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Resistance of tropical seedlings to drought is mediated by neighbourhood diversity

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Occasional periods of drought are typical of most tropical forests, but climate change is increasing drought frequency and intensity in many areas across the globe threatening the structure and functioning of these ecosystems. However, the effects of intermittent drought on tropical tree communities remain poorly understood and the potential impacts of intensified drought under future climatic conditions are even less well known. The response of forests to altered precipitation will be determined by the tolerances of different species to reduced water availability and the interactions among plants that alleviate or exacerbate the effects of drought. Here we report the response of experimental monocultures and mixtures of tropical trees to simulated drought that reveal a fundamental shift in the nature of interactions among species. Weaker competition for water in diverse communities allowed seedlings to maintain growth under drought while more intense competition among conspecifics inhibited growth under the same conditions. These results show that reduced competition for water among species in mixtures mediates community resistance to drought. The delayed onset of competition for water among species in more diverse neighbourhoods during drought has potential implications for the coexistence of species in tropical forests and the resilience of these systems to climate change.

Many types of tropical forests are characterized by constant temperature and humidity, typically experiencing regular rainfall evenly distributed throughout the year. However, rain forests often experience infrequent droughts, during El Niño Southern Oscillation (ENSO) years for example, although the effect of these events on forest structure and functioning is poorly understood[1,2]. On the one hand, drought could increase the success of some species putting them at an advantage, increasing dominance and potentially decreasing diversity[3]. Alternatively, drought could promote diversity by enhancing density-dependent mechanisms that favour uncommon species[4]. For example, drought may increase intraspecific competition for light, water and associated soil resources or predispose trees to pathogen infection or insect attack[5–7], both density-dependent mechanisms that can influence community diversity[8–10].

Although light is usually considered the most important resource gradient driving species distributions in tropical forests[7], climate change is projected to increase the severity and frequency of drought for substantial areas of tropical forest[1,11] thereby increasing the importance of water limitation as a driver of species distributions[12]. These changes pose a potential risk to these hyper-diverse ecosystems due to negative effects on reproduction[13], recruitment[13], growth[3,14] and survival[3,15]. Species diversity may provide an insurance effect against these alterations and provide stability under drought conditions[16,17] because species vary in their resistance and resilience to severe climatic disturbances[3,18]. Although, if conditions go beyond the physiological limits of even the tolerant species, then large-scale mortality will occur regardless[19]. However, there is limited empirical evidence regarding the direction and magnitude of the interactions between drought and tree diversity as research has largely focused on shifts of species distributions and functional composition[12,15,20].

Here we test how drought affects interactions among tropical tree seedlings in monocultures and mixtures of different species. We used rainfall-exclusion shelters to reduce soil water availability while altering tree seedling diversity by manipulating neighbourhood richness around focal individuals (Fig. 1). Ecological theory predicts that competition for limited resources is more intense when species and individuals are more similar and closely related[21,22]. Therefore, neighbourhood diversity consisted of three treatments in which a focal individual was surrounded by 3 individuals of the same, or 3 different, species as follows: 1) a focal seedling surrounded by seedlings of 3 different species than those used as the focal species (mixtures), 2) monocultures of a focal seedling surrounded by 3 seedlings originating from a different mature tree of the same species (non-sibling) and 3) monocultures of a focal seedling surrounded by 3 seedlings originating from the same mature tree as the focal seedling (sibling). The third neighbourhood represents the dense aggregated seedling communities that form under mature trees after mast seed production, a common reproductive strategy in these ever-wet tropical forests[23]. We used the rainfall-exclusion shelters for two intervals lasting 3 and 6 months over a two-year period in order to simulate drought intensity similar to supra-annual droughts in Malaysian Borneo[24] (Fig. 2). We monitored focal seedling growth and mortality and quantified the magnitude of drought response in leaf physiology while assessing nutrient concentrations to test if drought increased competition for water and nutrients.

Results

We found an interaction between the drought and diversity treatments in which the strength of competition was related to seedling neighbourhood diversity under drought but not ever-wet conditions (Fig. 3a). Specifically, in the monocultures (i.e. sibling and non-sibling treatments) relative growth rate (RGR) was significantly lower in the drought than in the ever-wet treatments, but seedlings in mixtures had RGRs that were statistically indistinguishable under drought and ever-wet conditions (Fig. 3b; Supplementary Table 1). These results are consistent with reduced competition for water in species mixtures relative to monocultures. Furthermore, average RGR over all species under drought was higher in mixtures than in monocultures (reduction in RGR due to non-sibling competition = -0.06 cm cm^{-1} yr^{-1}, -0.1 to -0.02 and reduction in RGR due to sibling competition = -0.04 cm cm^{-1} yr^{-1}, -0.07 to 0.003). These results indicate that overall mixtures and monocultures are significantly different under drought (see significant contrast × rainfall term in Supplementary Table 1), but the sibling treatment is only marginally different from the mixture (see neighbor × rainfall term in Supplementary Table 1). Although mortality was not severe (only 3% of the focal seedlings died), 80% of mortality occurred in the drought treatment.

Measurements of seedling physiology support intensified competition for water as the cause of lower growth rates in monocultures during drought. Our experimental drought caused seedlings in all neighbourhoods to close their stomata to levels of 44% conductance (95% CI: 35 – 55) of seedlings in ever-wet conditions (Fig. 4a; Supplementary Table 2). Therefore, seedlings in all neighbourhoods were responding to drier soils — at levels similar to seedlings after approximately 70 – 100 days of no water in a dry-down pot experiment[25] (Supplementary Fig. 1). Despite all neighbourhoods showing reduced (but not completely inhibited) stomatal conductance, leaf water potentials were significantly different among neighbourhoods under drought. Leaf water potentials of focal seedlings were only significantly lower in the drought than the ever-wet treatment in the non-sibling (reduction in leaf water potential due to drought = -0.3 MPa, 95% CI: -0.4 to -0.2) and sibling (reduction in leaf water potential due to drought = -0.2 MPa, 95% CI: -0.3 to -0.1) neighbourhoods (Fig. 4b). Conversely, the leaf water potential of focal seedlings in mixture neighbourhoods was statistically indistinguishable in the drought and ever-wet treatments (reduction in leaf water potential due to drought = -0.03 MPa, 95% CI: -0.1 – 0.1). In addition, under drought, seedlings in monoculture neighbourhoods had significantly lower leaf water potential than seedlings in mixtures (reduction in leaf water potential due to non-siblings = -0.2 MPa, 95% CI: -0.3 to -0.1 and siblings = -0.1 MPa, 95% CI: -0.2 to -0.02). These results indicate that competition for water was more intense between individuals of the same species than among seedlings of different species, which may be due to different rooting strategies or water use efficiencies that produce complementarity in mixtures[26].

Discussion

Two pathways to reduced plant growth under drought have been suggested: carbon limitation due to stomatal closure[27] and sink limitation (i.e. limited water or nutrient availability) that inhibits plant function and decouples growth and photosynthesis[28,29]. Previous research indicates that dipterocarps continue to photosynthesize during drought leading to accumulated nonstructural carbohydrates but eventually hydraulic failure[25,30–32]. Our results support the hypothesis that the mechanism limiting growth during drought — and eventually leading to mortality with increased drought severity — is water limitation that inhibits cell expansion or division and not carbon limitation due to stomatal closure[28–30]. Furthermore, although drought could also affect the availability or uptake of other soil resources, leaf nitrogen and phosphorus concentrations and N:P ratio[33] were statistically indistinguishable among all levels of competition and water availability (Supplementary Fig. 2 and Supplementary Table 3), which indicates competition for nutrients was similar among all neighbourhoods. The incomplete closure of stomata, the reduced leaf water potentials in monocultures and the lack of differences in leaf nutrients suggest that focal seedlings in diverse mixtures had delayed water limitation during drought (and not carbon or nutrients) thereby maintaining higher relative growth rates. In contrast, seedling growth in monocultures became more quickly limited by water during drought.

Surprisingly, under ever-wet conditions, growth of the focal seedlings was statistically indistinguishable among the three levels of diversity (Fig. 3a). Comparison of these growth rates with those of seedlings grown for two years at low density without competition in a nearby experiment[3] showed that RGR was reduced by about 38% (Fig. 3a). Competition — for resources other than water — appears to have had strong negative effects on seedling growth in general, but the effect was independent of diversity under ever-wet conditions, consistent with small differences among species at the seedling stage in an ever-wet climate[34]. More unexpectedly, our results suggest that intermittent drought induces competition for water among conspecifics, which raises the possibility that ENSO events may promote coexistence. Previous work has investigated the role of differences in species tolerance of drought — usually inferred through differences in drought-induced mortality — in determining their spatial distribution in tropical forests[12] and shifts in functional composition in response to drought[20]. However, our results lead us to hypothesize a potential stabilizing role of competition for water during intermittent drought — a type of hydrological realized niche — which may act as another driver of species distributions, in conjunction to and interacting with heterogeneity in light and nutrients[7,35].

Non-sibling and sibling neighbourhoods had similar effects on focal seedling growth. We did not observe competitive differences at the genotypic level (i.e. the contrast of mixtures versus monocultures explained the most variation among neighbourhoods). Instead, responses were mainly at the species level (Supplementary Fig. 3) and between mixtures and monocultures (see the significant species × contrast × rainfall term in Supplementary Table 1). Our diversity treatment was designed to vary genetic similarity of seedlings in a three-level gradient from most similar (siblings) to intermediate (non-siblings) to most dissimilar (mixtures), but the lack of effect between the sibling and non-sibling treatments could be explained by insufficient genetic dissimilarity among seed sources. For example, a high degree of out-crossing and long-distance pollen dispersal among mature trees would reduce variability among seed sources[36].

Our results are based on seedling responses under experimental conditions and require comparison with existing and future data from natural droughts. To impose competition our experiment required relatively high seedling densities, although these were within the range of seedling densities 4 years after a mast fruiting event, e.g. 3 – 75 seedlings m^{-2}. We used mid-day leaf water potential as an indicator of water limitation. The use of pre-dawn leaf water potential or loss of hydraulic conductivity may have provided more direct means of assessing water limitations on growth since mid-day water limitation can be overcome with diurnal refilling (although it might be expected that the recovery of water potential during the day would require greater refilling than in the pre-dawn period). Supra-annual ENSO droughts in our study system normally last for between 1 and 3 months[37]. In our experiment, rainfall-exclusion shelters were maintained for as much as 6 months to induce soil drying during natural tropical rainfall, which caused water movement through the soil and higher cloud cover and humidity than would be the case during an ENSO event. However, this application achieved soil water potentials similar to and slightly greater than an ENSO drought[24].

Seedling dynamics and recruitment into the sapling stage are an important process that influences the future structure and composition of the forest[3,38,39], and drought is likely to play a more prominent role in mediating those dynamics under climate change scenarios. Although these results at the seedling level have implications for future forest canopies, they may not directly relate to interactions among adult trees. In addition, tropical forest diversity is far greater than the number of species used in this experimental manipulation. However, the species were selected to encompass the range of functional traits found in the natural forest (Supplementary Fig. 4), and these species showed highly variable responses to both water availability and neighbourhood diversity that cannot be solely explained by traits[40]. Further research on drought responses of adult trees and more diverse tropical forest communities in general are needed to improve our understanding of the implications of a changing climate for this important ecosystem.

Our results have implications for two related areas of ecology. Our experimental demonstration of reduced competition for water among seedlings in diverse neighbourhoods suggests that intermittent drought may be a process that promotes and maintains diversity in these tropical rain forests as it has been shown to in a prairie grassland[4]. At the same time, our findings of differential responses of species to drought and of complementarity (reduced competition) among species in mixtures are consistent with the idea that diversity can also increase the resistance and stability of ecosystem functioning to extreme climatic events[3]. Interestingly, this suggests that intermittent drought may promote tree diversity in tropical forests, which in turn increases the resilience of the system to these drier conditions.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions: MOB came up with the concept, designed and carried out the experiment, analyzed the data and wrote the manuscript. GR and RO contributed to the logistics and implementation of the experiment in Sabah. AH contributed to the design, analysis and writing.

Author Information

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Figures

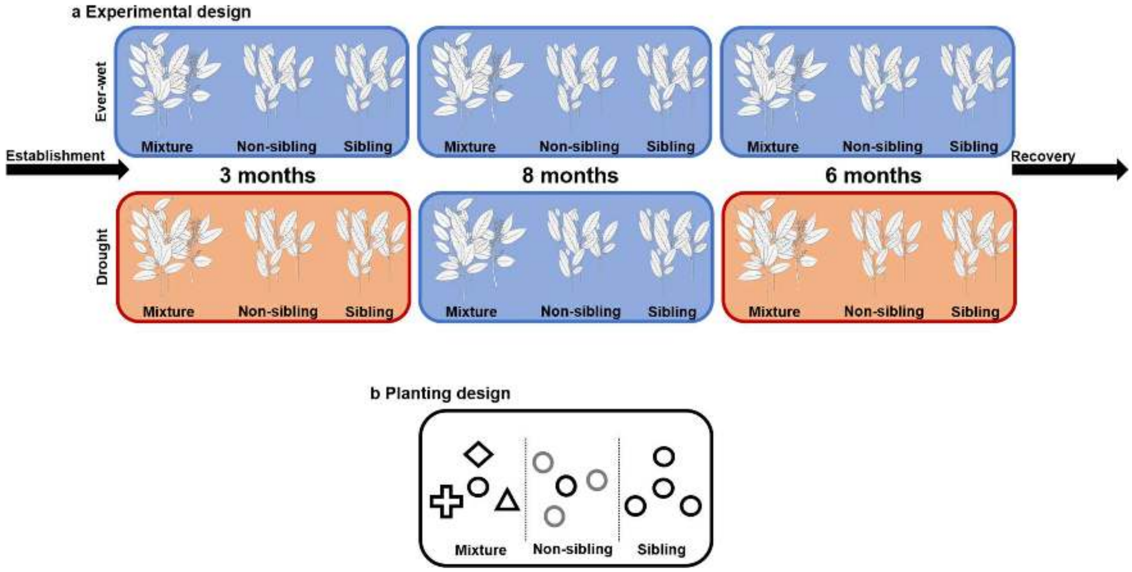

Fig. 1 Experimental and planting design. (a) The experimental design consisted of two sub-plots each with a distinct rainfall treatment: ever-wet (blue) and drought (red). (b) Within each rainfall treatment, there were three neighbourhood treatments: 1) mixtures with three different species than the focal seedling, 2) non-sibling monocultures with individuals from a different mature tree than the focal seedling and 3) sibling monocultures with individuals from the same mature tree as the focal seedling. These three conditions were replicated for each of the focal species (*Dryobalanops lanceolata*, *Hopea sangal*, *Parashorea malaanonan* and *Shorea parvifolia*) under both drought and ever-wet conditions in 20 plots. The mixture neighbourhoods were standardized for all focal species using three additional species (*Hopea nervosa*, *Parashorea tomentella* and *Shorea argentifolia*).

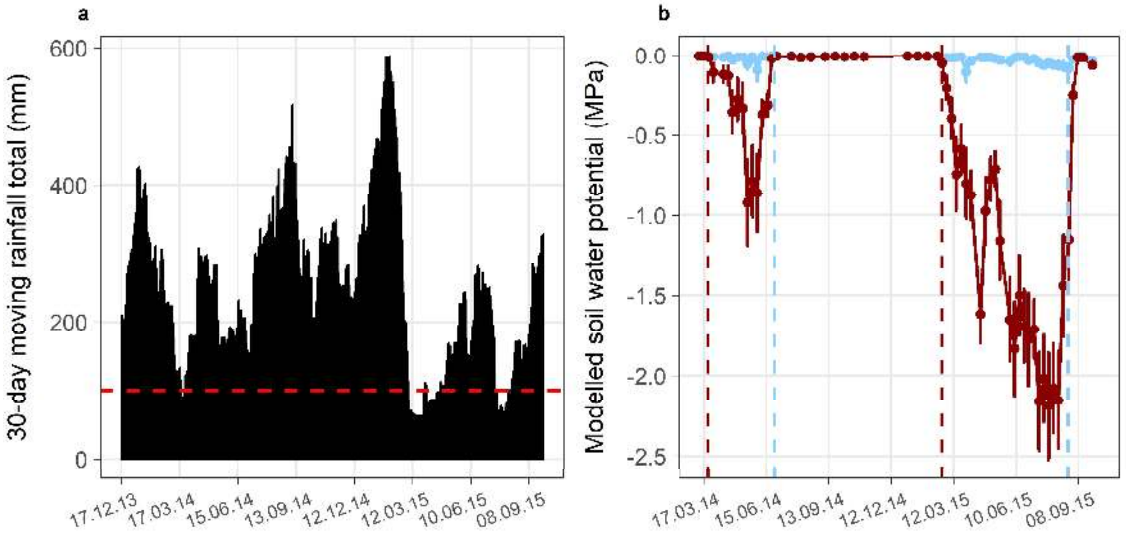

Fig. 2 Rainfall and soil water potential during the 2 years of the experiment. (a) The 30-day cumulative rainfall from the first measurement of height. The red dashed line is the predicted rainfall threshold for drought. (b) Modelled soil water potential (95% CI) during the two years of the experiment for drought (red lines and dots) and ever-wet (blue lines and dots) treatments (n = 20 for each rainfall treatment per sample after averaging 3 – 5 measurements per sub-plot). The vertical dashed lines represent the start (red) and end (blue) of the rainfall-exclusion shelters. The soil moisture was converted from volumetric soil moisture (%) to water potential (MPa) using the filter paper method. The soil water potential reached minimums similar to that measured during the El Niño droughts in 1997 and 1998[24].

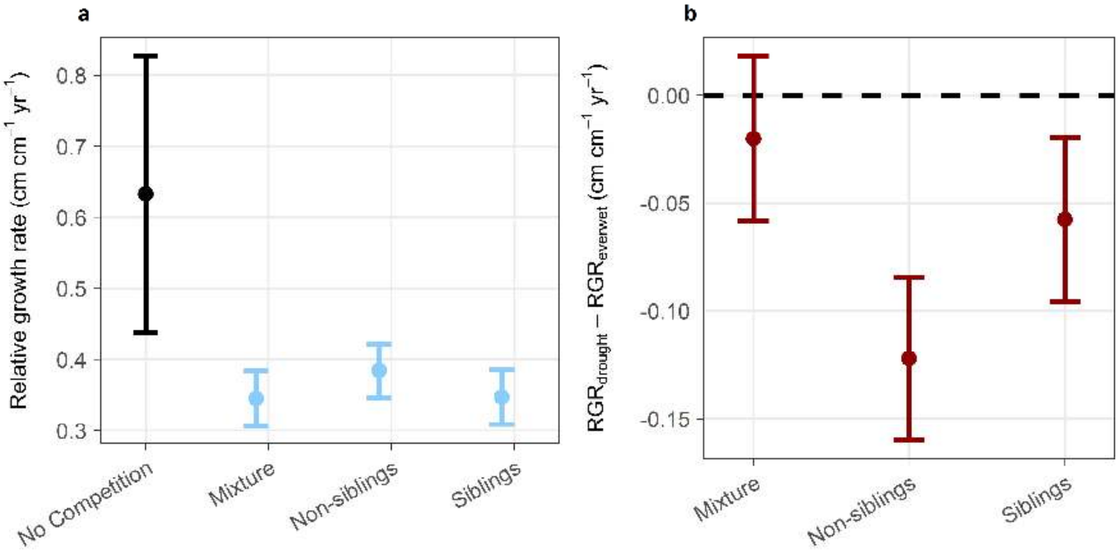

Fig. 3 Relative growth rate for each neighbourhood and water treatment. (a) Relative growth rate (95% CI) for seedlings under ever-wet (blue) conditions for mixture, non-sibling and sibling neighbourhoods (n = 80 for each neighbour × rainfall treatment). The black point is the estimated RGR (95% CI) without competition from a similar experiment in the Malua Forest[3]. It represents the maximum growth rate potential for seedlings of these species. (b) Difference in relative growth rate (95% CI) was statistically indistinguishable between drought and ever-wet seedlings — i.e. 95% CI in the difference crosses zero (black dashed-line) — with mixture neighbourhoods (reduction in RGR due to drought = -0.02 cm $\mathrm{cm^{-1}}$ $\mathrm{yr^{-1}}$, -0.06 – 0.02). However, growth was significantly reduced under drought in non-sibling (reduction in RGR due to drought = -0.12 cm $\mathrm{cm^{-1}}$ $\mathrm{yr^{-1}}$, 95% CI: -0.16 to -0.08) and sibling (reduction in RGR due to drought = -0.06 cm $\mathrm{cm^{-1}}$ $\mathrm{yr^{-1}}$, -0.1 to -0.02) neighbourhoods. RGR was calculated at a standardized average height of 50.75 cm to compare among individuals with initial size differences. A covariate for focal seedling size relative to average neighbour size was used to account for initial height differences among competing individuals.

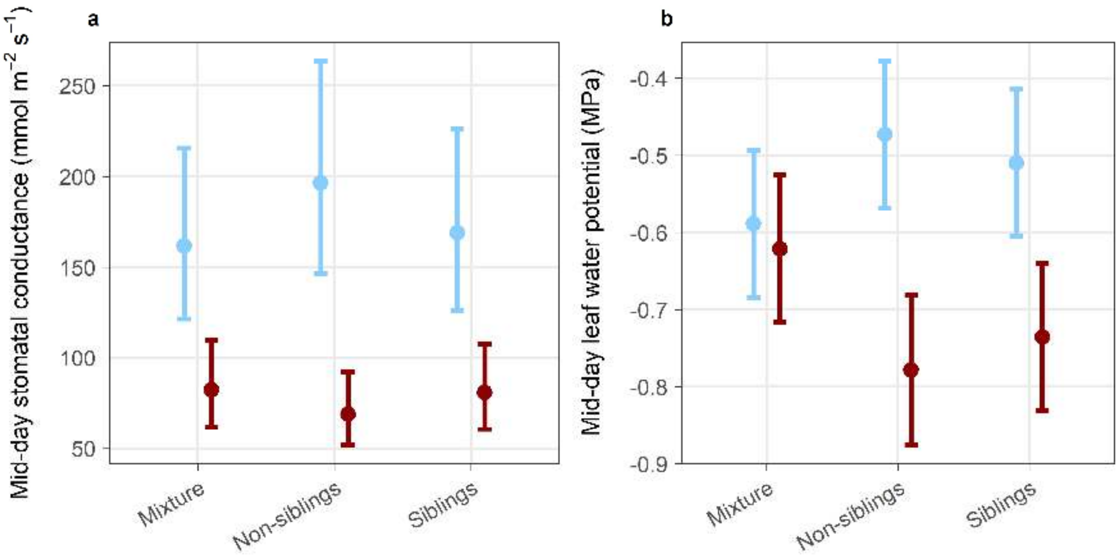

Fig. 4 Seedling water stress under rainfall and neighbourhood treatments. Physiological response of seedlings to drought (red) and ever-wet (blue) conditions with mixture, non-sibling and sibling neighbourhoods. (a) Mid-day stomatal conductance in the drought and everwet treatment (95% CI) was significantly lower in all neighbourhoods (n = 32 for each neighbourhood × rainfall treatment). Stomatal data was log-transformed but is presented on normal-scale after back transformation. (b) Leaf water potentials (95% CI) were significantly lower under drought for non-sibling and sibling neighbourhoods (n = 24 for each neighbourhood × rainfall treatment), but leaf water potential was statistically indistinguishable between drought and ever-wet conditions in mixtures.

Methods

Site description

We established the experiment in Malua Forest nearby to the Malua Field Station (N05º05’20’’ E117º38’32’’; 102 masl). This forest is located ≈22 km north of Danum Valley Field Center in Sabah, Malaysia. Eastern Sabah has historically had an aseasonal climate and for the last 25 years 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. The mean temperature during the experiment was 25.6 °C with an average daily low of 22.6 °C and high of 31.5 °C.

Experimental design

In May 2013, seedlings of four dipterocarp species (*Dryobalanops lanceolata*, *Hopea sangal*, *Parashorea malaanonan* and *Shorea parvifolia*) were planted into 20 plots randomly distributed across a small topographic gradient from 100 to 130 masl. The species were selected to represent a range of different functional traits and growth/allocation strategies (Supplementary Fig. 4 for trait differences among species). Seeds of the four species were collected in August and September 2010, and seedlings were grown in a standard nursery environment with 5% sunlight for the two years prior to being planted into the forest. Seeds were collected from three different mature trees for every species except *H. sangal* which only had two mature trees. Each plot consisted of two sub-plots. Within each sub-plot, we planted three focal seedlings of each species (20 plots x 2 sub-plots x 4 species x 3 seedlings = 480 focal seedlings). For each species within each plot, the focal seedlings originated from the same mature tree, and seedlings from each mature tree were planted as focal seedlings in 8 – 12 plots (depending on seedling quantities). Seedlings that died in the first 5 months were replanted (all plants were alive and healthy at the first measurement in December 2013).

Neighbourhood treatments

Each focal seedling was randomly assigned one of three neighbourhoods: 1) seedlings of different species (mixture), 2) seedlings of the same species but from a different mature tree (non-sibling) and 3) seedlings of the same species and from the same mature tree (sibling). To standardize the interspecific competition for all focal species, three dipterocarp species that were not used as focal seedlings (*Hopea nervosa*, *Parashorea tomentella* and *Shorea argentifolia*) were planted as the neighbourhood. These species were selected because they span a similar spectrum of growth strategies to that of the focal species. The neighbourhoods consisted of three seedlings planted in a triangle pattern at approximately 15 cm from the focal seedling (480 focal seedlings x 3 neighbours = 1440 neighbourhood seedlings). Sub-plots had a total of 48 seedlings in an area of 1.5 × 2 m for an overall density of 16 seedling m^{-2}, but concentrated densities around focal seedlings (based on planting distance) could be estimated at 42 seedling m^{-2}. However, these values fall within the natural densities (mean = 22 seedlings m^{-2} and range = 3 – 75 seedlings m^{-2}) monitored for 4 years after a mast fruiting event in 81 plots at the Malua Forest Reserve.

Rainfall exclusion treatment

From 23 March to 27 June 2014 and 23 February to 24 August 2015, rainfall-exclusion shelters were built over one sub-plot in every plot. The rainfall-exclusion shelters were made of clear polyethylene sheeting draped over the plots (covering an area of approximately 1.8 x 2.3 m) at a height of approximately 3 meters. The rainfall-exclusion shelters were designed to remove 100% of rainfall within the sub-plot. Small aluminum barriers (10 cm high and buried 5 cm in the soil) were placed upslope from every drought sub-plot to prevent overland flow into the rainfall exclusion shelter during heavy rain events. Sub-plots without rainfall-exclusion shelters were watered by hand if a period of 3 days of no rain occurred naturally. This watering was also done for both sub-plots when rainfall-exclusion shelters were absent in an effort to limit the drought treatment to only the periods when rainfall-exclusion shelters were present. Because the shelters prevented leaves and woody debris from falling into the sub-plot, we added surrounding litter on a weekly basis in order to maintain litter levels approximately equal to that of the sub-plot without an exclusion shelter (i.e. a constant layer of litter with no bare soil).

Environmental conditions

Volumetric soil moisture content was measured weekly at a depth of approximately 10 – 15 cm (equivalent to approximately half of the rooting depth of the seedling based on a root growth experiment) during the drought at three to five locations in each sub-plot with an ML3 Theta Probe and HH2 moisture meter (Delta-T Devices, Burwell, Cambridge, UK). The frequency of these measurements was decreased to biweekly when the rainfall-exclusion shelters were removed and monthly during the rainiest period from November to February. The relationship between soil water potential and volumetric soil moisture content was determined using the filter paper method[1,2]. A single batch of Whatman no. 42 filter papers were used in measuring the gravimetric water content in the filter paper that allowed calculation of soil matric potential using the equations from Deka et al. 1995[1]. Soils were dried to levels between 2 and 50% volumetric soil moisture, which were used to calculate a drying curve relating volumetric soil moisture and soil matric potential. Two equations were defined (above and below 25% volumetric soil moisture) because soil matric potential declined at a faster rate below this threshold.

Photosynthetically active radiation using quantum sensors (Delta-T Devices, Burwell, Cambridge, UK) was measured in each sub-plot for 24 hours and compared to simultaneous measurements of direct sunlight at the Malua Field Station, in order to assess the light differences among plots and between sub-plots within a plot. Light was statistically indistinguishable between sub-plots (difference between sub-plots with and without rainfall-exclusion shelters = 0.9%, 95% CI: -0.8 – 2.5) and ranged from 1% to 10% among plots. Temperature was measured simultaneously with light and was statistically different between sub-plots (difference between sub-plots with and without rainfall-exclusion shelters = 0.2 °C, 95% CI: 0.0 – 0.4), but this difference is likely biologically unimportant in this climate with persistent high temperatures and humidity.

Seedling measurements

Beginning in December 2013 (after mortality from planting shock had subsided), we measured all seedlings for height, diameter at base (1 cm above the soil) and counted all leaves. Seedling deaths were recorded for both the focal and neighbourhood seedlings. These measurements were done approximately every 80 days between December 2013 and October 2015.

In June 2015 during the second drought period, one mature leaf was removed from every focal seedling weighed wet, photographed to calculate leaf area and then dried at 64 °C for one week and weighed again. Specific leaf area was calculated from each leaf measurement for each focal seedling. Leaves were selected based on 3 criteria: 1) young but fully developed, 2) in direct sunlight and 3) without herbivory. However, in plots where these criteria could not be met, leaves in similar conditions across the rainfall and neighbourhood treatments were selected to allow comparisons. Furthermore, a subset of 192 focal seedlings from 8 plots were measured for mid-day (between the hours of 11:00 and 13:00) stomatal conductance using a porometer (model SC-1, Decagon Devices, Inc., Pullman, WA, USA) and 120 of those seedlings were also measured for mid-day leaf water potential using a Scholander pressure chamber (model 670, PMS Instrument Co., Corvallis, Oregon, USA). Analysis of the nitrogen and phosphorus content in leaves was done for each species in each neighbourhood and each rainfall treatment to test the effect of neighbourhood and drought on nutrient uptake. For this analysis plots were pooled (based on similar light conditions) into 5 groups in order to have enough leaf biomass per sample (4 species x 3 neighbourhoods x 3 rainfall treatments x 5 groups = 120 nutrient analysis samples).

Statistical analysis

To estimate relative growth rate for each seedling, height was log transformed and analyzed as a function of time (a continuous variable in years; days since the first measurement divided by 365.25) in a mixed-effects model with random intercepts and slopes for individuals (a random factor with 480 levels). These relative growth rate values were then analyzed as a function of species (a fixed factor with four levels; *Dryobalanops lanceolata*, *Hopea sangal*, *Parashorea malaanonan* and *Shorea parvifolia*), neighbourhood treatment (a fixed factor with three levels; siblings, non-sibling and mixture), rainfall treatment (a fixed factor with two levels; ever-wet and drought), all two-way interactions and a neighbourhood × rainfall × species interaction. Covariates for initial seedling height (a continuous variable in cm) to account for initial height differences among focal seedlings and relative size (a continuous variable; seedling height relative to average neighbour height) to account for initial differences between focal seedlings and their neighbourhood were used to control for differential size effects. We also used an *a priori* contrast to test whether mixture and monoculture neighbourhoods accounted for most of the variation in neighbourhood treatments at every interaction level. Random effects were used for plot (a random term with 20 levels), sub-plot nested in plot (a random term with 40 levels), species nested in sub-plot nested in plot (a random term with 160 levels) and neighbourhood treatment nested in sub-plot nested in plot (a random term with 120 levels). See Supplementary Table 1 for the ANOVA table and variance components. We also performed this analysis separately for each year of the drought to validate that the results were consistent across years and not solely a cumulative effect (Supplementary Fig. 5 for this validation).

Mid-day leaf water potential and stomatal conductance were analyzed as a function of species (a fixed factor with four levels; *Dryobalanops lanceolata*, *Hopea sangal*, *Parashorea malaanonan* and *Shorea parvifolia*), neighbourhood treatment (a fixed factor with three levels; siblings, non-sibling and mixture), rainfall treatment (a fixed factor with two levels; ever-wet and drought) and the interaction between neighbourhood and rainfall treatments. Random effects were used for plot (a random term with 20 levels), sub-plot nested in plot (a random term with 40 levels), species nested in plot (a random term with 80 levels) and neighbourhood treatment nested in sub-plot nested in plot (a random term with 120 levels). The stomatal conductance data were log-transformed to meet assumptions of linearity.

Leaf N concentration and leaf P concentration were analyzed the same as mid-day leaf water potential but with a modified random error structure because plots were pooled. Random effects were used for group (a random term with 5 levels), sub-plot nested in group (a random term with 10 levels), species nested in group (a random term with 20 levels), neighbourhood nested in group (a random term with 15 levels), neighbourhood treatment nested in sub-plot nested in plot (a random term with 30 levels). All analyses were performed with the asreml-R package (ASReml 3, VSN International, UK) in the R statistical software (version 3.3.2; http://r-project.org).

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request and will be publicly available on www.searrp.org.

Code availability

All R script will be made available in the Supplementary Information.

Method references

1. Deka, R. et al. Use and accuracy of the filter-paper technique for measurement of soil matric potential. *Eur. J. Soil Sci*. **46**, 233–238 (1995).
2. O’Brien, M. J., Philipson, C. D., Tay, J. & Hector, A. The influence of variable rainfall frequency on germination and early growth of shade-tolerant dipterocarp seedlings in Borneo. *PLoS One* **8**, e70287 (2013).

Supplementary Information

Supplementary Table 1. RGR ANOVA.
Supplementary Table 2. ANOVA of leaf water potential and stomatal conductance.
Supplementary Table 3. ANOVA of leaf nutrients.

Supplementary Fig. 1. Stomatal changes with drought.
Supplementary Fig. 2. Leaf nutrients.
Supplementary Fig. 3. Species level growth differences.
Supplementary Fig. 4 Functional trait differences among species.
Supplementary Fig. 5 Growth response for each year of the experiment.
Supplementary Fig. 6 Revised Figure 2 presenting plot level differences.

R Code Growth.
R Code Leaf Physiology.
R Code Nutrients.

Resistance of tropical seedlings to drought is mediated by neighbourhood diversity

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Supplementary Table 1. The ANOVA table (above) and variance components (below) from the linear mixed-effects model of seedling relative growth rate.

Source of variation	**d.f.**	**denominator d.f.**	**F**
Initial height	1	329.9	867.9***
Size relative to neighbour	1	390.8	3.21†
Light	1	36.7	11.61**
Species	3	62	8.94***
Mix-mono contrast	1	81.6	0.56
Neighbour treatment	1	76.7	0.04
Rainfall treatment	1	18.2	3.96†
Species x contrast	3	236.1	2.68*
Species x neighbour	3	227.2	0.43
Species x rainfall	3	56.9	0.63
Contrast x rainfall	1	76.3	4.43*
Neighbour x rainfall	1	75.6	2.91†
Species x contrast x rainfall	3	226.1	3.73*
Species x neighbour x rainfall	3	225.9	1.33
Variance components	**Var.**	**SE**	
Plot	0.016	0.007	
Sub-plot:plot	0.005	0.003	
Species:plot	0.008	0.002	
Neighbour:sub-plot:plot	0.000	0.001	
Species:sub-plot:plot	-0.001	0.002	
Residual variance	0.028	0.003	

d.f.: degrees of freedom (note effective df can be fractional); F: conditional F-statistic; Var.: variance component estimate; SE: standard errors of variance component; †P<0.1, *P < 0.05, **P < 0.01, ***P < 0.001

Supplementary Table 2. The ANOVA table from the linear mixed-effects model of (a) leaf water potential and (b) stomatal conductance (presented as in Supplementary Table 1).

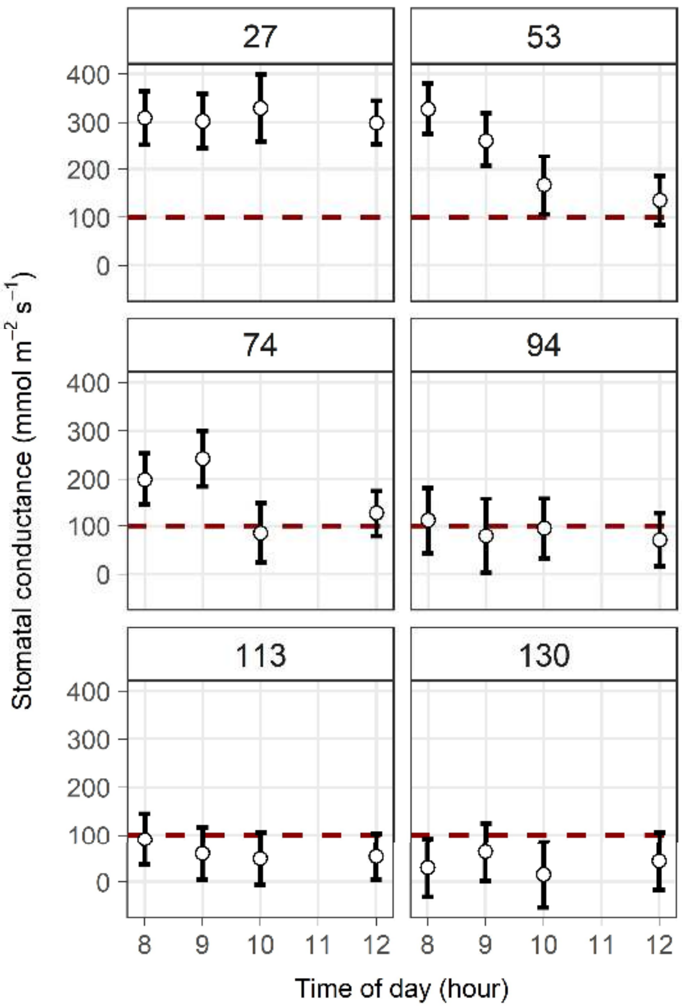
Source of variation	**d.f.**	**denominator d.f.**	**F**
A			
Species	3	14.9	10.8***
Neighbour treatment	2	20.1	0.2
Rainfall treatment	1	5	32.9**
Neighbour x rainfall	2	20.1	8.1**
Variance components	**Var.**	**SE**	
Plot	0.006	0.005	
Sub-plot:plot	0.001	0.002	
Species:plot	0.001	0.004	
Neighbour:sub-plot:plot	-0.008	0.003	
Residual variance	0.061	0.009	
b			
Species	3	21.1	3.1†
Neighbour treatment	2	28.2	0.0
Rainfall treatment	1	7	32.5***
Neighbour x rainfall	2	28.3	1.4
Variance components	**Var.**	**SE**	
Plot	-0.01	0.04	
Sub-plot:plot	0.05	0.04	
Species:plot	0.11	0.05	
Neighbour:sub-plot:plot	0.04	0.03	
Residual variance	0.26	0.03	

d.f.: degrees of freedom (note effective df can be fractional); F: conditional F-statistic; Var.: variance component estimate; SE: standard errors of variance component; $^\dagger P<0.1$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

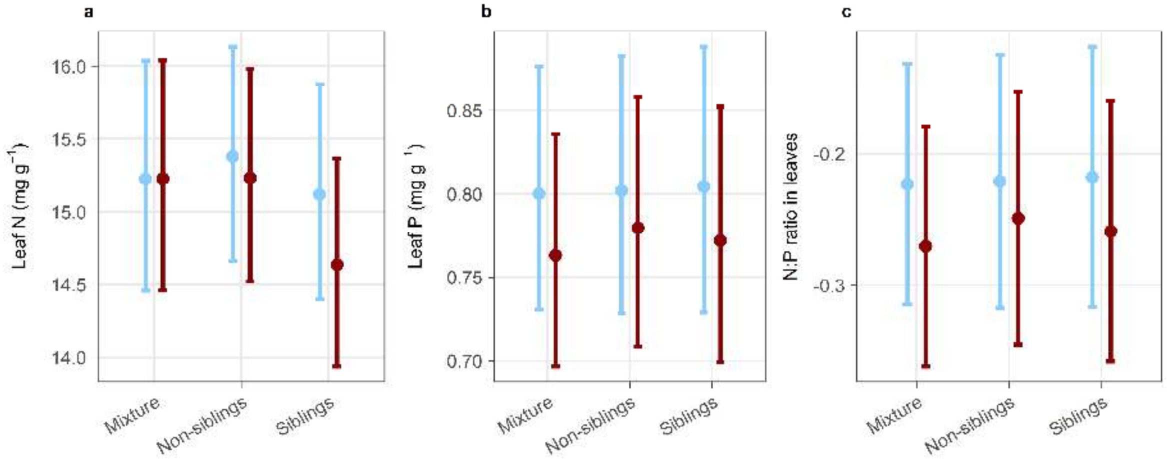
Supplementary Table 3. The ANOVA table from the linear mixed-effects model of (a) leaf nitrogen, (b) phosphorus and (c) nitrogen to phosphorus ratio.

Source of variation	**d.f.**	**denominator d.f.**	**F**
a			
Species	3	12	14.2***
Neighbour treatment	2	5.1	6.7*
Rainfall treamtent	1	4	0.5
Neighbour x rainfall	2	7.6	0.3
Variance components	**Var.**	**SE**	
Group	0.001	0.001	
Sub-plot:group	0.000	0.001	
Neighbour:group	-0.001	0.001	
Species:group	0.002	0.001	
Neighbour:sub-plot:group	0.001	0.001	
Mixture variance	0.007	0.002	
Sibling variance	0.006	0.001	
Non-sibling variance	0.005	0.001	
b			
Species	3	12	10.2**
Neighbour treatment	2	8.3	0.1
Rainfall treamtent	1	3.9	4.3
Neighbour x rainfall	2	8.6	1.0
Variance components	**Var.**	**SE**	
Group	0.007	0.006	
Sub-plot:group	-0.001	0.001	
Neighbour:group	-0.002	0.002	
Species:group	0.003	0.002	
Neighbour:sub-plot:group	0.004	0.003	
Mixture variance	0.009	0.003	
Sibling variance	0.017	0.004	
Non-sibling variance	0.014	0.004	
c			
Species	3	12	57.61***
Neighbour treatment	2	19.4	1.18
Rainfall treamtent	1	19.2	2
Neighbour x rainfall	2	17.8	0.31
Variance components	**Var.**	**SE**	
Group	0.59	0.53	
Sub-plot:group	0.00	NA	
Neighbour:group	0.02	NA	
Species:group	-0.04	0.24	
Neighbour:sub-plot:group	0.09	0.34	
Mixture variance	3.21	0.84	
Sibling variance	3.52	0.94	
Non-sibling variance	3.81	0.95	

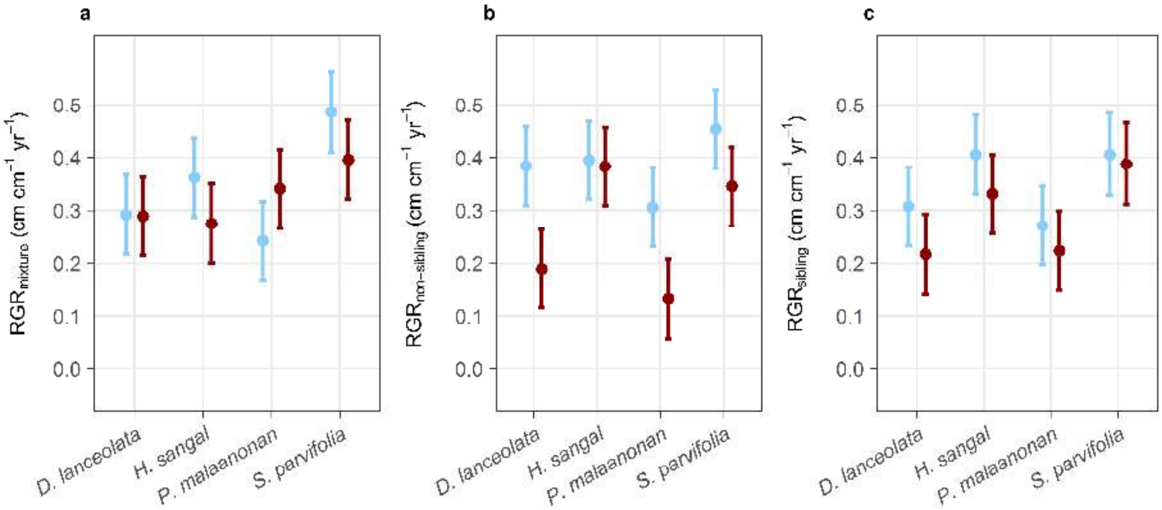
d.f.: degrees of freedom (note effective df can be fractional); F: conditional F-statistic; Var.: variance component estimate; SE: standard errors of variance component; $^{\dagger}P<0.1$, *P < 0.05, **P < 0.01, ***P < 0.001



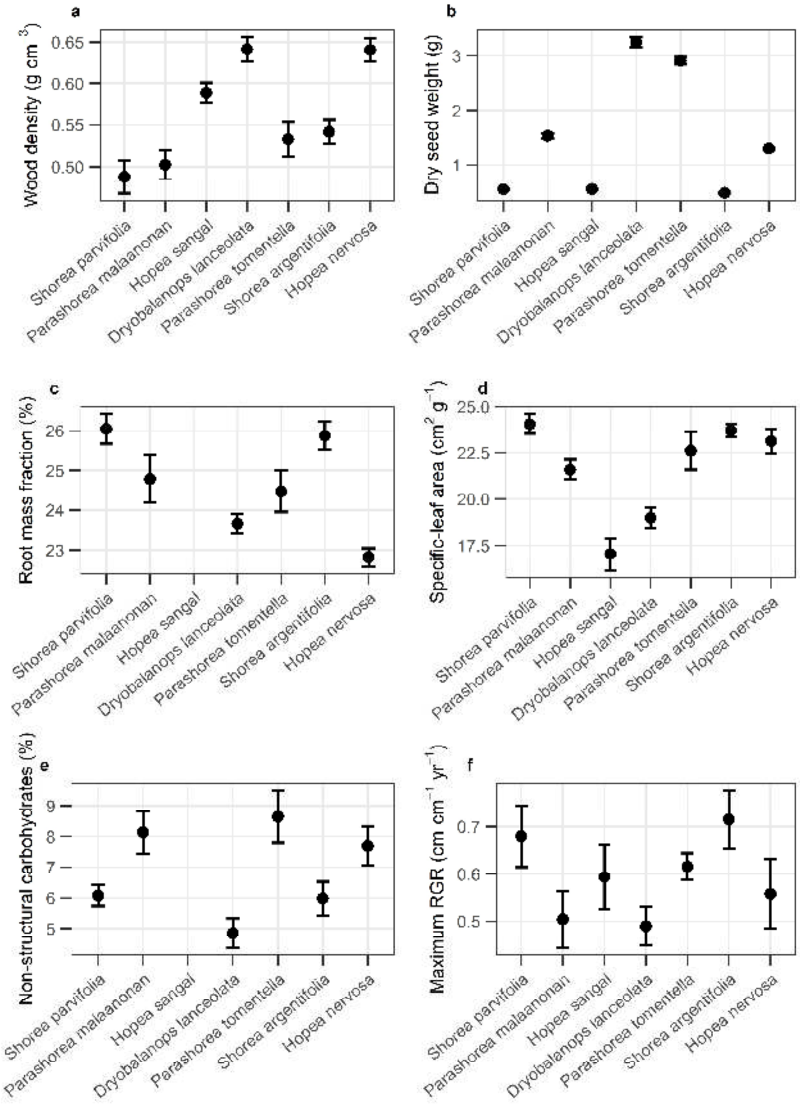
Supplementary Fig. 1 Stomatal conductance from a dry-down pot experiment using these species. Each panel is the stomatal conductance (95% CI) from 7:00 in the morning to 13:00 in the afternoon through the course of the dry-down. The panels are the mean days since the start of no watering, and the red line is at 100 mmol m^{-2} s^{-1}, which is about the threshold the seedlings under rainfall exclusion shelters reached in our experiment. By approximately 90 days, little fluctuation in stomatal conductance occurred during the course of the day. These species only fully close their stomata in severely dry soils and even at that point stomatal leakage continues to occur.



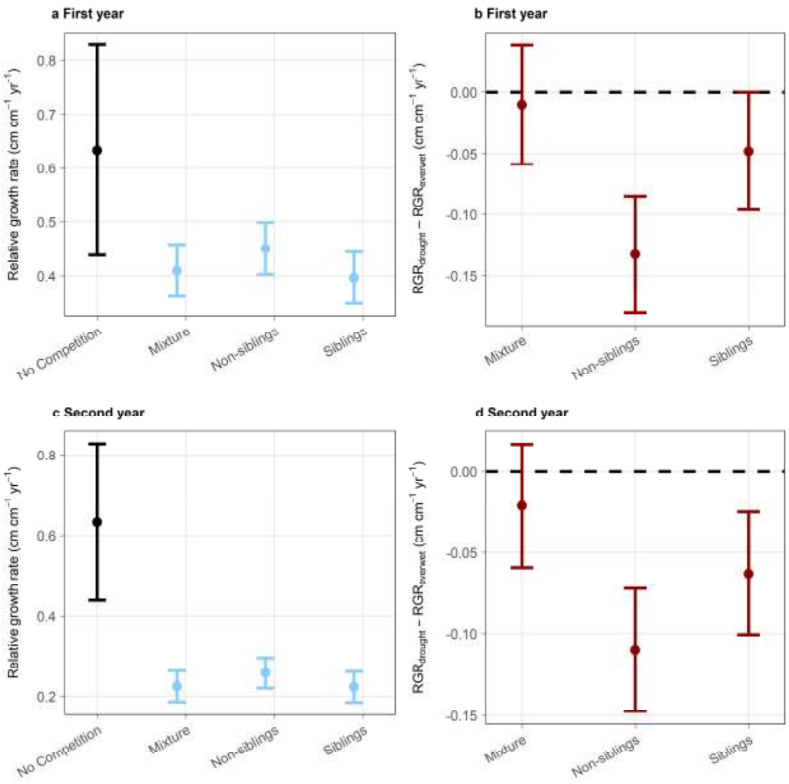
Supplementary Fig. 2 Leaf nutrient concentrations. (a) Leaf nitrogen concentration (95% CI) was similar in all treatments. (b) Leaf phosphorus concentration (95% CI) was significantly indistinguishable among all treatment combinations. (c) N:P ratio in the leaves (95% CI) was significantly indistinguishable among all treatment combinations



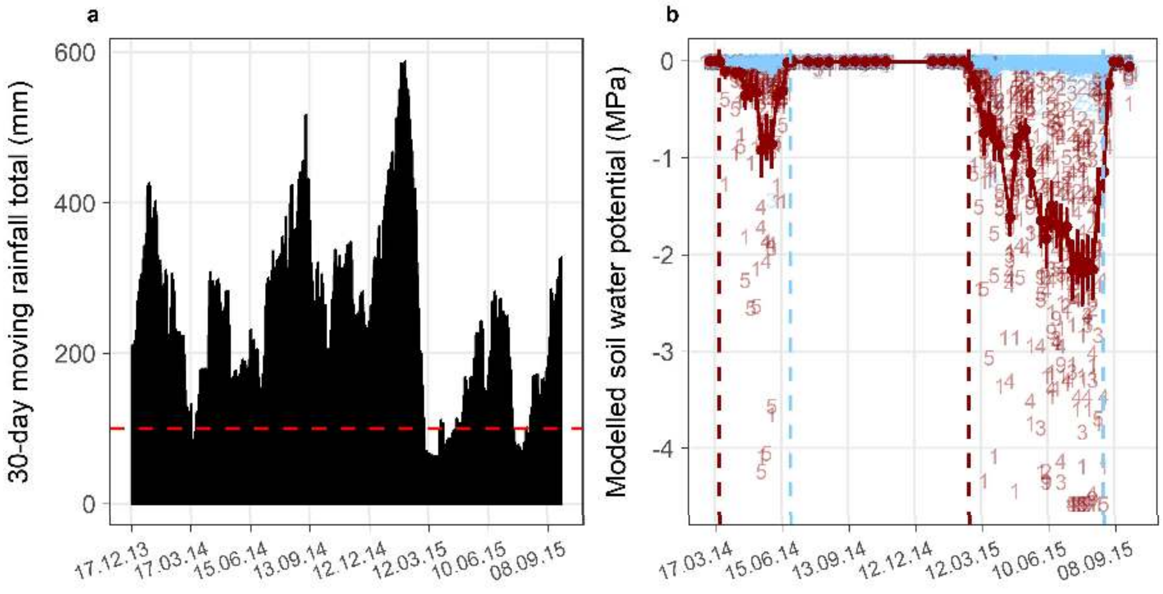
Supplementary Fig. 3 Relative growth rate (RGR) of each species. (a) Three of the four species had lower a relative growth rate (95% CI) under drought than everwet in the mixture treatment. In (b) non-sibling and (c) sibling neighbourhoods all species had lower RGR in drought relative to everwet treatments. However, the magnitude of the effect depended on the species and neighbourhood (see significant species × contrast × rainfall interaction in Supplementary Table 1).



Supplementary Fig. 4 Functional trait differences among species. The mean (s.e.) for six functional traits of seven species used in the experiment. The first four species (from left to right) were focal species (*Shorea parvifolia*, *Parashorea malaanonan, Hopea sangal* and *Dryobalanops lanceolata*) and the last three were used as neighbors in the mixture neighbourhoods (*Parashorea tomentella*, *Shorea argentifolia* and *Hopea nervosa*). The data compiled for these trait estimates were collected from seedlings of previous experiments at the Malua Field Station [1–6].



Supplementary Fig. 5 Separate growth response for each year of the experiment. (a and c) Relative growth rate (95% CI) for seedlings under ever-wet (blue) conditions for mixture, non-sibling and sibling neighbourhoods. The black point is the estimated RGR (95% CI) without competition from a similar experiment in the Malua Forest[3]. It represents the maximum growth rate potential for seedlings of these species. (b and d) Difference in relative growth rate (95% CI) was statistically indistinguishable between drought and ever-wet seedlings with mixture neighbourhoods. However, growth was significantly reduced under drought in non-sibling and sibling neighbourhoods. The effect of drought and competition was stronger in the second year.



Supplementary Fig. 6 Rainfall and soil water potential during the 2 years of the experiment. (a) The 30-day cumulative rainfall from the first measurement of height. The red dashed line is the predicted rainfall threshold for drought. (b) Modelled soil water potential (95% CI) during the two years of the experiment for drought (red lines and dots) and ever-wet (blue lines and dots) treatments. The vertical dashed lines represent the start (red) and end (blue) of the rainfall-exclusion shelters. The soil moisture was converted from volumetric soil moisture (%) to water potential (MPa) using the filter paper method. The numbers represent the measured percentage of direct sunlight in that subplot (i.e. a 1 equals 1% light or 9 equals 9% light).

References

1. O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J. & Hector, A. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nat. Clim. Chang.* **4,** 710–714 (2014).

2. O'Brien, M. J., Burslem, D. F. R. P., Caduff, A., Tay, J. & Hector, A. Contrasting nonstructural carbohydrate dynamics of tropical tree seedlings under water deficit and variability. *New Phytol.* **205,** 1083–1094 (2015).

3. O'Brien, M. J., Ong, R. & Reynolds, G. Intra-annual plasticity of growth mediates drought resilience over multiple years in tropical seedling communities. *Glob. Chang. Biol.* **doi,** 10.1111/gcb.13658 (2017).

4. O'Brien, M. J., Philipson, C. D., Tay, J. & Hector, A. The influence of variable rainfall frequency on germination and early growth of shade-tolerant dipterocarp seedlings in Borneo. *PLoS One* **8,** e70287 (2013).

5. Philipson, C. D. *et al.* Light-based regeneration niches: Evidence from 21 dipterocarp species using size-specific RGRs. *Biotropica* **44,** 627–636 (2012).

6. Saner, P. *et al.* Growth rates and relative change in non-structural carbohydrates of dipterocarp seedlings in response to light acclimation. *Plant Ecol. Divers.* **9,** 491–504 (2016).

R Code Growth

```
rm(list=ls(all=TRUE))
require(lattice)
require(nlme)
require(ggplot2)
require(asreml)
require(pascal)
require(grid)

SEM <- function(x) sqrt(var(x,na.rm=TRUE)/length(na.omit(x)))
cv <- function(x) ( 100*sd(x,na.rm=TRUE)/mean(x,na.rm=TRUE))

dat <- read.table("GrowthDataCompiled.txt", header=T)

dat <- dat[order(dat$plot,dat$treat,dat$jiran,dat$spp,dat$samp),]
lm1 <- asreml.nvc(tinggi~
day,
random=~pid:day,
na.method.X="omit",
na.method.Y="omit",
control=asreml.control(maxiter=30),
family=asreml.gaussian(link="identity",dispersion=NA),data=dat)
lm1 <- update(lm1)
test.asreml(lm1)
slopes <- summary(lm1,all=T)$coef.ran[1:480,1]+summary(lm1,all=T)$coef.fix[1,1]

dax <- subset(dat, day < 0.01)
dax <- dax[order(dax$pid),]
dax <- subset(dax, select=c(plot,treat,jiran,mama,spp,spp.no,initial,jir,size,relate))
dax$rgr <- slopes

dax$id <- with(dax, paste(spp,treat,sep=":"))
dax$mid <- with(dax, as.factor(paste(spp,mama,sep=":")))
dax$size <- dax$initial/dax$jir

dx <- read.table("Light.txt", header=T)
dx$id <- with(dx, paste(plot,treat,sep=":"))
dx <- with(dx, aggregate(light, list(id),mean,na.rm=T))
colnames(dx) <- c("id","light")
dax$id <- with(dax, paste(plot,treat,sep=":"))
dax <- merge(dax,dx,by.x="id",by.y="id",all.x=T)

dax <- dax[order(dax$jiran),]
dax$jiran <- relevel(dax$jiran, ref="C")
dax$treat <- relevel(dax$treat, ref="A")

dax$plot <- as.factor(dax$plot)
dax$mama <- as.factor(dax$mama)
dax$spp.no <- as.factor(dax$spp.no)
dax$id <- as.factor(dax$id)

lm1 <- asreml.nvc(rgr~initial+
size+
light+
spp+
relate+
jiran+
treat+
spp:relate+
spp:jiran+
spp:treat+
relate:treat+
jiran:treat+
spp:relate:treat+
```

```
spp:jiran:treat,
random=~plot+
        plot:treat+
        plot:spp+
        plot:treat:spp+
        plot:treat:jiran,
na.method.X="omit",
na.method.Y="omit",
control=asreml.control(maxiter=30),
keep.order=T,
family=asreml.gaussian(link="identity",dispersion=NA),data=dax)
lm1 <- update(lm1)
test.asreml(lm1)
summary(lm1,all=T)$coef.fix

nd1 <- predict(lm1,classify = "jiran:treat:initial:relate",
average=c("spp","size","light","plot"),levels=list(initial=50.75))$predictions$pvals

nd1 <- subset(nd1, is.na(predicted.value)==F)

nd <- data.frame(jiran=nd1$jiran,treat=nd1$treat)
nd$rgr <- with(nd1, predicted.value)
nd$Up <- with(nd1, predicted.value + 1.96*standard.error)
nd$Low <- with(nd1, predicted.value - 1.96*standard.error)

nd <- nd[order(nd$jiran),]

dt <- dax[,-1]
dt$pnt <- 0.9
dt[which(dt$jiran == "C" & dt$treat=="B"),14] <- 1.1
dt[which(dt$jiran == "S" & dt$treat=="B"),14] <- 2.1
dt[which(dt$jiran == "M" & dt$treat=="B"),14] <- 3.1
dt[which(dt$jiran == "S" & dt$treat=="A"),14] <- 1.9
dt[which(dt$jiran == "M" & dt$treat=="A"),14] <- 2.9
dt$jiran <- as.factor(dt$jiran)

dt$treat <- as.character(dt$treat)
dt[which(dt$treat == "A"),2] <- "Everwet"
dt[which(dt$treat == "B"),2] <- "Drought"
dt$treat <- as.factor(dt$treat)

nd$treat <- as.character(nd$treat)
nd[which(nd$treat == "A"),2] <- "Everwet"
nd[which(nd$treat == "B"),2] <- "Drought"
nd$treat <- as.factor(nd$treat)

dt$jiran <- as.character(dt$jiran)
dt[which(dt$jiran == "M"),3] <- "Siblings"
dt[which(dt$jiran == "S"),3] <- "Intraspecific"
dt[which(dt$jiran == "C"),3] <- "Interspecific"
dt$jiran <- as.factor(dt$jiran)

nd$jiran <- as.character(nd$jiran)
nd[which(nd$jiran == "M"),1] <- "Siblings"
nd[which(nd$jiran == "S"),1] <- "Intraspecific"
nd[which(nd$jiran == "C"),1] <- "Interspecific"
nd$jiran <- as.factor(nd$jiran)
nd$pnt <- c(0.9,1.1,2.9,3.1,1.9,2.1)

###No competition RGR
nd7 <- data.frame(jiran=as.factor("Interspecific"),treat=as.factor("Everwet"),rgr=as.numeric(0.6332351),
Up=as.numeric(0.6332351 + 2*0.09744224),Low=as.numeric(0.6332351 - 2*0.09744224),pnt=as.numeric(0))
nd7[1,1] <- "Interspecific"
nd7[1,2] <- "Everwet"

1-(mean(nd$rgr[1],nd$rgr[3],nd$rgr[5])/nd7$rgr)
1-(mean(nd$rgr[2],nd$rgr[4],nd$rgr[6])/nd7$rgr)
```

```
1-(nd$rgr[1]/nd7$rgr)
1-(nd$rgr[2]/nd7$rgr)

1-(nd$rgr[5]/nd7$rgr)
1-(nd$rgr[6]/nd7$rgr)

dp <- read.table("MaxRGR.txt",header=T)
dp$pnt <- 0

pd <- position_dodge(width=0.8)
plots <- list()
plots[[length(plots)+1]] <- ggplot(data = nd[nd$treat=="Everwet",],aes(pnt,rgr,group=treat))+
geom_errorbar(data=nd[nd$treat=="Everwet",], aes(pnt,rgr,ymax=Up,ymin=Low,colour=treat),size=1,width=0.2)+
geom_errorbar(data=nd7, aes(pnt,rgr,ymax=Up,ymin=Low),colour="black",size=1,width=0.2)+
geom_point(data=nd[nd$treat=="Everwet",],aes(pnt,rgr,colour=treat,fill=treat),shape=21,size=2.5)+
geom_point(data=nd7,aes(pnt,rgr),colour="black",fill="black",shape=21,size=2.5)+
ggtitle("a")+
xlab(expression(paste("")))+
ylab(expression(paste("Relative growth rate (cm ",cm^-1," ",yr^-1,")")))+
scale_x_continuous(breaks=c(0,1,2,3),limits=c(-0.2,3.2),labels=c("0"="No Competition","1"="Mixture","2"="Non-
siblings","3"="Siblings"))+
#scale_y_continuous(breaks=c(-0.25,0,0.25,0.5,0.75,1),limits=c(-0.26,1.01))+
scale_colour_manual(values=c("Everwet"="skyblue1","Drought"="darkred"),guide="none")+
scale_fill_manual(values=c("Everwet"="skyblue1","Drought"="darkred"),guide="none")+
theme_set(theme_bw())+theme(panel.grid.minor=element_blank(),legend.position="none")+
theme(strip.background=element_rect(theme_bw()),
axis.text.x = element_text(margin=margin(0.1,0.1,0.1,0.1,"cm"),angle=30,size=9,vjust=1,hjust=1),
axis.text.y = element_text(margin=margin(0.1,0.1,0.1,0.1,"cm"),size=9),
axis.title.y = element_text(size=9,hjust=0.5),
axis.title.x = element_text(size=9,hjust=0.5),
strip.text.x=element_text(size=11),
strip.text.y=element_text(size=11,angle=-90),
plot.margin = unit(c(0.5,0.5,0.1,0.1), "lines"),
axis.ticks=element_line(size=0.2),
plot.title=element_text(size=9,hjust=-0.05,face="bold"))
#dev.off()

nd1 <- data.frame(diff = c(nd$rgr[2]-nd$rgr[1],nd$rgr[4]-nd$rgr[3],nd$rgr[6]-nd$rgr[5]),
Low = c(nd$rgr[2]-nd$Up[1],nd$rgr[4]-nd$Up[3],nd$rgr[6]-nd$Up[5]),
Up = c(nd$rgr[2]-nd$Low[1],nd$rgr[4]-nd$Low[3],nd$rgr[6]-nd$Low[5]),pnt = c(1,3,2))

nd2 <- data.frame(diff = c(nd$rgr[4]-nd$rgr[2],nd$rgr[6]-nd$rgr[2]),Low = c(nd$rgr[4]-nd$Up[2],nd$rgr[6]-nd$Up[2]),
Up = c(nd$rgr[4]-nd$Low[2],nd$rgr[6]-nd$Low[2]))

plots[[length(plots)+1]] <- ggplot(data= nd1,aes(pnt,diff))+
geom_point(data=nd1,aes(pnt,diff),colour="darkred",fill="darkred",shape=21,size=2.5)+
geom_hline(aes(yintercept=0),linetype=2,colour="black",size=1)+
geom_errorbar(data=nd1, aes(pnt,diff,ymax=Up,ymin=Low),colour="darkred",size=1,width=0.2)+
ggtitle("b")+
xlab(expression(paste("")))+
ylab(expression(paste("",RGR[drought]," – ",RGR[everwet]," (cm ",cm^-1," ",yr^-1,")")))+
scale_x_continuous(breaks=c(1,2,3),limits=c(0.8,3.2),labels=c("1"="Mixture","2"="Non-siblings","3"="Siblings"))+
theme_set(theme_bw())+theme(panel.grid.minor=element_blank(),legend.position="none")+
theme(strip.background=element_rect(theme_bw()),
axis.text.x = element_text(margin=margin(0.1,0.1,0.1,0.1,"cm"),size=9,angle=30,vjust = 1,hjust=1),
axis.text.y = element_text(margin=margin(0.1,0.1,0.1,0.1,"cm"),size=9),
axis.title.y = element_text(size=9,hjust=0.5),
axis.title.x = element_text(size=9,hjust=0.5),
strip.text.x=element_text(size=11),
strip.text.y=element_text(size=11,angle=-90),
plot.margin = unit(c(0.5,0.5,0.1,0.1), "lines"),
axis.ticks=element_line(size=0.2),
plot.title=element_text(size=9,hjust=-0.05,face="bold"))

plotCols = 2 # Number of columns of plots
plotRows = 1 # Number of rows needed, calculated from # of cols
```

```
# Allocate 15x5 cm for each plot
#tiff(filename = "RGR_DeltaRGR_Rev.tif",width=16.5, height=8.5, units="cm",res=600,pointsize=12, compression="lzw")
postscript("Figure3.eps", height=3.3, width=6.85,pointsize=12,horizontal = FALSE, onefile = FALSE, paper = "special")

# Set up the page
grid.newpage()
pushViewport(viewport(layout = grid.layout(plotRows, plotCols,widths=unit(c(0.48,0.52),"null"))))
vplayout <- function(x, y)
    viewport(layout.pos.row = x, layout.pos.col = y)

# Make each plot, in the correct location
for (i in 1:length(plots)) {
    curRow = ceiling(i/plotCols)
    curCol = (i-1) %% plotCols + 1
    print(plots[[i]], vp = vplayout(curRow, curCol ))
}

dev.off()
```

R Code Leaf Physiology

```
rm(list=ls(all=TRUE))
require(lattice)
#require(lme4)
require(nlme)
require(ggplot2)
require(asreml)
require(pascal)
require(grid)

SEM <- function(x) sqrt(var(x,na.rm=TRUE)/length(na.omit(x)))
cv <- function(x) ( 100*sd(x,na.rm=TRUE)/mean(x,na.rm=TRUE))

###Leaf traits
das <- read.table("LeafMoisture.txt", header=T)
dax <- read.table("Stomata.txt", header=T)

das$air <- das$air* -1
das$plot <- as.factor(das$plot)
dax$plot <- as.factor(dax$plot)

das <- das[order(das$treat),]
lm2 <- asreml.nvc(air~
spp+
jiran+
treat+
jiran:treat,
random=~plot+
        plot:treat+
        plot:spp+
        plot:treat:jiran,
na.action.X="na.omit",na.action.Y="na.omit",data=das)
lm2 <- update(lm2)
test.asreml(lm2)
summary(lm2, all=T)$coef.fix

nd <- predict(lm2,classify = "jiran:treat")$predictions$pvals
nd <- subset(nd, is.na(predicted.value)==F)

nd2 <- data.frame(jiran=nd$jiran,treat=nd$treat)
nd2$air <- with(nd, predicted.value)
nd2$Up <- with(nd, predicted.value + 1.96*standard.error)
nd2$Low <- with(nd, predicted.value - 1.96*standard.error)
nd2 <- nd2[order(nd$jiran),]

dax$angin <- log(dax$angin)

dat <- dat[order(dat$treat),]
lm3 <- asreml.nvc(angin ~
spp+
jiran+
treat+
jiran:treat,
random=~plot+
        plot:treat+
        plot:spp+
        plot:treat:jiran,
na.action.X="na.omit",na.action.Y="na.omit",data=dax)
lm3 <- update(lm3)
test.asreml(lm3)
summary(lm3, all=T)$coef.fix

nd <- predict(lm3,classify = "jiran:treat")$predictions$pvals
nd <- subset(nd, is.na(predicted.value)==F)
```

```
nd3 <- data.frame(jiran=nd$jiran,treat=nd$treat)
nd3$angin <- with(nd, predicted.value)
nd3$Up <- with(nd, predicted.value + 1.96*standard.error)
nd3$Low <- with(nd, predicted.value - 1.96*standard.error)
nd3 <- nd3[ order(nd$jiran),]

nd3$angin <- exp(nd3$angin)
nd3$Up <- exp(nd3$Up)
nd3$Low <- exp(nd3$Low)
```

R Code Nutrients

```
rm(list=ls(all=TRUE))
require(lattice)
require(nlme)
require(ggplot2)
require(asreml)
require(pascal)
require(grid)

SEM <- function(x) sqrt(var(x,na.rm=TRUE)/length(na.omit(x)))
cv <- function(x) ( 100*sd(x,na.rm=TRUE)/mean(x,na.rm=TRUE))

###Leaf traits
dat <- read.table("Nutrients.txt", header=T)
dat$pid <- with(dat, paste(spp,spp.no))
dat$plot <- as.factor(dat$plot)
dat$np <- dat$n/dat$p
dat$n <- log(dat$n)
dat$p <- log(dat$p)

dat$relate <- 0
dat[which(dat$jiran == "M"),14] <- "Intra"
dat[which(dat$jiran == "S"),14] <- "Intra"
dat[which(dat$jiran == "C"),14] <- "Inter"
dat$relate <- as.factor(dat$relate)

dat$jiran <- relevel(dat$jiran, ref="C")
dat <- dat[order(dat$jiran),]
lm1 <- asreml.nvc(n~spp+jiran+treat+jiran:treat,
random=~plot+
plot:spp+
plot:jiran+
plot:treat+
plot:treat:jiran,
rcov=~at(jiran):units,
keep.order=T,
na.action.X="na.omit",na.action.Y="na.omit",data=dat)
test.asreml(lm1)
summary(lm1, all=T)$coef.fix

lm2 <- asreml.nvc(p~spp+jiran*treat,
random=~plot+
plot:spp+
plot:jiran+
plot:treat+
plot:treat:jiran,
rcov=~at(jiran):units,
na.action.X="na.omit",na.action.Y="na.omit",data=dat)
test.asreml(lm2)
summary(lm2, all=T)$coef.fix

lm3 <- asreml.nvc(np~spp+jiran*treat,
random=~plot+
plot:spp+
plot:jiran+
plot:treat+
plot:treat:jiran,
rcov=~at(jiran):units,
na.action.X="na.omit",na.action.Y="na.omit",data=dat)
lm3 <- update(lm3)
test.asreml(lm3)
summary(lm3, all=T)$coef.fix
```