

Intra-annual plasticity of growth mediates drought resilience over multiple years in tropical seedling communities

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Funding information

Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: P2ZHP3_161986, P300PA_167758; Stiefel-Zangger fund

Abstract

Precipitation patterns are changing across the globe causing more severe and frequent drought for many forest ecosystems. Although research has focused on the resistance of tree populations and communities to these novel precipitation regimes, resilience of forests is also contingent on recovery following drought, which remains poorly understood, especially in aseasonal tropical forests. We used rainfall exclusion shelters to manipulate the interannual frequency of drought for diverse seedling communities in a tropical forest and assessed resistance, recovery and resilience of seedling growth and mortality relative to everwet conditions. We found seedlings exposed to recurrent periods of drought altered their growth rates throughout the year relative to seedlings in everwet conditions. During drought periods, seedlings grew slower than seedlings in everwet conditions (i.e., resistance phase) while compensating with faster growth after drought (i.e., recovery phase). However, the response to frequent drought was species dependent as some species grew significantly slower with frequent drought relative to everwet conditions while others grew faster with frequent drought due to overcompensating growth during the recovery phase. In contrast, mortality was unrelated to rainfall conditions and instead correlated with differences in light. Intra-annual plasticity of growth and increased annual growth of some species led to an overall maintenance of growth rates of tropical seedling communities in response to more frequent drought. These results suggest these communities can potentially adapt to predicted climate change scenarios and that plasticity in the growth of species, and not solely changes in mortality rates among species, may contribute to shifts in community composition under drought.

KEYWORDS

climate change, drought frequency, forest dynamics, phenological shifts, plant–climate interactions, recovery, resistance

1 | INTRODUCTION

Forests across the globe are experiencing reduced or more variable precipitation (Chadwick, Good, Martin & Rowell, 2015; Forzieri et al., 2014) leading to increased tree dieback (Lewis, Brando, Phillips, van der Heijden & Nepstad, 2011; Peng et al., 2011; Steinkamp & Hickler, 2015). The response of a forest community to novel precipitation

patterns is the result of the resistance and recovery of the species and individuals comprising the community (Mitchell et al., 2016). Therefore, assessing both the immediate response of a forest and the overall recovery of the forest is important for understanding the long-term effects on composition and ecosystem function (Anderegg et al., 2015; van der Sande et al., 2016). However, most research has focused solely on the resistance phase (i.e., the immediate

impacts of a drought; Potts, 2003; Lewis et al., 2011; Rowland et al., 2015) with much less attention on the postdrought recovery of forest communities or legacy effects (Anderegg et al., 2013, 2015; Cole, Bhagwat & Willis, 2014; Hartmann, Adams, Anderegg, Jansen & Zepfel, 2015), which is important for understanding long-term vegetation shifts under novel precipitation patterns (Martinez-Vilalta & Lloret, 2016).

The impact of drought on plant communities, and in turn ecosystem function, depends on the intensity, duration, timing and frequency of drought events (Mitchell et al., 2016). The response of a plant community to these components of drought consists of the loss of a function during drought (i.e., resistance) and the return of the function after drought (i.e., recovery), which are the features of resilience (Cole et al., 2014; Lloret, Keeling & Sala, 2011; Mitchell et al., 2016). Within this concept, alterations to any of these four characteristics of drought under climate change will potentially affect ecosystem functions. However, the relative importance of these characteristics is dependent on other variables such as the community composition (i.e., traits of the species; Li et al., 2015; O'Brien et al., 2017), abiotic factors (e.g., soil type; Nakagawa et al., 2000; Potts, 2003), biotic interactions (Desprez-Loustau, Marçais, Nageleisen, Piou & Vannini, 2006; McDowell et al., 2011), historical drought regime (Cole et al., 2014; Mitchell et al., 2016) and postdrought environmental conditions (Lloret, Escudero, Iriondo, Martínez-Vilalta & Valladares, 2012; Lloret et al., 2011).

Many forests throughout the world are shifting from communities assembled by differences in light or nutrients to communities assembled by differences in water availability (Hartmann, 2011), especially everwet tropical forests that have rarely experienced water limitation historically (Cole et al., 2014; Lewis et al., 2011; Phillips et al., 2010). This shift in the limiting resource may alter competitive dynamics and the demographic rates of species (e.g., growth and mortality) and in turn impact species distribution and community composition (Anderegg & HilleRisLambers, 2016; Kroiss, HilleRisLambers & D'Amato, 2015; Martinez-Vilalta & Lloret, 2016; van der Sande et al., 2016). The lowland tropical forests of South-East Asia, especially those occurring on the relatively aseasonal island of Borneo, may be particularly sensitive to these altered precipitation patterns because rainfall is generally high and evenly distributed over the year (Phillips et al., 2010; Walsh & Newbery, 1999), and drought normally occurs on relatively infrequent cycles at supra-annual intervals (Gibbons & Newbery, 2003; Sakai et al., 2006; Walsh & Newbery, 1999). Experimental manipulation of the rainfall regime is a useful approach to test the effects of altered precipitation patterns on seedling communities in this everwet system, especially given the relative paucity of historical observational data relating drought and stand dynamics. Seedling communities are also important for the long-term recovery and resilience of forest ecosystems as climate change alters the overstorey composition and structure (O'Brien, Philipson, Tay & Hector, 2013; Potts, 2003). In addition, climate change alters seedling regeneration dynamics (establishment and recruitment) through interactions with herbivores and pathogens, which are drivers of community assembly processes

in tropical forests (Bagchi et al., 2014; Bell, Freckleton & Lewis, 2006). For example, drought may predispose seedlings to mortality by pathogens and herbivores thereby enhancing vegetation shifts beyond the direct effects of drought (McDowell et al., 2011).

In this study, we altered the drought frequency for seedling communities in a tropical forest that, in recent history (i.e., the last 10–20,000 years; Heaney, 1991; Bird, Taylor & Hunt, 2005), has primarily experienced infrequent supra-annual droughts associated with El Niño Southern Oscillation events (ENSO). We applied rainfall exclusion shelters yearly for three consecutive years to achieve water limitation similar to that measured during the 1997–98 ENSO event and assessed resistance and recovery of the seedling communities in response to this yearly drought return interval. Therefore, we manipulated the frequency and intensity of drought but ignored the timing of drought—which we assumed to be less important in this aseasonal tropical forest. Developed from the conceptual framework proposed by Körner (2006) with regard to CO₂ manipulation experiments, we propose four growth responses of seedlings to more frequent drought: (1) no effect of drought on growth, (2) an initial decline in growth followed by a compensatory recovery of growth, (3) a reduced growth followed by a recovery parallel to growth in everwet conditions or (4) a reduced and declining growth relative to seedlings in everwet conditions (see Figure 3 in Körner, 2006 for scenarios). In addition, we expected drought to increase seedling death relative to everwet conditions.

2 | MATERIALS AND METHODS

2.1 | Site

The experiment was conducted near the Malua Field Station (N05°05'20" E117°38'32"; 102 masl) in the c. 33,000 hectare Malua Forest Reserve located approximately 22 km north-west of Danum Valley Field Centre in Sabah, Malaysia (Tuck et al., 2016). Malua was initially logged in the mid-1980s and, except for the 500 hectare Sabah Biodiversity Experiment site, was relogged in 2005. Eastern Sabah has historically had an aseasonal climate and an average monthly rainfall (SE) of 240 mm (33) and an average yearly total of 2900 mm (90), as recorded at Danum Valley Field Centre from 1986 to 2014. There have been severe drought events occurring irregularly since the early 1980s in the area (e.g., 1986–1987, 1991–1992 and 1997–1998, Walsh & Newbery, 1999). The mean daily minimum temperature measured at the Malua Field Station during the experiment was 22.7°C, and the mean daily maximum temperature was 31.6°C. The mean mid-day humidity was 59%, and the mean nighttime humidity was 95%.

2.2 | Experimental design

In December 2011, we established 12 plots along a topographic gradient from 100 masl at a small stream to 130 masl on top of a low ridge. Soil texture across the gradient showed little variability with a mean (SE) of sand, silt and clay content equal to 20% (2), 11% (1)

and 65% (3), respectively. Each plot consisted of two identical subplots (90×120 cm) planted approximately 70 cm apart. We planted communities of 20 species (Table S1) consisting of one seedling per species in each subplot (40 seedlings at each paired plot and a density of 19 seedlings/m² per subplot; 480 seedlings in total). Prior to planting, competing understorey vegetation within the plot area was removed to ground level and was continuously removed during the experiment. Species were randomly assigned to a planting point in each subplot at 30×30 cm spacing. Therefore, among plots, species had unique neighbors but within plots, neighbors were identical in each subplot. The species selected comprised seventeen species of the *Dipterocarpaceae* family, one from the *Fabaceae* family and two from the *Bombacaceae* family. The *Dipterocarpaceae* seedlings included one species from the genus *Dryobalanops*, three species from the genus *Hopea*, two species from the genus *Parashorea* and 11 from the genus *Shorea* (see Table S1 for species details). Seedlings were planted from 15-month-old nursery stock, which were grown in polyethylene pots in a nursery under 5% light. Seeds were sourced from Malua and adjacent forest reserves during the mast fruiting event of August 2010 (O'Brien et al., 2013).

Seedlings established for ~2 months, and during this time, no mortality was observed. In February 2012, a rainfall exclusion shelter was constructed over one subplot in each plot. Clear plastic polyethylene sheeting was used to create the shelters 1.5 m above the seedlings covering approximately 1.5×1.8 m (i.e., an additional 30 cm of area on all sides of the plot). Aluminum sheeting 10 cm high was inserted 5 cm into the soil upslope from each plot to prevent overland water flow into the plots during heavy rainfall events. Exclusion shelters remained in place for ~90 days and were then removed. Although 90 days seems like an excessively severe drought, the natural conditions during this time remained rainy and cloudy. Therefore, 90 days were necessary to simulate reduced soil water availability in the field while during a natural drought soil drying would occur more rapidly. In February 2013 and 2014, the shelters were returned to the same subplots and left for approximately 100 days for each year. During experimental drought periods, control subplots received natural rainfall and were also given supplementary irrigation (~10 L per subplot) in the event of no rain for 3 days. Furthermore, both subplots were irrigated in the event of 3 days with no rainfall during the nondrought periods of the experiment. This irrigation regime ensured that control subplots (everwet treatments) remained wet relative to the rainfall excluded subplots (drought treatments). Neither subplot experienced drought when rainfall exclusion shelters were not present. With this design and irrigation regime, we ensured that the seedling community only experienced drought because of the rainfall exclusion shelters (see Fig. S1 for soil water potential during the experiment).

2.3 | Environmental conditions

We measured photosynthetically active radiation using quantum sensors (SKP 210; Skye instruments LTD, Llandrindod Wells, Powys, UK) in each subplot for 24 hr. These data were compared to

simultaneous measurements of direct sunlight at the Malua Field Station in order to assess the light differences among plots and between subplots within a plot. Light was similar between subplots, but among plots, light ranged from 0.3% to 13% (Fig. S2).

Volumetric soil moisture content was regularly measured at the soil surface at three locations in each subplot during the first drought and at a depth of 15 cm during the second and third drought using a ML2x Theta Probe and HH2 moisture meter (Delta-T Devices, Burwell, Cambridge, UK). The relationship between soil water potential and volumetric soil moisture content was determined using the filter paper method (Deka et al., 1995; O'Brien et al., 2013). At the end of the second and third drought period, we measured the mid-day leaf water potential of three to five seedlings of each species in everwet and drought treatments to test whether seedlings were responding to reduced soil water availability. We chose not to remove leaves in the first year because most seedlings had very few leaves.

2.4 | Seedling monitoring

The height of each seedling was measured at the time rainfall exclusion shelters were applied (beginning in February 2012) and during removal of shelters every year for 3 years. Height was also measured 340 days after the final period of rainfall exclusion shelters (May 2015). Relative growth rate (RGR) was calculated as the natural log difference in height between the beginning and end of a period divided by the number of days between measurements. This calculation was carried out for each period (three periods with rainfall exclusion shelters and three periods with no rainfall exclusion shelters for a total seven measurements including the initial measurement). Dead seedlings were also recorded at each census.

2.5 | Statistical analysis

Mean soil water potential during each drought was analyzed as a function of treatment (fixed factor with two levels; drought and everwet), period (fixed factor with three levels; first, second and third drought) and treatment \times period with a linear mixed-effects model. We used random terms for plot, treatment nested in plot and period nested in plot (Table S2a). Mid-day leaf water potential was analyzed as a function of treatment, period and treatment \times period with a linear mixed-effects model. We used random terms for plot, treatment nested in plot and species (Table S2b).

Relative growth rate (RGR) was calculated based on a standardized height to account for differences in seedling size across species and through time. To do this, RGR was analyzed as a function of initial height at the start of each time-point (a continuous variable) and time-point (fixed factor with six levels) with random effects for subplot nested within plot nested within time-point and individual seedling. We applied an auto-regressive correlation structure to account for the fact that a measurement of seedling height at a time-point is not independent of seedling height at a previous time-point. From this analysis, we estimated RGR from the extracted random term

estimates for every seedling during each time-point while controlling for height differences among seedlings (i.e., RGR calculated at the mean height of 60 cm; Table S3a).

We tested the effect of treatments on the growth by analyzing these size-standardized estimates of RGR as a function species (fixed factor with 20 levels), period (fixed factor with two levels; during and after rainfall exclusion shelters), year (fixed factor with three levels) and treatment (fixed factor with two levels; everwet and drought). We also tested the two-way interactions of species \times treatment, year \times period and treatment \times period as well as the three-way interaction of treatment \times year \times period. We used random effects for plot, treatment nested in plot, period nested in plot, year nested in plot, treatment nested in period nested in plot, treatment nested in year nested in plot, species nested in plot and species nested in treatment nested in plot (Table S3b). From this analysis, differences in RGR between drought and everwet treatments during the different temporal phases can be used to calculate resistance and recovery (i.e., the difference in RGR between seedlings in the drought and everwet plots during drought periods is resistance and after drought periods recovery). The difference in average growth between drought and everwet treatments over the entire year or over the entire experiment is therefore resilience as it encompasses both the resistance (drought) and recovery (post-drought) phases.

We also assessed average recovery of each species from the second and third year of drought (the average difference in growth between individuals in drought and everwet treatments after the removal of rainfall exclusion shelters) as a function of average resistance (the average difference in growth between individuals in drought and everwet treatments during rainfall exclusion shelters) using a linear model (Table S4) to test whether more resistant species recovered better. We removed the first year from this analysis because soil water availability was statistically indistinguishable between treatments in that year (Figure 1a).

Probability of seedling survival was analyzed as a function of species, period, year, treatment, species \times treatment, year \times period, treatment \times period and treatment \times year \times period with a binomial distribution (1 = alive and 0 = dead) and a complimentary log-log link function. We used random effects for plot, treatment nested in plot, species nested in plot, year nested in plot and treatment nested

in period nested in plot (Table S5). Furthermore, an offset, calculated as the natural log of the number of days since the last census divided by 30 (to assess survival on a monthly scale), was used to account for different time intervals between censuses. We also tested the effect of seedling size on survival by analyzing binomial survival as a function of average height throughout the experiment. We used random terms for plot and treatment nested in plot. All analyses were performed with the asreml-R package (ASReml 3, VSN International, UK) in the R statistical software (version 3.3.1; <http://r-project.org>).

3 | RESULTS

Soil water potential was significantly lower with rainfall exclusion shelters (-0.08 MPa, 95% CI: -0.1 to -0.06) than without (-0.01 MPa, 95% CI: -0.03 to 0.1). Although soil water potential was statistically indistinguishable between treatments in the first year, the difference between treatments increased with each following year that the exclusion shelters were applied (Figure 1a). Leaf water potentials showed the same pattern as soil water potential (Figure 1b) with seedlings under rainfall exclusion shelters having significantly lower water potentials (-0.61 MPa, 95% CI: -0.68 to -0.54) than seedlings without rainfall exclusion shelters (-0.48 MPa, 95% CI: -0.54 to -0.41). The increasing drought conditions with each year are likely due to improved methods of applying the rainfall exclusion shelters, increased competition in the communities as seedlings grew larger and required more water and lower rainfall during the period of exclusion in the second and third year ($>1,200$ mm in year one and <900 mm in year two and three).

Except for the first year when only marginal decreases in soil water were measured, RGR was significantly lower in the drought treatment when rainfall exclusion shelters were present (i.e., resistance; difference in RGR between drought and everwet treatments in the second drought = -1.1×10^{-4} cm cm $^{-1}$ day $^{-1}$, 95% CI: -1.3×10^{-4} to -8.6×10^{-5} and in the third drought = -2.8×10^{-5} cm cm $^{-1}$ day $^{-1}$, 95% CI: -4.8×10^{-5} to -7.8×10^{-6} ; Figure 2a). However, these significantly lower RGRs in the drought treatments switched to significantly higher RGRs after the rainfall exclusion shelters were removed (i.e., recovery; difference in postdrought RGR

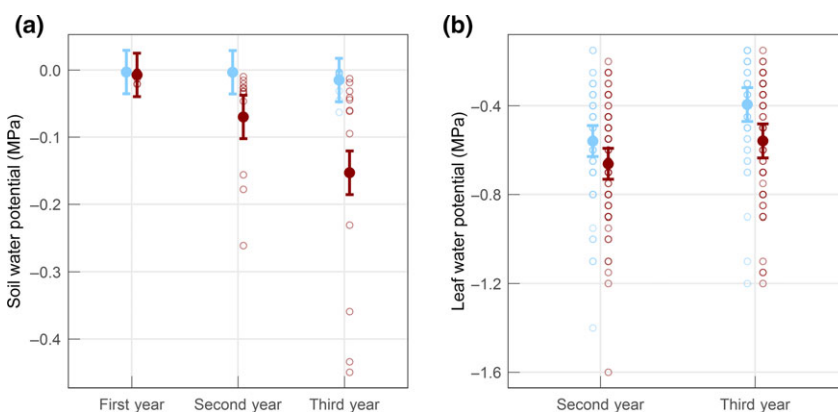


FIGURE 1 Mean soil water potential and minimum leaf water potential during rainfall exclusion periods. (a) Soil water potential (95% CI) modeled from volumetric water content using the filter paper method for everwet (blue) and drought (red) treatments. (b) Mid-day leaf water potential measured after approximately 75 days of rainfall exclusion for the second and third year of drought [Colour figure can be viewed at wileyonlinelibrary.com]

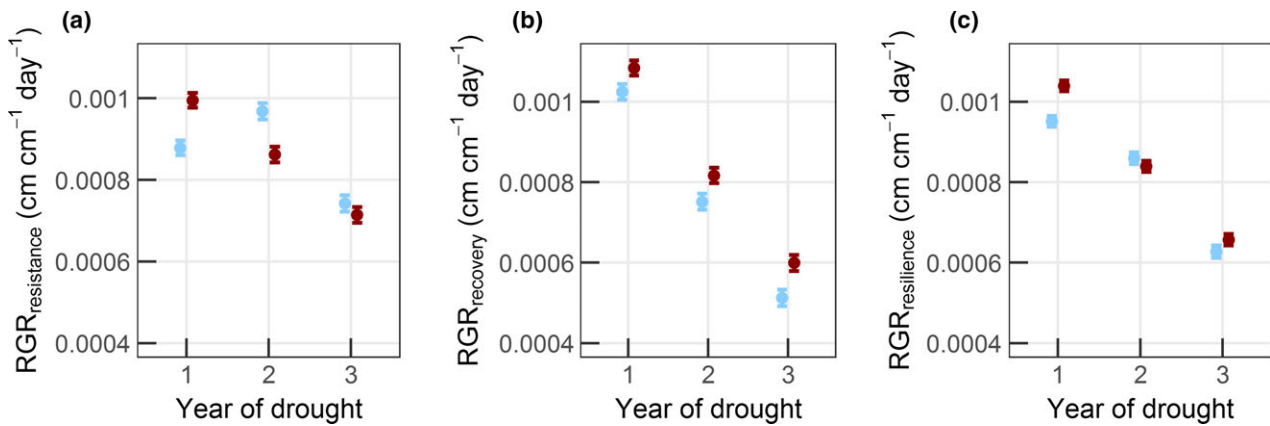


FIGURE 2 Relative growth rate (RGR) for everwet and drought treatments. (a) RGR (95% CI) was significantly lower in drought (red) than everwet (blue) treatments when rainfall was excluded for the second and third year (i.e., the resistance phase). The first year likely showed a different pattern because the rainfall exclusion shelters were not effective at achieving significant differences in soil water that year (Fig. 2a). (b) Following the removal of rainfall exclusion shelters (i.e., the recovery phase), drought treatments grew significantly faster than everwet treatments. (c) Average annual RGR (i.e., resilience of each year) for seedlings in the drought treatment had significantly lower RGR in year two but significantly higher growth in year three. The observed RGRs were removed for readability [Colour figure can be viewed at wileyonlinelibrary.com]

between drought and everwet treatments in the second year = $6.6 \times 10^{-5} \text{ cm cm}^{-1} \text{ day}^{-1}$, 95% CI: 4.5×10^{-5} – 8.6×10^{-5} and postdrought RGR in the third year = $8.7 \times 10^{-5} \text{ cm cm}^{-1} \text{ day}^{-1}$, 95% CI: 6.6×10^{-5} – 1.1×10^{-4} ; Figure 2b). In year two, postdrought RGR only partially compensated for the reduction in RGR during the drought (postdrought RGR was 62% of the RGR reduction during rainfall exclusion shelters), but in year three, postdrought RGR overcompensated for the reduction in RGR during the drought (postdrought RGR was 310% of the RGR reduction during rainfall exclusion shelters). Therefore, annual RGR for seedlings in the drought treatment had significantly lower growth in year two but significantly higher growth in year three (i.e., resilience; Figure 2c). Trends and differences were similar if the first year (when the drought treatments were not effective) was excluded from the analysis (Fig. S3).

The magnitude and direction of the effect of drought on RGR was significantly different among species (Figure 3). Only three species had a significantly lower RGR during drought (Figure 3a) while 13 species had a significantly higher postdrought RGR (Figure 3b). However, if the first year is removed from the analysis (when soil water potential was only marginally reduced in the drought treatment; Figure 1a), then the number of species with a significantly lower RGR during drought increased to 13 species of the 20 species (Fig. S4). Regardless of these temporal variations in RGR, the overall differences in RGR between drought and everwet treatments over 3 years (i.e., multiyear resilience) were statistically indistinguishable from zero for twelve species, exemplifying postdrought compensatory recovery (Figures 3c and S4c). Therefore, even though intra-annual RGR was statistically different between drought and everwet treatments, average multiyear RGR was similar. Furthermore, recovery significantly increased with resistance across species (Figure 3d) whereby more resistant species had better recovery. This analysis also showed that three species were overall negatively impacted by drought, and five species were overall positively affected by drought while all other species were compensating

growth reductions during drought proportionally with increased post-drought growth.

Although seedling survival was high in both drought (86% survived; 33 seedlings died) and everwet (82% survived; 41 seedlings died) treatments, a cyclical pattern in probability of survival was observed in both treatments (Figure 4a). The probability of survival was significantly higher during the period with rainfall exclusion shelters (February to July) than in the months that followed. Overall probability of survival was statistically indistinguishable between drought treatments (78% chance of survival per month, 95% CI: 67–88) than in everwet treatments (71% chance of survival per month, 95% CI: 60–82). We also tested the correlation between percent direct sunlight of a plot and the total number of seedlings alive at the last census for each treatment in each plot. Light was marginally positively correlated with total living seedlings for the everwet treatment (spearman $\rho = .51$, $p = .09$) and was significantly correlated for the drought treatment (spearman $\rho = .62$, $p = .03$). Species were significantly different in their survival with a range from 46% to 94% (Figure 4b). Survival rates were lower for smaller seedlings (below 90% probability of survival for seedlings <56 cm tall, 95% CI: 83.4–89.8; Fig. S5), and seedlings that died were on average smaller than seedlings that lived (difference in height between dead and alive seedlings = 13.1 cm, 95% CI: 3.9–22.2).

4 | DISCUSSION

Our yearly rainfall manipulation in an everwet tropical forest showed that seedlings subjected to recurrent drought can adjust their intra-annual growth rates while maintaining annual growth rates similar to communities under everwet conditions. Seedlings slowed their growth rates during drought and then increased growth rates in recovery periods when water availability was not limiting. Within the

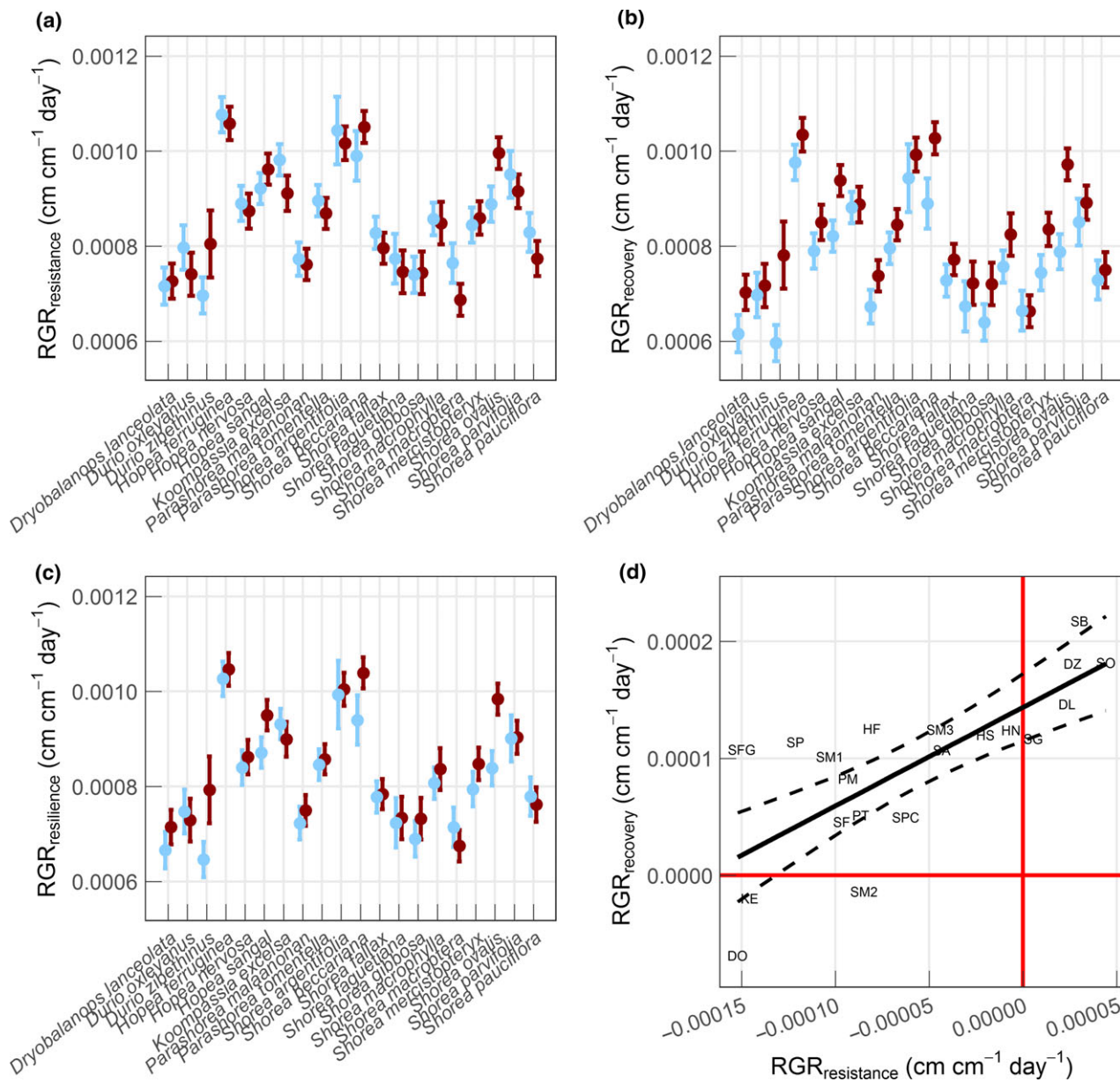


FIGURE 3 RGR during and after rainfall exclusion for all species. (a) Mean RGR (95% CI) during periods of rainfall exclusion shelters (resistance) was highly variable among species with some showing significantly faster growth in drought (red) than everwet (blue) treatments while others were showed significantly slower growth. (b) Mean RGR after periods of rainfall exclusion shelters (recovery) was also highly variable among species. (c) This intra-annual variability led to statistically indistinguishable RGR between drought and everwet treatments for most species over the 3.5 years of the experiment (resilience). (d) Recovery significantly increased with resistance. Three species showed overall negative effects of drought, twelve species showed proportionally compensatory effects whereby faster growth after drought offset slower growth during drought and five species showed overall positive effects. Species codes are the first letter of genus and specific epithet (Table S1 [Colour figure can be viewed at wileyonlinelibrary.com])

context of the four hypotheses proposed in the introduction—i.e., no effect, short-term reduction with compensatory recovery, short-term reduction and no compensating recovery or reduction and decline (Körner, 2006)—three species showed a reduced and declining growth rate with drought relative to everwet conditions, and twelve species showed an initial decline followed by a compensation that allowed recovery to similar growth rates of everwet conditions. Surprisingly, five species had an overall higher growth rate during resistance and recovery periods relative to seedlings in everwet

conditions, which implies they benefited from imposed droughts likely due to reduced competition for light due to the negative effects on other species (i.e., potentially shading effects were reduced as a consequence of defoliation and slower growth in drought-impacted species). The probability of seedling survival followed a cyclical pattern with periods of higher and lower survival probability that was independent of soil water availability. We found that absolute survival was correlated with light, indicating low light superseded the effects of drought. Our results indicate that intra-

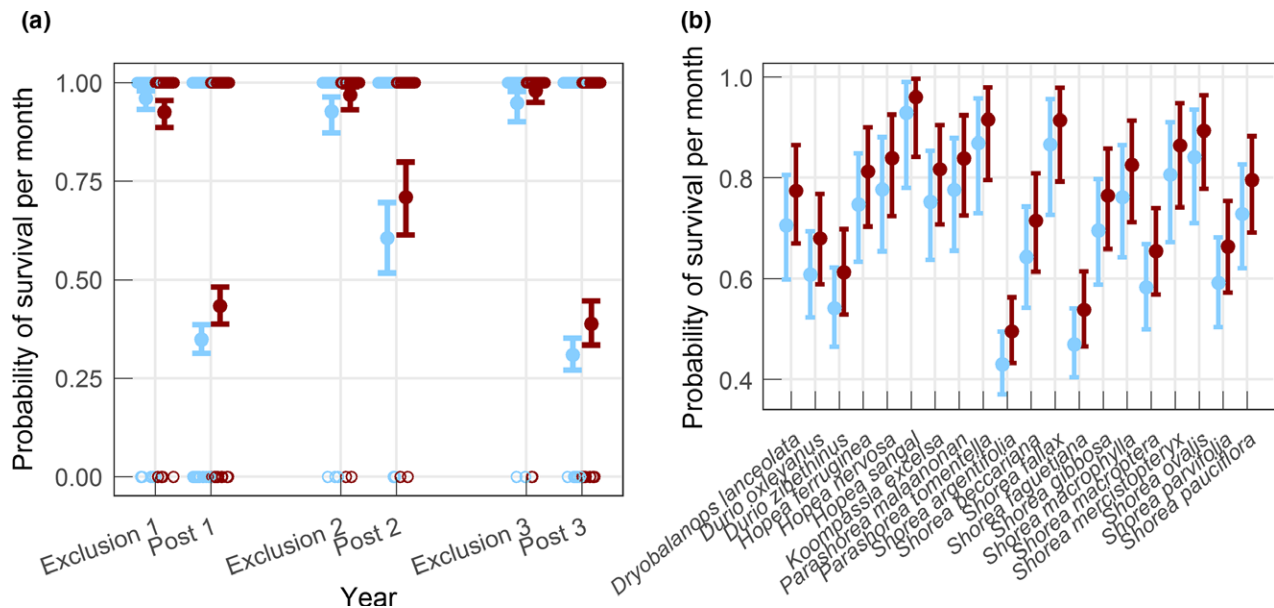


FIGURE 4 Survival trends at the treatment and species level. (a) Probability of survival (95% CI) was higher in drought treatment during all time periods except the first period with rainfall exclusion, but average probability of survival over the entire experiment was not significantly different between drought and everwet treatments (Table S5). Interestingly, we found a cyclical trend with more death occurring between August and January than from February to July. (b) Similar to growth, species were highly variable in their probability of survival [Colour figure can be viewed at wileyonlinelibrary.com]

annual plasticity in growth rates is a mechanism to compensate for reduced soil water availability and maintain annual and multiyear growth rates.

4.1 | Intra-annual growth plasticity

The plasticity of seedling growth under frequent interannual drought supports studies in other systems that found plant communities shift the timing of leaf, flower and fruit production as a strategy in response to climatic changes in temperature and precipitation (Cleland, Chuine, Menzel, Mooney & Schwartz, 2007; Peñuelas et al., 2012). Therefore, even in tropical forests with 20,000 years of fairly everwet conditions (Bird et al., 2005; Heaney, 1991), tree species were able to temporally adjust functions to resist and recover from recurrent drought. One potential mechanism promoting this plasticity in growth may be an active shift from a growth to a storage strategy in response to water limitation (Wiley & Helliker, 2012). This response may also occur passively (Körner, 2015) as a consequence of plant growth being more sensitive to drought than photosynthesis (Muller et al., 2011; Tardieu, Granier & Muller, 2011), and as growth is inhibited by low water availability, photosynthesis continues causing photosynthates to passively accumulate. Regardless of whether active storage or passive accumulation occurs, this excess of nonstructural carbohydrates could be available for rapid growth at the onset of rainfall following a drought, and many of the species used in this experiment have been shown to accumulate nonstructural carbohydrates during drought (O'Brien, Burslem, Caduff, Tay & Hector, 2015; O'Brien, Leuzinger, Philipson, Tay, & Hector, 2014). In support of this argument, O'Brien et al. (2015) showed that seedlings had reduced nonstructural carbohydrates under fluctuating water relative to regularly watered control seedlings but

maintained growth similar to controls. Therefore, nonstructural carbohydrate dynamics may support recovery following drought.

An additional mechanism mediating this temporal shift in growth may be the negative effect of drought on soil microbial abundance and activity (Maestre et al., 2015; Manzoni, Schimel & Porporato, 2011; Vogel, Eisenhauer, Weigelt & Scherer-Lorenzen, 2013) and, in turn, seedling access to soil nutrients (He & Dijkstra, 2014; Sardans, Peñuelas, Prieto & Estiarte, 2008). During drought, nutrients may accumulate in the soil and then become available at the onset of rain and the return of soil microbial activity. Seedling competition may also contribute to the shift in growth rates. Drought may delay direct competition among seedlings for light and soil resources. In other words, seedlings achieved faster growth when water was not limiting in drought treatments while seedlings in everwet conditions were growing continuously and directly competing earlier in time.

4.2 | Interspecific differences in drought response

Although seedling communities under drought conditions maintained annual growth rates at a similar level to those under everwet conditions, interspecific variation in resilience of growth was observed. Most species showed a neutral (12 species), or positive (five species), growth response to frequent drought. The positive relationship between resistance and recovery suggests a shift in the competitive differences among species (Table S1). For example, the rank height of *Durio oxleyanus* dropped from 3 in everwet condition to 10 in drought conditions while *Shorea ovalis* moved from 19 in everwet conditions to 13 in drought conditions. We did not find a mechanism to explain this relationship (i.e., resistance, recovery and resilience were not correlated with functional traits such as wood density,

nonstructural carbohydrates or specific-leaf area). These changes in growth rates may lead to shifts in demographic rates, but the effect on demographic rates is dependent on the interactions between more frequent drought and herbivores, pathogens and light that drive community assembly (Bagchi et al., 2014; Bell et al., 2006; Lloret et al., 2012; McDowell et al., 2011). However, direct tests of the interactive effects of drought and these factors will be necessary to understand vegetation shifts in a changing climate (Martinez-Vilalta & Lloret, 2016).

Three species showed overall negative responses to frequent drought with average growth rates significantly lower than that of seedlings in everwet conditions during both the resistance and recovery phase. These species were biologically distinct (i.e., each comes from a different family), suggesting that the factors which contributed to slower growth under drought were unique. *Koompassia excelsa* is a legume and may be particularly sensitive to decreases in microbial activity inhibiting nitrogen fixation in nodules (Serraj, Sinclair & Purcell, 1999), which supports the findings of Gei and Powers (2015) in tropical dry forests. The poorest performer under drought, *Durio oxleyanus*, has already been shown to be highly sensitive to low soil water availability as a result of its low nonstructural carbohydrate concentration in the stem and low wood density relative to other species (O'Brien et al., 2014, 2015). *Shorea macroptera* was one of the slowest growing species regardless of the treatment, which contrasts previous work on this species which found it to have intermediate growth rates (Philipson et al., 2012, 2014). However, those studies were carried out with limited or no seedling competition either within managed planting lines of the Sabah Biodiversity Experiment (Philipson et al., 2014) or in pots in controlled shade houses (Philipson et al., 2012). This difference may indicate that *S. macroptera* is unable to compete well for limiting resources when seedling densities are higher. This diverse spectrum of species showing a negative response suggests mechanisms underlying drought sensitivity were likely the result of a complex interaction of variables (e.g., a suite of traits that confer resistance and resilience) and not a single trait axis (O'Brien et al., 2017).

4.3 | Survival rates

Survival showed a cyclical pattern with periods of high survival followed by periods of low survival throughout the 3 years. This cycle was surprising because of the aseasonal climate of Borneo (Walsh & Newbery, 1999). However, rainfall was much greater from August to January (6200 mm, period of low survival probability) than from February to July (5100 mm; period of high survival probability) during the experiment (Fig. S1). There was also 100 fewer rainless days and 26 more days with high rainfall (>30 mm in 24 hr) in the periods with low probability of survival. This excessive rainfall may have enhanced mortality through poor abiotic conditions in the soil or by promoting soil pathogen infection and spread.

There were only minor differences in mortality between treatments and therefore, little evidence that mortality was mediated by

drought. Light had a positive effect on survival, and plots with <1% light had double seedling mortality (51 of 200, 26%) as compared to plots with more than 1% light (23 of 280, 8%). These results support Philipson et al. (2014) which showed a decrease in mortality with higher light. The cyclical mortality pattern may represent thresholds in time whereby extended low light conditions cause a negative carbon balance and lead to seedling death (Hoch, 2015; Sevanto, McDowell, Dickman, Pangle & Pockman, 2014). Specifically, small seedlings had lower survival rates than larger seedlings potentially due to being outcompeted by larger seedlings for water or nutrients or shading by larger neighbors. Multiple variables are likely contributing to this pattern and interacting with light including pathogens (Augspurger & Kelly, 1984) and competition (e.g., density- or size-dependent mortality; Peters, 2003).

In our manipulation of recurrent interannual drought, species responses in a tropical aseasonal forest ranged from reduced to enhanced growth rates relative to everwet conditions. Intra-annual fluctuations in growth followed rainfall patterns with reduced growth rates during drought (i.e., resistance phase) and compensatory growth rates postdrought (recovery phase), which maintained annual and multiyear growth similar to seedlings in everwet conditions (i.e., resilience). Therefore, forest dynamics, and potentially vegetation shifts, under novel climate conditions may be mediated by differences among species in their growth plasticity and not solely by mortality rates, which indicates communities may be more robust to altered drought regimes than predicted. These results suggest that even tropical forests with a historically irregular, infrequent and weak drought regime can adapt to more frequent drought.

ACKNOWLEDGEMENTS

MOB was supported by the Stiefel-Zangger fund and a Swiss National Science Foundation Mobility Fellowship (P2ZHP3_161986 and P300PA_167758). This work contributes to the University Research Priority Program on Global Change and Biodiversity at the University of Zurich. The Southeast Asia Rainforest Research Partnership contributed to the field work with research assistant support, especially from Musa, Udin, Achung, Fauzi, Asri, Weldy, Vendi, Redley, Eglee, Danil, Remy, Abu, Jude, Jolu and Philip. We thank Erick Calderon for feedback and Cam Wagg for revisions on earlier versions of the manuscript. This is article number 17 of the Sabah Biodiversity Experiment.

AUTHOR CONTRIBUTIONS

MOB designed and carried out the experiment, analyzed the data and wrote the manuscript. RO and GR provided conceptual development and logistical help for working in Sabah, Borneo.

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How to cite this article: O'Brien MJ, Ong R, Reynolds G.

Intra-annual plasticity of growth mediates drought resilience over multiple years in tropical seedling communities. *Glob Change Biol*. 2017;23:4235–4244.

<https://doi.org/10.1111/gcb.13658>