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Restoration Ecology

A pre-adaptive approach for tropical forest restoration during climate change using naturally occurring genetic variation in response to water limitation

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Running head: Genetic variation in response to drought

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Abstract

Effective reforestation of degraded tropical forests depends on selecting planting material suited to the stressful environments typical at restoration sites that can be exacerbated by increased duration and intensity of dry spells expected with climate change. While reforestation efforts in non-tropical systems are incorporating drought-adapted genotypes into restoration programs to cope with drier conditions such approaches have not been tested or implemented in tropical forests. As the first effort to examine genetic variation in plant response to drought in a tropical wet forest, we established a watering experiment using five replicated maternal lines (i.e. seedlings from different maternal trees) of five Dipterocarp species native to Borneo. Apart from the expected species level variation in growth and herbivory (3-fold variation in both cases), we also found intraspecific variation so that growth in some cases varied 2-fold, and herbivory 3-fold, among genetically different maternal lines. In two species we found that among-maternal line variation in growth rate was negatively correlated with tolerance to water limitation, i.e. the maternal lines that performed the best in the high water treatment lost proportionally more of their growth during water limitation. We argue that selection for tolerance to future drier conditions is not only likely to impact population genetics of entire forests, but likely extends from forest trees to the communities of canopy arthropods associated with these trees. In tropical reforestation efforts where increased drought is predicted from climate change, including plant material resilient to drier conditions may improve restoration effectiveness.

Implications for Practice

- Restoring degraded tropical forests by supplementing existing genetic diversity with a larger proportion of drought tolerant genotypes is a promising strategy to increase functional and community stability and provide insurance towards predicted drier environments.
- A larger proportion of drought tolerant genotypes may be incorporated into reforestation projects simply via bet hedging by collecting seeds from a diversity of maternal lines.
- Experiments such as ours may be a useful first step towards screening genotypes for drought resilience to improve reforestation effectiveness during climate change.

Key words: Climate change, Dipterocarpaceae, Drought tolerance, Genetic variation, Herbivory, Tropical forest restoration, Reforestation

Introduction

The need for reforestation of degraded tropical forests has been well established, now formalized in multi-national, multi-billion dollar agreements such as the Bonn Challenge to bring 350 million hectares of the world's deforested and degraded land into restoration by 2030. In degraded forests, a lack of plant water availability is often encountered due to a combination of soil compaction leading to decreased water infiltration, and low canopy cover resulting in increased solar radiative input to soils and hence, high evaporation (Hanson et al. 2004; Ilstedt et al. 2007). Many tropical forests are also exposed to novel environmental conditions such as increasing frequency and duration of droughts and high temperatures from climate change (Walsh 1996; Sugden 2019). The combination of deforestation and increasing aridity from climate change creates extreme water-stress in plants (Tobin et al. 1999; Walsh & Newbery 1999) that subsequently affects plant-insect interactions (Price 1991; Huberty & Denno 2004; Gutbrodt et al. 2011), composition of associated communities (Huberty &

Denno 2004) and potentially overall biodiversity. Restoring biodiversity to degraded forests using plant material adapted to current conditions and conditions of the future may reduce the possibility of maladaptation to rapidly changing environments. Maintaining local adaptation is likely to have cascading effects to biodiversity and ecosystem function (Falk 2017).

The historically widespread practice of using local seed sources that are likely to be adapted to local abiotic and biotic environments during reforestation has recently been called into question due to concerns that climate change is likely to cause local maladaptation (Havens et al. 2015; Gellie et al. 2016). Although mixed seed sources to increase genetic diversity are sometimes advocated, local seed sources are still dominating restoration efforts globally (Jalonen et al. 2018). Assisted migration, i.e. amending local genetics with trees from more arid environments has been suggested (McLachlan et al. 2007) and implemented in many temperate regions (Aitken & Whitlock 2013), especially where local economies depend on sustained timber production (Savva et al. 2008; Wang et al. 2010). In addition to assisted migration, there is also potential to screen genotypes from within a population to identify those most tolerant to changing conditions such as drought and increased heat. In fact, in tropical systems this may be more appropriate as within population genetic variation is often higher than among population variation (Schierenbeck et al. 1997; Degen & Sebbenn 2014). Using drought adapted genotypes to increase their frequency in a restored population, in essence, a form of genetic high-grading, has potential to pre-adapt populations to ongoing climate change. While many temperate and arid regions of the world are using genetic approaches to increase conservation effectiveness during climate change (Wang et al. 2010), we are unaware of any such efforts in tropical ecosystems.

Due to the rarity of studies in the tropics evaluating intra-specific variation in plant function (Thomas et al. 2014), especially in response to increasing aridity, it is not currently possible to assess the value of approaches such as assisted migration or pre-adaptation in tropical reforestation. However, while direct adaptation to drought may seem unlikely in wet tropical forests with extremely high precipitation, the amount and seasonality of rainfall varies extensively throughout tropical regions, and plant species distribution patterns are correlated with rainfall even in wet tropical forests (Engelbrecht et al. 2005), together suggesting the potential for genetic variation in response to water availability. Furthermore, increased duration and frequency of dry seasons from climate change increases plant stress and affects seedling mortality (Tobin et al. 1999; Gilbert et al. 2001; Engelbrecht et al. 2006), potentially resulting in natural selection for drought tolerance. Thus, it is likely that genetic variation exists, and this variation can be exploited to increase reforestation effectiveness.

Encouraging the value of genetic resources in reforestation has been important for the success of many restoration projects in various regions and ecosystems outside the tropical zone (Grady et al. 2011; Grady et al. 2015; Zucchi et al. 2017). The use of common garden experiments where plant performance of different genetic stock are tested in different environments has proven valuable to generate knowledge about how plant trait-functional relationships in different environments can help determine which genetic material is best suited to current and future climates (Grady et al. 2011; Grady et al. 2013) and how climate interacts with host genetics to influence associated organisms (Axelsson et al. 2015). Despite predictions of high genetic variability within tropical tree species, genetic approaches have not yet been well tested in tropical ecosystems (but see review by Thomas et al. 2014). Recent genetic research indicates that fine scale genetic structure is common in tropical trees (Kettle et al. 2011; de Morais et al. 2015), that traits related to ecosystem function vary among genotypes (at least among dioecious species; Hultine et al. 2016), and that genetic variation in plant traits shapes entire communities of associated epiphytes and canopy invertebrates (Zytynska et al. 2010; Zytynska et al. 2011). Subsequently, tropical tree species should contain large amounts of genetic variation that could be utilized to ensure that initial phases of restoration efforts are as effective as possible. A better understanding of the degree to which tropical tree genetic variation is involved in forming functional traits that are related to drought tolerance can be used to improve restoration effectiveness.

It is generally accepted that tree species with plant traits involved in rapid resource acquisition such as high foliar nitrogen, specific leaf area, and photosynthetic rates, are a feature of more productive environments, and that species with these traits will be relatively intolerant of stresses such as low light, nutrient deficiency, drought, and high temperatures (Wright et al. 2004). Slow growing species, with lower water and nutrient demand, may do better in harsher environments. Plant traits and growth rate are also likely to interact with herbivores. Generally acquisitive traits are associated with high herbivory rates, likely due to high nutrient levels and less investment to defensive compounds (Pringle et al. 2011). However, with stress, and potential resource allocation tradeoffs among growth and defensive chemistry investment (Roff & Fairbairn 2007; Züst & Agrawal 2017), it is possible that herbivores switch to prefer the most stressed trees (Price 1991; Huberty & Denno 2004). Thus, climate change may simultaneously impact traits associated with drought tolerance and resistance to herbivory (van Asch et al. 2007). However, most previous work on these functional trade-offs address variation among species (Kitajima 1994; Baraloto et al. 2005; Wright et al. 2010; Gustafsson et al. 2016) and less is currently known to what extent similar patterns apply to variation within species (but see Eichenberg et al. 2015; and Senior et al. 2019).

We designed a nursery experiment as a first step towards building a screening tool to identify genotypes that are best able to tolerate drought and herbivory, and maintain function in a changing climate, and to examine genetic variation in performance characteristics of tree species used in tropical forest restoration. In Sabah, Malaysian Borneo, we exposed five replicated maternal-lines from five species (*Dryobalanops keithii*, *D. lanceolata*, *Shorea leprosula*, *S. parvifolia*, and *Parashorea smythiesii*) of the *Dipterocarpaceae* family to differing watering regimes and evaluated variation in their performance. We explicitly tested three main hypotheses related to the influence of variation both among species and within species on plant growth and foliar herbivory: 1) variation exists both among species and among maternal lines in growth rate and susceptibility to herbivory, and that the expression depends on water availability i.e. with reduced water we expect reduced growth and higher herbivory; 2) among species and among maternal line variation in growth rate is negatively correlated with the response to reduced water availability, i.e. plants with the highest growth during high water availability are impacted the most by reduced water availability; 3) Among species and among maternal line variation in growth response to reduced water availability influences herbivory so that plants that are tolerant to water limitation experience less herbivory compared to plants that are impacted the most by water limitation.

This study is novel in being the first to evaluate genetic variation in plant responses to varying water levels in wet tropical forests (but for dry tropical forests see; Ramirez-Valiente & Cavender-Bares 2017). Furthermore, we assess genetic variation in herbivory, and thus begin to evaluate the impacts of genes on plant traits that cascade to impact invertebrate communities and ecosystem processes. Our study is part of an ongoing Sow-A-Seed INIKEA reforestation project initiated in 1998 in lowland mixed-dipterocarp forest of Sabah, Malaysia, where our group has contributed to planting over three million trees; results from this study will be useful for informing future management efforts.

Materials and Methods

Experimental Design

We collected plant material from five different mother trees from each of five species (all in the *Dipterocarpaceae* family) that are commonly used in reforestation efforts in mixed dipterocarp forests of Borneo. Plant material of *Dryobalanops keithii* and *D. lanceolata* were collected as wildings (juvenile plants naturally regenerating in the forest) whereas we collected seeds from mother trees of *Shorea leprosula*, *S. parvifolia*, and *Parashorea smythiesii*. Mother trees used for germplasm collection were separated from other collections from conspecific mature trees by at least 100 m to ensure that collected materials were distinct half-sib families (i.e. maternal lines). Mother trees were located within 45 km of each other in the vicinity of the village of Lusaong, Sabah, Malaysia within the INIKEA restoration area, and along the road to Maliau Basin. Wildings were directly planted into polyethylene bags (6 cm diameter by 40 cm height) the same day that they were field collected. Seeds were germinated on seed-beds in the INIKEA nursery immediately following collection at the Luasong Forestry Centre, (4°37.43’N, 117°12.15’E), and after germination they were planted into polyethylene bags as above. Planting soil was a standard nursery mixture of mineral soil and compost at a ratio of 1:1. The compost was produced by mixing saw dust, dry grass and urea into locally collected mineral soil, and kept for about 6 months prior to using for potting. Seedlings were grown in a shade house and watered daily for 6 months before being exposed to a watering experiment. The shade house included mesh screen approximately 2.5 m height as a ceiling and was open to the air around the perimeter, thus allowing for herbivore entrance to the shade house. The climate in Luasong is humid tropical equatorial with high precipitation throughout the year, even though a wetter season usually occurs from October to February (Peel et al. 2007). Measured mean annual precipitation was 2565 mm (SD 338 mm) for the years 2004 to 2016 according to a weather station in Luasong.

To test for variation among maternal lines in response to variation in water availability we set up a rainout shelter experiment in the nursery using plants from the above described maternal lines still in the polyethylene bags. The rainout shelter was constructed from water proof plastic and erected just below the shading cloth approximately 2.5 m above the ground. Underneath the rainout shelter we positioned 20 metal mesh frames used in the nursery to prevent plants from falling over. The 1.5 × 1.5 m frames were positioned one meter apart in 10 rows by 2 columns. We assigned to each frame one plant from each of five maternal lines from each of the five species randomly in a 5 × 5 configuration with plants spaced by 0.3 m. Two adjacent frames were assigned to a block and within each block one frame was randomly assigned to a high water treatment and the other to a low water treatment. The water treatment was designed to reflect variation in water availability and included plants being watered with approximately 0.5 L of water applied twice per day for the high water treatment and 0.5 L of water applied one time per day for the low water treatment. The high twice a day watering treatment is equivalent with operational practice in the nursery designed to facilitate good growth and avoid wilting. The watering experiment was conducted in 2017 for three months, from June to August. We observed no plant mortality during the experiment.

To assess relative growth rate of the plants, we measured height and diameter at root collar (DRC; ~ 3 cm above soil surface) of all seedlings at the start of the experiment and then again after plants had been subjected to the watering treatment for 3 months. From these measurements we then derived relative growth rates (RGR) of each plant using the formula

$$RGR = \frac{lnW_2 - lnW_1}{t_2 - t_1}$$

Where ln is the natural logarithm, t_1 is time one, t_2 is time two, W_1 is the size measurement of height or DRC at time one, W_2 is the size measurement of height or DRC at time two.

To assess foliar herbivory on plants during the experiment, we marked four randomly selected leaves on each of the 500 plants. Leaves were photographed at the start of the watering treatment and then again after plants were subjected to the watering treatment for 3 months. Photographs were processed using Digimizer Image Analysis Software (https:///www.digimizer.com) to calculate the proportion of leaf area removed by herbivores relative to the total leaf area. We calculated the proportion of foliar herbivory on the plants during the experiment by subtracting the proportion of leaf area removed by herbivores at the start of the experiment from the proportion of leaf area removed by herbivores at the end of the experiment. To avoid negative scores (occurring through sampling errors when foliar herbivory was close to zero) we converted foliar herbivory to proportional classes in 5% intervals (<0 = 0, > 0 and up to 5 = 5, > 5 and up to 10 = 10, and so on). Leaf damage was then averaged per plant before analyses. Based on the total number of leaves on each plant and the mean leaf area, the four photographed leaves accounted on average for 28 percent of the total leaf area of each plant.

To estimate the among-maternal line variation in response of RGR and herbivory to watering treatment, we calculated response ratios (Hedges et al. 1999) of the different maternal lines using the formula

$$Response\ ratio = \frac{\mu_{lw}}{\mu_{hw}}$$

Where μ_{lw} is either the RGR or herbivory of plants exposed to the low water treatment and μ_{hw} either the relative growth rates or herbivory of plants exposed to the high water treatment. The response ratio thus describes the response in the low water treatment relative to the response in the high water treatment. For these analyses, we used relative height growth to represent among maternal line variation in growth as it revealed more variation compared to DRC.

Statistical Analyses

To test our first hypothesis (H1) that variation exists in growth and susceptibility to herbivory, and that the expression of these traits depends on water availability we conducted Analyses of Variances (ANOVAs). These analyses were conducted in the R package stats using the aov function and we performed separate analyses at the species- and maternal levels. First, to test for species level variation in growth rate we used a model including species (S), water treatment (WT) and their interaction (S × WT) as predictors separately for both relative height and relative diameter growth. We checked assumptions of normality and homogeneity of variance using histograms and residual plots and log transformed relative height growth as data did not conform to assumptions. When species significantly affected responses either alone or in interaction with water treatment we explored those differences using Tukey HSD tests ($p < 0.05$). To test for species level variation in herbivory we conducted beta regressions using the function betareg in the R package betareg, again with species, water treatment and their interaction as predictors, and used off-zero adjustment constant of 0.0001. When species significantly affected responses either alone or in interaction with water treatment we explored those differences with Tukey HSD tests ($p < 0.05$). Second, to test for variation among maternal lines in growth rate and herbivory we repeated the above analyses on each species separately and included maternal line (M), water treatment (WT) and their interaction (M × WT) as predictors. As we were interested in the general influence of maternal line variation and not the influence of specific maternal lines we interpreted a significant effect of maternal line either alone or in combination with WT as support for genetic variation in trait expression. In all of the above analyses we included block to control for potential environmental influence within the experiment.

To test whether the growth response to watering treatment, (i.e. RGR response ratio defined as the ratio in RGR between low and high water treatments), was associated with fast growth (H2), we used correlation analyses first for species level variation and then for each species separately to test for maternal level variation. These analyses were conducted in the R package devtools using the cor.test function. In these analyses we used Spearmans ρ non-parametric correlation to test for correlations between mean RGR of plants in the high water treatment and RGR response ratio.

To test if plant varieties that were affected the most from the low water treatment, i.e. with the highest RGR response ratio, were also most susceptible to herbivory (H3), we used Spearmans ρ non-parametric correlation analyses first for species level variation and then for each species separately to test for maternal level variation. These analyses were conducted in the R package devtools using the cor.test function. In the analyses on species level variation, we correlated mean species level RGR response ratio with mean species level leaf damage response ratios (the ratio of leaf area consumed per each species in high water versus low water treatments). For the maternal level variation we correlated mean maternal line level RGR response ratio with mean maternal level leaf damage response, for each species separately. All statistical tests were performed in R version 3.5.3 (R Core Team 2018) and evaluated at the alpha = 0.05 significance level.

Results

Species level variation

In our analyses of species level variation we found partial support for our first hypothesis (H1) that growth and herbivory vary among species, and that the expression of these traits depends on water availability. Plant growth differed significantly among species and between treatments both for height ($R^2 = 0.36$, $p < 0.0001$ for both species and water treatments) and diameter growth ($R^2 = 0.24$, $p < 0.0001$ and $p = 0.009$, respectively). The growth response to water treatment was similar among species as indicated by a non-significant interaction between species and water treatment on diameter and height growth ($p = 0.243$ and $p = 0.900$, respectively). Subsequent species comparisons showed that species varied approximately 3 fold in height growth, and that *P. smytheisii* had the fastest height growth followed in decreasing order by *S. leprosula* and *S. parvifolia*, and *D. lanceolata* and *D. keithii* (Fig. 1). The water treatment caused a general decrease in relative height growth of 21% (RGR decreased from 0.029 ± 0.001 to 0.023 ± 0.001 mm/day) and 13% for relative diameter growth (RGR decreased from 0.0023 ± 0.0001 to 0.0020 ± 0.0001 mm/day).

For herbivory, we found that it differed among species (Psuedo $R^2 = 0.16$, $p < 0.0001$) so that leaf damage varied 3-fold among species. The species experiencing the highest leaf damage was *S. parvifolia* and *S. leprosula* followed by *P. smythiesii*, and then *D. lanceolata* and *D. keithii* (Fig. 1). We also found a close to significant effect of water treatment on herbivory ($p = 0.060$) so that plants in the low water treatment experienced higher herbivory than the high water treatment (Fig 1). There was no interaction between species and the watering treatment on herbivory ($p = 0.547$).

In our analyses on species level variation we found no support for our second hypothesis (H2) that the growth response to reduced water availability is negatively correlated to variation in growth rate. The species level mean response to water reduction was not related to the species mean relative growth in high water treatment (Spearmans ρ: rho = 0.3, $p = 0.683$), i.e. fast and slow growing species responded similarly to water reduction and species that grew the fastest with high water treatments continued to have the highest growth during low water (Fig. 1).

In our species level analyses we found no strong support for hypothesis (H3) that herbivory would be highest on species suffering the most from water limitation. Although the correlation between mean species level growth response ratio and mean species was negative, the trend was moderately significant (Spearmans ρ: rho = -0.9, $p = 0.083$). Species that lost more of their growth potential with reduced water were not necessarily more responsive in terms of herbivory (Fig. 1).

Maternal level variation

In our maternal level analyses, we found strong support for our first hypothesis (H1) that growth and herbivory vary among maternal lines, and that the expression of these traits depends on water availability. Four out of five species expressed variation among maternal lines in growth rate and/or herbivory, and in some cases expression depended on water treatment. Height and diameter growth varied significantly among maternal lines in four and three out of the five species, respectively (Table S1). In some species this variation was substantial, e.g. in *P. smythiesii*, *S. leprosula* and *S. parvifolia* the mean relative height growth of fast growing maternal lines was more than double that of slow growing maternal lines ($p < 0.002$, Fig 2). The exception to the general influence of maternal line on relative growth rates was *D. lanceolata* in which the maternal line effect was insignificant for both height and diameter growth ($p = 0.953$ and $p = 0.617$, respectively). Furthermore, in *D. keithii* relative height growth was affected by a significant interaction between maternal line and water treatment ($p = 0.033$; Table S1). In one maternal line of *D. keithii* the low water treatment caused a ~60% reduction in growth whereas other lines maintained their growth potential even with low water (Fig. 2). Herbivory was significantly affected by maternal line in two species, *P. smythiesii and S. parvifolia* (Table S1). In these species herbivore-susceptible maternal lines experienced up to 3 times higher herbivory than unsusceptible lines, e.g. herbivory levels varied between 0.7% and 2.2 % and between 1.1% and 3.1%, respectively. The single effect of water treatment was close to significant for one species *D. lanceolata* (Pseudo $R^2 = 0.30$, $p = 0.056$) and in *S. leprosula* there was a close to significant interaction between maternal line and watering treatment on herbivory (Pseudo $R^2 = 0.19$, $p = 0.077$, Table S1).

We found partial support for our second hypothesis (H2) that the growth response to reduced water availability is negatively correlated to maternal line variation in growth rate. Both *D. keithii* and *D. lanceolata* showed strong negative correlations between relative height growth with high water and the response to water limitation (Spearmans ρ: r = -1.0, $p < 0.017$ and r = -0.9, $p = 0.083$, respectively). Maternal lines with high growth potential during high water had proportionately less growth during water stress. We found no such relationship in *P. smytheisii*, *S. leprosula* and *S. parvifolia* (Fig. 3).

We found very limited support for our third hypothesis (H3) that herbivory would be highest on maternal lines suffering the most from water limitation. Only *S. parvifolia* had a negative and significant correlation among maternal lines between proportional loss of growth with water stress and herbivory (Spearmans ρ: rho = -0.9, $p < 0.083$, Fig. 4). We note that this result should be interpreted cautiously as only a moderately significant trend was identified.

Discussion

We present the first study to demonstrate that trees from wet tropical forests exhibit not only species but also genetic variation in functionally important characteristics such as growth rate and susceptibility to herbivory, and that the expression of these characteristics often depends on water availability. In the cases where we found that performance varies in response to decreasing water, it is likely that increasing aridity from climate change will alter plant functioning differently depending on species and genotypic identity. It follows that plant material selection strategies to maintain function during decreased water availability and during reforestation of degraded landscapes could benefit by considering this species and genetic variation. Genetic variation has been used in non-tropical systems to enhance growth in forestry timber production systems (Savva et al. 2008; Wang et al. 2010) and in the design of assisted migration approaches focusing on conservation (Grady et al. 2011; Grady et al. 2015; Zucchi et al. 2017). Even with genetic material collected from a localized spatial scale and from the same population with all germplasm collected from within a 45 km range, we present examples of genetic variation in growth corresponding to changes in water availability. As such, we believe there is potential for considering genetic variation in response to environmental variation relevant for ongoing restoration efforts confronted by climatic change in tropical forests. Our results suggest that approaches such as assisted migration and supplementing drought-adapted species and genotypes (pre-adapting) into reforestation programs has potential to increase reforestation effectiveness.

Genetic strategies for reforestation in the tropics

Demonstrating that genetic variation exists in plant functioning to drier conditions represents a first step for developing new strategies for reforestation in tropical forests. This has previously not been possible due to the overall lack of studies evaluating intra-specific variation in tropical trees (but see; Ramirez-Valiente & Cavender-Bares 2017), and a strategic use of genetic resources is not currently being widely applied to reforestation efforts in the tropics (Thomas et al. 2014). Our results suggest that it is possible to select genetic resources in tropical forests that are best suited to different environmental conditions by taking advantage of local standing variation. For instance, in designing a reforestation project concerned with climate change, it may be useful to increase the frequency of drought tolerant genotypes on the landscape. This may be achieved simply by collecting propagules from a diverse origin to increase the probability that plant material with desired characteristics is included in restoration (Dunwiddie et al. 2009), or by using an approach such as in this study by screening genotypes for drought resilience. In the case of our study, these trees would still be “local”, but the out-planted population would be enhanced for drought tolerance during the genotype selection process, at least during the seedling stage – a critical time in restoration efforts where fast growth rate is key to avoiding mortality from competition with weeds. Our study does not examine the long-term consistency of genetic variation in drought tolerance from juvenile to mature, to old trees. Using locally derived genetic material that is enhanced in this way, rather than using assisted migration, may be more tenable in tropical forests where more arid provenances for seed collecting may not be available or may be geographically distant. While many temperate and arid regions of the world are considering assisted migration during reforestation, we recommend taking advantage of local or within population variation in drought tolerance during tropical reforestation efforts.

In addition to promoting drought tolerance on landscapes during reforestation efforts, our research also highlights the potential for incorporating genetic variation in timber production of native tropical tree species. In large parts of the tropics, exotic tree species are often preferred over natives in plantation forestry due to their high productivity potential directly as a result of using breeding programs to identify fast-growing genotypes (Piotto et al. 2004). However, using genetic resources to increase the productivity potential of the most promising native tree species could potentially make them competitive options especially during climate change. Even with planting material from a narrow geographical range of 45 km we demonstrate a 2 to 3 times difference in growth rates and up to 3 times difference in susceptibility to herbivory among maternal lines. Although we recognize that growth rates in our short duration study may not correlate to growth rates in larger harvestable trees, our results do provide evidence of genetic variation in growth of native hardwood trees that should be further explored for increasing incentives to substitute native trees for more commonly used exotic trees. By incorporating variation in productivity potential during water limitation it may be possible to better maintain productivity during projected climate change scenarios. Although there are cases when exotics do provide environmental benefits (D'Antonio & Meyerson 2002) the added conservation value of native species is evident. Conservation benefits of native trees is supported both empirically (Tallamy & Shropshire 2009; Narango et al. 2017) and from co-evolutionary theory, i.e. native tree species share an evolutionary history with associated communities and are often foundational to ecosystem processes and native biota (Thompson 2005). When conservation is part of the management goal it would be useful to consider foundational status of species used in restocking. We suggest that incorporating genetic variation into native species plantation forestry or agroforestry can enhance the economic value of such approaches and at the same time provide increased conservational benefits.

Genetically determined functional trade-offs and correlations

A striking result of this study is that trait correlations of importance for basic ecological theories such as trade-offs and plant stress hypothesis were only expressed on the intraspecific level and not among species. Most previous work on functional trade-offs address variation among species (Kitajima 1994; Baraloto et al. 2005; Wright et al. 2010; Gustafsson et al. 2016) but see Eichenberg et al. (2015) for intraspecific trade-offs among defensive traits. However, we found no support for an interspecific level trade off, e.g. species that performed the best during high water continued to do so also during water reduction and the species that suffered the most from water limitation were not necessarily more susceptible to herbivory. In contrast, we found evidence for intraspecific tradeoffs, i.e. in the two Dryobalanops species (*D. keithii* and *D. lanceolata*) we found that high among-family variation in growth potential was negatively correlated to tolerance to water limitation. In other words, the maternal lines that grew fastest in well-watered conditions grew the slowest with reduced water availability (Fig. 3). A negative relation between fast growth in optimal conditions and tolerance to water stress suggests a tradeoff in performance in different environmental conditions. This highlights the potential for an intraspecific level functional trade-off between growth and tolerance to drought.

We found no general influence of maternal line variation of plant stress on herbivory. Although two species, *S. parvifolia* and *P. smythiesii* did show negative correlations so that the maternal lines that lost the most in growth with reduced water, also experienced the highest leaf damage, other species showed opposite positive trends. As such we can neither corroborate nor dispute the plant vigor hypothesis suggesting that herbivores should prefer vigorous plants over stressed plants (Price 1991). Instead we speculate that the influence of plant stress on susceptibility to herbivory may vary among different plant species as a consequence of different life history characteristics and their associated communities of herbivores. For example, the plant vigor hypothesis was formulated from observations with galling insects that arguably perform better on fast growing large plants compared to slow growing small plants (Roininen et al. 1988; Price 1991). Nevertheless, Huberty and Denno (2004) and Galway et al. (2004) both found that the outcome of plant stress-plant vigor experiments depend on insect feeding guild, whereby gallers predominantly prefer vigorous fast-growing plants but leaf chewers tend to prefer stressed plants (Galway et al. 2004). Furthermore, it has been suggested that insect herbivory increases on moderately water-stressed plants because water limitation may influence nutrient composition of plant tissue (Huberty & Denno 2004) and consequently, among species variation in physiological response to stress is likely to influence herbivory in different ways. We recognize that our study was conducted on seedlings and may not apply to older trees; however, we note that the establishment phase of regeneration and reforestation efforts is a critical phase likely to strongly influence the long-term outcomes of species interactions. Understanding the community context of evolutionarily mediated interactions such as those among plants and between plants and other trophic levels is important for predicting the effects of climate change on such interactions and considering adaptive management strategies for mitigating potentially negative effects.

Community-wide consequences

A better knowledge of how genetically controlled plant characteristics impact communities is important for predicting the full consequences of climate change on ecosystems, e.g. both drought and damage from insects are important in a climate change perspective. In one of our species, *D. keithii,* we found large among maternal line variation in growth that was correlated strongly to the relative growth response to water limitation. It seems like maternal lines with inherently slow growth maintained their growth potential better than fast growing genotypes during water limitation (Table S1, Fig. 2). Although resource allocation tradeoffs among growth and investment to defensive chemistry predict that fast growth should be associated with high herbivory (Roff & Fairbairn 2007; Züst & Agrawal 2017) we found no evidence for this in our study. Nevertheless, in cases where such correlations occur we expect that climate change, via natural selection for drought tolerance, to simultaneously influence a range of attributes important for the function of the system. For example drought may select for plants that are slow growing with cascading influences to other plant properties, such as susceptibility to herbivory. Plant resistance and other genetically controlled traits are expected to have pronounced effects on associated communities and ecosystem processes (Whitham et al. 2003). Selection for one function could thus influence others and have important eco-evolutionary consequences (Johnson et al. 2009; Turcotte et al. 2012). In cases when plant functionality is genetically determined, such as shown here, and relate to traits under selection we expect that selection for one function could influence others and have important eco-evolutionary consequences that need to be understood to predict the full consequences of ongoing climate change on ecosystem function.

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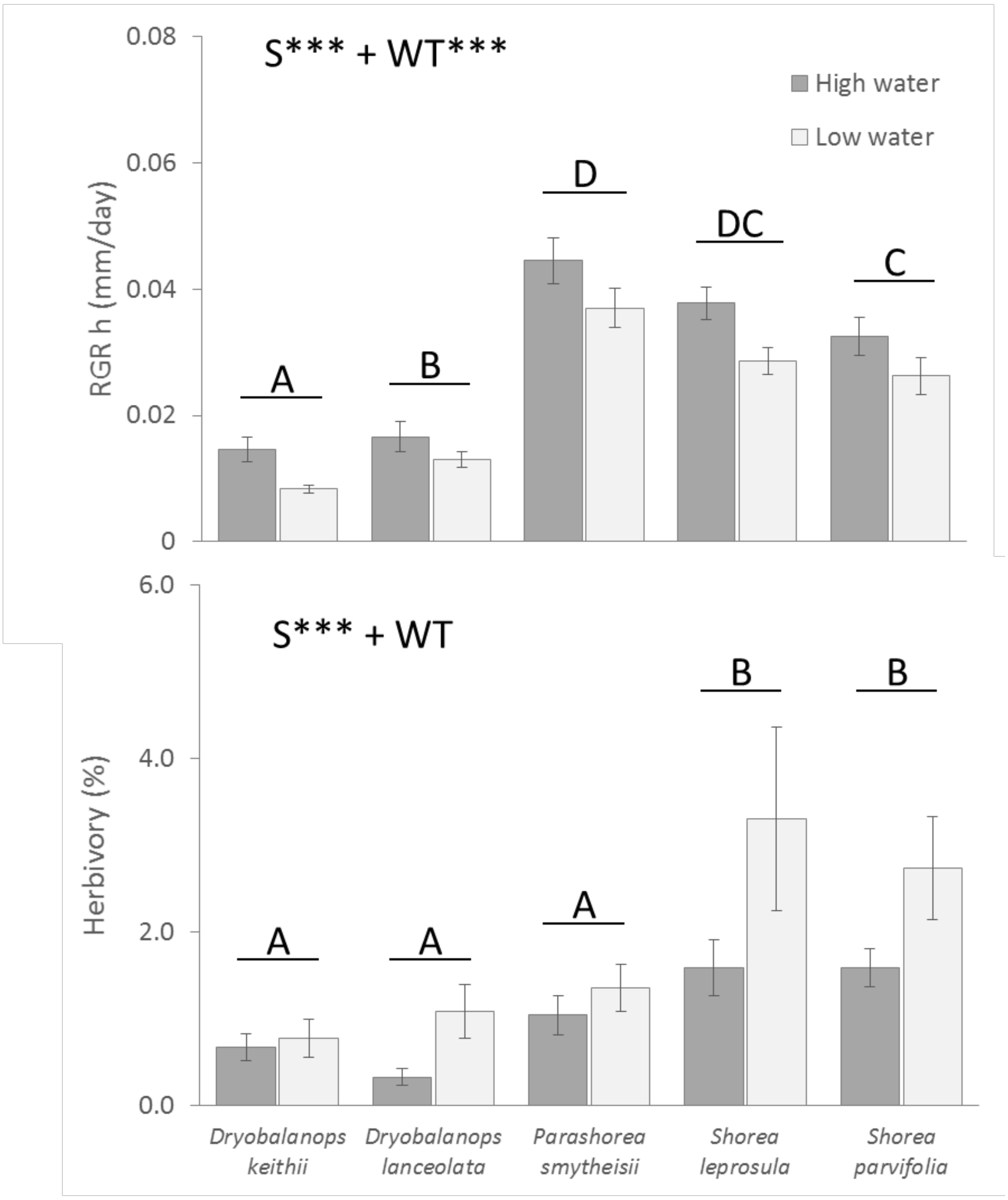

Figure 1. Mean relative height growth rates (RGR h ± SE) and herbivory (% ± SE) of seedlings from five different dipterocarp species growing in a nursery exposed to two watering treatments. Letter combinations in upper left corner indicate significant effects; single effects of species (S), water treatment (WT), combined effects of species and water treatment (S + WT), and interaction effects (S x WT). In each case, an asterisks indicates

level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Significance among species differences is indicated by different capital letters above paired bars (Tukey HSD, $p < 0.05$). The effect of water treatment was close to significant for herbivory ($p = 0.060$).

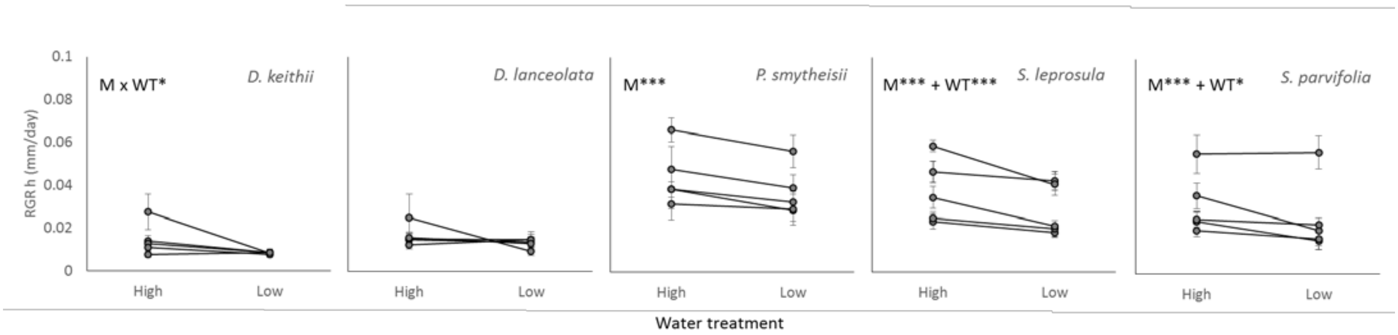

Figure 2 Among-maternal line variation in relative height growth (RGR h; mean ± SE) in seedlings from five different diperocarp species exposed to low and high water treatments in a nursery in Luasong, Sabah, Malaysia. Letter combinations in upper left corner indicate significant effects; single effects of maternal line (M), water treatment (WT), effects of both maternal line and water treatment (M + WT), and interaction effects (M x WT). In each case, an asterisks indicates level of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

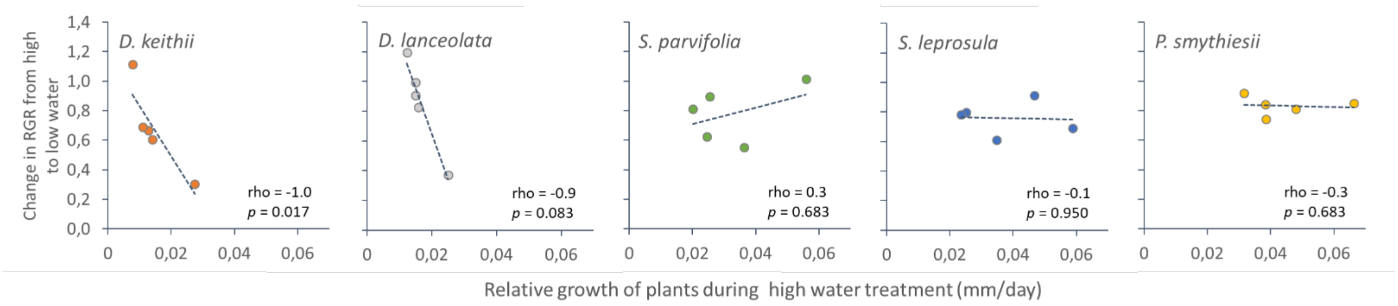

Figure 3. Relationship between maternal line level relative height growth rate of plants growing in a high water treatment and proportional change in growth with reduced water in a low water treatment of seedlings from five replicated maternal lines from five dipterocarp tree species in a nursery experiment. Statistics relates to the correlation coefficient and significance level of Spearmans ρ. Mean values for each of the five maternal lines are derived from ten individual plants per maternal line growing in each watering treatment.

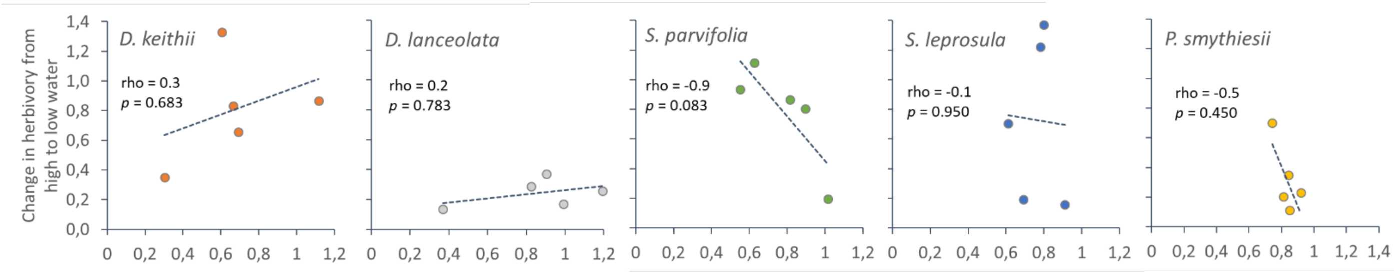

Figure 4. Relationship between maternal line level variation in proportional change in RGR between high and low water treatments and the maternal line level variation in proportional change in herbivory between high and low water treatments for five maternal lines from five dipterocarp tree species grown in a nursery experiment in Sabah, Malaysia. Statistics relates to the correlation coefficient and significance level of Spearmans ρ. Mean values for each of the five maternal lines are derived from ten individual plants per maternal line growing in each watering treatment.