaptative variation towards drought resistance, but this might not hold in other bioclimatic zones where adaptive pressures and thus ecological variability is different. Strong seasonality in tropical dry forests exerts selective pressures on hydraulic strategies and has resulted in diversification along the hydraulic safety-efficiency axis with diverse strategies to maximise tree vital rates (González-M. *et al.* 2021; Oliveira *et al.* 2021). The degree of adaptive variation along the water use axis might be comparable to other dry climatic systems (e.g. temperate drylands reported in Vasey *et al.* (2022)) but it may not apply to the wet or everwet tropics, where tree-environment relations and evolutionary strategies may be substantially different. Therefore, we caution that our results suggestive of community-level insurance effects under drought be interpreted carefully across forest types that may be structured primarily by nutrient limitation, fires, herbivory or pathogens. However, our inference on the effects of drought timing could be generalisable across wet and dry tropics in the light of emerging evidence that despite low seasonality in climatic conditions, everwet forest species also show seasonal growth patterns (Giraldo *et al.* 2023).

Despite consistent observations of growth declines at the plot level across drought events, we show that this scale obscures a variety of ecological responses at the species and tree level that are heterogeneous across drought events. Our finding that a wet season drought had bigger impact calls into question the generality of the findings of Zuidema *et al.* (2022), which found that in species with tree-ring chronologies, dry season drought was most impactful. (Care must be taken in interpretation, however, as the 2015-2016 wet season ENSO drought was stronger (Fig 1)). *Afzelia xylocarpa*, one of the few annual-ring-forming species in HKK is noteworthy with the most distinct response across the two events; it had the highest (positive) sensitivity in the dry season drought, but a large negative sensitivity in the wet season drought (Fig S5). More generally, past analyses of tree ring and census estimates of drought sensitivity in seasonally dry tropical forests may have been limited towards fast growing (measurable using tape) or few dry-associated species (that form annual tree rings) - and therefore capturing only the more dramatic effects. In contrast, our analyses reveal a range of responses, including the contrasting influence of deciduousness in the two different droughts, showing that ecological and evolutionary strategies may result in heterogeneous consequences. Distinct responses of species and individuals to drought characteristics suggests potential spatiotemporal insurance effects among tropical tree response to drought in alignment with recent global analyses (Liu *et al.* (2022)).

Drought sensitivity is often defined as a static species trait but our study reveals expanded dimensions of drought responses with possible consequences for management and restoration. Despite net decreased growth at the plot level (in agreement with landscape-scale in Aguirre-Gutiérrez *et al.* (2022) and Bennett *et al.* (2023)), we show evidence that the same strategies are not uniformly successfully across spatiotemporal climatic variation. Static traits are often used to explain and predict forest responses to drought, especially in the tropics where long-term records are few (Guillemot *et al.* 2022; Vico *et al.* 2017). More inclusive frameworks for drought responses like Trugman *et al.* (2021) (on mortality) encompass ecological complexity and covarying traits with environment like, but they assume consistent sensitivity of individual trees across events. Our results, however, demonstrate an additional temporal dimension of variation, at least partially attributable to drought characteristics. Our results indicate that drought responses in tropical trees may not be a fixed response across events, but jointly shaped by species adaptations and local environmental conditions. Given these inconsistencies, diverse stands that may represent greater variation in ecological and evolutionary strategies, may have mechanisms for stable functioning under future droughts.

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