Linking individual-level functional traits to tree growth in a subtropical forest

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Abstract. Forging strong links between traits and performance is essential for understanding and predicting community assembly and dynamics. Functional trait analyses of trees that have correlated single-trait values with measures of performance such as growth and mortality have generally found weak relationships. A reason for these weak relationships is the failure to use individual-level trait data while simultaneously putting that data into the context of the abiotic setting, neighborhood composition, and the remaining axes constituting the overall phenotype. Here, utilizing detailed growth and trait data for 59 species of trees in a subtropical forest, we demonstrate that the individual-level functional trait values are strongly related to individual growth rates, and that the strength of these relationships critically depends on the context of that individual. We argue that our understanding of trait–performance relationships can be greatly improved with individual-level data so long as that data is put into the proper context.

Key words: cold season; functional traits; growth rate; long-term; neighborhood; short-term growth; soil nutrients; warm season.

INTRODUCTION

The assembly and dynamics of ecological communities is ultimately governed by demographic performance (Rees et al. 2001, Silvertown 2004). A key goal in community ecology is, therefore, to quantify the intrinsic and extrinsic factors that best predict individual performance. Identifying the relative influence of the abiotic and biotic environment and the aspects of organismal form and function that are related to such interactions is necessary for a predictive and mechanistic understanding of how individual performance scales up to produce the emergent patterns of community assembly and dynamics (e.g., Massey et al. 2006, Enquist et al. 2007, Martinez-Vilalta et al. 2010, Bai et al. 2012, Swenson 2013, Iida et al. 2014a, b).

Despite the importance of linking organismal traits to the abiotic and biotic environment and individual-level demographic performance, most trait-based analyses of tree demography have uncovered relatively weak statistical relationships (Poorter et al. 2008, Herault et al. 2011, Sterck et al. 2012). We propose four reasons why these relationships are not as strong as originally expected. First, trait–demography relationships must be placed into the context of the present abiotic and biotic environment. Specifically, the performance of an individual given its trait values can only be predicted with information regarding the identity of the neighboring individuals with which it interacts and the abiotic environment (e.g., Milla et al. 2009, Auger and Shipley 2013). Further, it is well known that soil nutrient and water content can greatly influence individual tree growth (e.g., Vitousek et al. 1993, Baker et al. 2003, Paoli and Curran 2007), but this information is frequently not considered in functional-trait-tree demography research. Second, in seasonal environments, the factors that most affect demography are likely to change with the seasons and such detail is often not considered. Third, often only univariate trait–demography relationships have been explored, but it is more likely that the entire multivariate phenotype and not only a single trait determine individual performance (e.g., Marks and Lechowicz 2006, Enquist et al. 2007, Swenson 2012, 2013). Last, trait–demography statistical relationships are often quantified at the species level using mean demographic rates and mean trait values, but individuals within species may vary substantially in their traits and performance, due to genetic and environmental differences, suggesting that trait–demography relationships will be strongest when analyzing data on the individual and not the species level (von Oheimb et al. 2011, Auger

and Shipley 2013, Iida et al. 2014a, b). Individual-based studies are therefore needed to understand how functional traits and the abiotic and biotic environment simultaneously govern demographic performance.

Critical to plant trait–demography research is that the traits being integrated should be those closely related with the ability to acquire limiting resources, thereby dictating competition, growth, or tolerance to abiotic and biotic interactions. This includes traits related to structure, wood economics, and leaf economics and where species land on a fast (i.e., acquisitive) to slow (conservative) strategy spectrum (e.g., Wright et al. 2004, Enquist et al. 2007, Chave et al. 2009). Typically, ecologists have used easily measured traits for these purposes, but it is likely that allocation and relatively "hard" traits, such as crown dimensions and hydraulics, are more strongly linked with performance and better reflect where species fall along an acquisitive to conservative strategy (Chave et al. 2009, Russo et al. 2010, Westbrook et al. 2011, Fan et al. 2012). For example, trees with large crown diameters are expected to have faster growth rates as height and crown size are closely related with canopy light interception and overall allocation to resource capture (Poorter et al. 2005, King et al. 2006). Additionally, individuals with higher hydraulic conductivity generally have lower wood density and have faster volumetric growth rates (Fan et al. 2012, Iida et al. 2014a, b). In other words, allocation and hard trait data may be extremely valuable and informative for trait–demography research, but there is a tremendous risk in losing this value when aggregating the data up to the species level. More research is needed that measures those aspects of plant form and function that are more mechanistically linked to individual performance and more information is needed regarding whether individual-level analyses are indeed more informative than analyses using aggregated species-level data.

Large (i.e., >1 ha) long-term forest dynamics plots with regular inventories of tree growth provide the essential infrastructure necessary to link the demographic performance of individuals to their abiotic and biotic environment and traits in a robust manner. Here we use a long-term forest dynamics plot in subtropical China to explore the causal relationships between functional traits, abiotic environment, and neighborhood composition of individual trees on the explanatory side and the growth of these individuals as the dependent variable for 59 woody species. We predict that (1) functional traits measured at individual level are directly related to tree growth; (2) the functional trait values of individuals are the result of intrinsic and extrinsic factors linked to abiotic and biotic environments, making these environmental variables indirectly linked to growth via the traits measured; (3) the importance of trait, abiotic, and biotic factors to tree growth is sensitive to intra- and inter-annual variation in climate and the relative strength of these interactions will not be consistent across seasons or years; (4) abiotic variables should be directly related to neighborhood composition, which itself influences the trait values of individuals; and (5) traits measured on the individual level will explain more of the variation in individual growth rates than mean trait values calculated from the aggregation of individual-level data (i.e., species-level mean trait data). Here we present, to our knowledge, the first study to address these predictions by measuring traits, the environment, and growth at the individual level in a natural forest stand.

METHODS

Study site

The study was conducted in the 24-ha Gutianshan forest dynamics plot (GTS FDP) in evergreen, broad-leaved, old-growth, subtropical forest at the Gutianshan Nature Reserve, Kaihua, China (29°15′ N, 118°07′ E). The GTS FDP is a part of the Chinese Forest Biodiversity Monitoring Network and the Smithsonian's Center for Tropical Forest Science Network. All free-standing woody trees with a diameter at breast height (DBH) ≥1 cm were mapped, tagged, and identified to species (Legendre et al. 2009). In the present study, we used data from the 2005 and 2010 censuses. GTS FDP has distinct seasons with a relatively warm and wet season from April to September and a cold and dry season from October to March. The average annual rainfall is 1964 mm and the mean annual temperature is 15.3°C (Yu et al. 2011). The plot is topographically rugged with altitude ranging from 446 to 715 m.

Target trees and growth rates

To quantify tree growth on finer temporal scales, we installed dendrometer bands on over 1,300 individual trees within the GTS FDP representing 80 species. The dendrometers allowed us to quantify variation in growth on shorter time scales than is typical for other studies of tree growth in large forest dynamics plots (Yan et al. 2006, O'Brien et al. 2008). The trees with dendrometer bands were sampled according to a standard protocol where 50 randomly selected quadrats were selected across the 24-ha GTS FDP, each being 40 × 40 m in area with a central nesting of subplots 15 × 15 m, 12 × 12 m and 8 × 8 m in size (Muller-Landau and Dong 2008). Quadrats and sub-quadrats of different sizes were used for sampling trees with DBH 40–50, 20–40, 10–20, and 5–10 cm, respectively, on which dendrometers were placed. Additionally, trees with a DBH > 50 cm were randomly selected from all over the 24-ha plot. Trees that died during the study period, trees with damaged dendrometer bands, species with a single individual in the data set, and species with incomplete trait or growth data at the individual level were eliminated from the analyses. This resulted in a reduced data set containing 822 individual trees belonging to 59 species. DBH values ranged from 3.1 cm to 87.4 cm in this reduced data set (Fig. 1 and Appendix S1: Table S1).
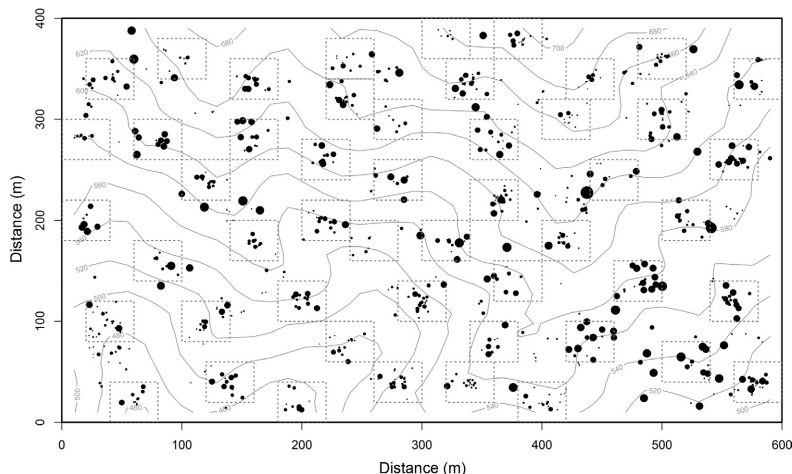
FIG. 1.   Locations of the target trees with dendrometer bands (dots on the map) in the 24-ha plot (600 × 400 m). Differently sized dots indicate different diameters at breast height. Elevation contour lines are shown at the 10-m scale. The 40 × 40 m quadrats plotted with dashed lines were randomly placed to sample trees for installing dendrometer bands (see *Methods* for detailed description).

Each tree with a dendrometer was visited twice per year, in March and September, and the growth increment was measured using a digital caliper. These circumference increments were transformed into diameter increments divided by the time interval to produce an annual tree growth rate, assuming linear growth over the time interval (AGR; mm/yr). All of the dendrometers were installed in September 2009. The measurements used in this study were obtained in the time period between September 2010 and September 2013. This included seven measurements or six time intervals per tree. However, the first measurement was excluded because the spring keeping the dendrometer band tight had slipped in some trees and needed time to settle, making initial measurements unreliable. According to the temperature of the region, we defined April to September as the warm season and October to March as the cold season. We calculated growth rate as the average annual growth rate summarized across seasons (mm/yr, AGR-2), the average annual growth rate just during the warm season (mm/yr, AGR-W) and the average annual growth rate just during the cold season (mm/yr, AGR-C; Appendix S1: Fig. S1). We also wanted to compare these dendrometer growth data to the growth data taken during the normal 5-yr interval censuses (i.e., the growth from 2005 to 2010 for the same individuals). Thus, we calculated the average annual growth rate for all 822 individuals (mm/yr, AGR-5) and included these measurements in our analysis (Appendix S1: Fig. S1). For biological and statistical reasons (see Stoll et al. 1994), we analyzed absolute rather than relative growth rates.

Tree functional traits

We measured functional trait values for each of the 822 trees in our reduced data set. These data were used for all of our individual-level analyses. For each of the 822 target trees, we measured two architectural traits, height and crown diameter (CD); two stem traits, wood density (WD) and xylem-specific hydraulic conductivity (Ks); and five leaf traits, leaf area (LA), specific leaf area (SLA), stomatal density (SD), leaf nitrogen content (LN), and leaf phosphorus content (LP). These functional traits are thought to be leading indicators of plant functional strategies and are expected to be linked to individual tree performance (e.g., Westoby et al. 2002, Wright et al. 2004, 2010, Poorter et al. 2008, Chave et al. 2009). Height and CD were measured using an altimeter pole together with a laser telemeter (Nikon Laser rangefinder 550, Tokyo, Japan) and a compass (Harbin Compass DQL-9, Harbin, China). Individual WD was quantified using the density of the nearest branch attached to the main trunk. Previous work has shown this to be a strong predictor of the main stem WD (Swenson and Enquist 2008). Thus, measuring branch WD allowed researchers to estimate individual WD without having to conduct potentially very destructive measurements such as coring the main stem or radially sectioning a stem (Swenson and Enquist 2008). The branch WD was calculated as oven-dried mass (80°C, 48 h) divided by water-displaced volume of three to five segments cutting from three separate branches for each tree. The Ks of each tree was calculated as the maximum rate of water flow through a branch segment per xylem cross-sectional area. The water flow rate was measured by a set of self-made equipment amenable to working in a field laboratory. We used three to five uniform, straight, healthy, and sun-exposed branches with diameters ~0.45 mm and with lengths ~15 cm for each individual tree (Sperry et al. 1988, Ding et al. 2011). The LA and SLA measurements followed the same methodologies as used in Liu et al. (2012) where 5–10 fresh, healthy, and

intact leaves were sampled for each tree, scanned for area, and dried 48 h at 60°C to measure mass. Leaf stomatal density was determined as the number of stomata per unit area using lamina impressions (Sachs and Novoplansky 1993, Ding et al. 2011). The sampled leaves were fresh and healthy leaves without any dirt or damage to the lower epidermis. Three impressions from each leaf were taken back to the lab and the number of stomata was counted under a microscope (Nikon 80i). LN and LP were determined using Kjeldahl method (Kjeltec 2200, FOSS, Höganäs, Sweden) and Mo-Sb colorimetric method (UV-2550 Spectrophotometer; Shimadzu, Kyoto, Japan) separately in the lab.

Environmental factors

Four topographic factors (elevation, convexity, slope, and aspect) and 11 soil nutrients (N, Fe, Mn, Zn, Cu, K, P, Ca, Mg, B, Al), and soil pH were used in our study. Briefly, elevation was quantified at every 20 m in the GTS FDP and convexity, slope, and aspect of each 20×20 m subplot was determined. These data were then used to assign values to each of the target trees. Soil nutrients were similarly quantified with the exception of soil cores being taken every 30 m in a large grid with three additional samples taken around these points in random distances and directions. These data were then used with kriging to provide soil nutrient maps for the plot. A more detailed description for the measurement of these factors can be found in Legendre et al. (2009) and Zhang et al. (2011).

Neighborhood composition

The composition of the neighborhood, specifically the identity, number, size of, and distance to neighboring trees, are expected to be related to target tree performance. For example, a high density of conspecific neighbors should negatively influence performance via competition for shared resources or shared pests. Therefore, we quantified conspecific and heterospecific total basal area and abundance for neighboring trees for each target individual within 10 m to characterize the biotic environment of individual trees. As neighborhood competition is often considered to be asymmetric, we only analyzed the larger neighboring individuals (neighbors with DBH larger than the focal tree; we also provided one model with all neighbors in Appendix S1: Fig. S3). The variables measured were conspecific basal area (BA-c), heterospecific basal area (BA-h), conspecific abundance (AB-c), and heterospecific abundance (AB-h).

Statistics

Pearson correlation analysis for growth rates.—We calculated Pearson correlations to test the pairwise relationships between AGR-5, AGR-2, AGR-W, and AGR-C and to evaluate the seasonal variation of tree growth and variation in long- and short-term growth (Fig. 2).

All variables were log-transformed or squared-root transformed in order to normalize them prior to analysis. The goal of this approach was to determine how well measurements from censuses separated by longer periods of time were correlated with more frequent measures and whether species growth between seasons in a year was correlated. Because species are non-independent entities due to shared descent, phylogenetic comparative methods may be necessary if the traits under investigation have phylogenetic signal. In our previous work in this forest plot, we have shown that the functional traits in this forest lack phylogenetic signal (Liu et al. 2013). We therefore did not perform phylogenetically controlled comparisons (e.g., independent contrasts).

Structural equation model relating individual-level growth and traits at individual/species level and growth to the abiotic and biotic environment.—One of our motivations for this study was to explore the causal relationship among abiotic environmental factors, neighborhood composition, functional traits, and growth rates. To this end, we used structural equation models (SEMs) to estimate the path coefficients and variation of dependent variables. We hypothesized that abiotic environmental factors and neighborhood composition first jointly affect the functional trait values of a target individual tree and functional traits will directly and ultimately affect tree growth rate. In other words, we expected that abiotic and biotic environment affect tree growth indirectly via their effect on plant traits. Nevertheless, we also tested direct environmental effects on growth rates by including direct pathways in the SEMs. Alternative pathways investigated included the direct effect of abiotic environmental factors on neighborhood composition and plant traits. We assumed that functional traits, environmental factors, and neighborhood composition were latent variables in the SEMs, each related to the real measured variables. Additionally, we wanted to test whether individual-level traits are better predictors of tree growth than species-level traits. To address this, we made another SEM where all other variables were the same as in the individual-level traits SEM, but trait values were substituted with species-level mean traits values. Then we could compare the predictive power between these two SEMs. The model was fit using maximum likelihood as implemented in the R package lavaan (Rosseel 2012).

Linear regression model relating functional traits to growth rates.—A final goal of our study was to explore whether the growth rate of an individual was more strongly predicted by the traits measured on that individual rather than the mean trait value for that species without any contextual information (i.e., knowledge of values for other traits on the individual or the abiotic and biotic environment). Trait values at species level were calculated as the mean value of all individual trees with dendrometer for each species. Four functional traits (height, SLA, Ks, and SD) were selected according to our results in SEMs.
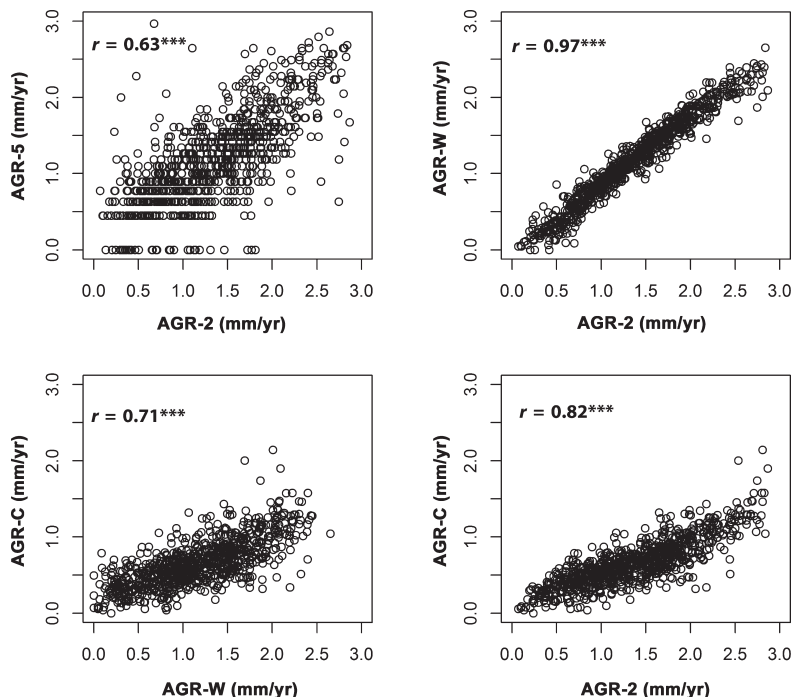
FIG. 2. Pearson correlations between annual growth rates for the same individual using different measurement protocols (***$P < 0.001$). AGR-5, annual average growth rate calculated from a 5-yr census interval; AGR-2, annual average growth rate calculated from a 2-yr census interval using dendrometer data; AGR-W, annual average growth rate for the warm season using dendrometer data; AGR-C, annual average growth rate for the cold season using dendrometer data.

Linear regression models were used to evaluate growth–trait relationships using trait values at both individual and species levels. All analyses were conducted using R statistical software (R Development Core Team 2008).

RESULTS

Relationship between different growth rates

The annual growth rate calculated from a 2-yr census interval using dendrometers (AGR-2) was significantly related to the annual growth rate calculated from a 5-yr census interval using diameter tapes (AGR-5) and the annual growth rate measured using dendrometers in the warm (AGR-W) and cold (AGR-C) seasons for individual trees (Fig. 2). There was a particularly strong positive relationship between AGR-2 and AGR-W ($r = 0.97$, $P < 0.001$) and a weaker one between AGR-2 and AGR-C ($r = 0.82$, $P < 0.001$). AGR-W and AGR-C were also significantly correlated ($r = 0.71$, $P < 0.001$), with AGR-W > AGR-C (Fig. 2). The positive but not very strong relationship between AGR-5 and AGR-2 ($r = 0.63$, $P < 0.001$) showed that the long-term measurements based on diameter tapes and more frequent measurements using dendrometers were significantly correlated, but with substantial variation left unexplained (Fig. 2). The absolute growth rate varied considerably among individuals within species and among different species (Appendix S1: Fig. S1).

Relationship between growth rates, functional traits, environmental factors and neighborhood competition effects

Results from the individual-level trait SEM showed that the strongest statistical relationships in the four best structural equation models (SEMs), one for each type of annual growth rate, was between functional trait and growth rates. The SEMs all supported strong positive direct relationships between functional trait and growth rates, with coefficients much larger than direct effects from environmental factors and neighborhood composition (Fig. 3). The functional traits that were cumulatively positively related to the traits latent variable, that were predictive of AGR-5, AGR-2, AGR-W, and AGR-C were tree height, SLA, Ks, and SD. The other traits were not included in our most strongly supported SEMs. The environment latent variable had a significant but weaker direct relationship with all types of annual growth rates and also directly and negatively related with the neighborhood composition (Fig. 3). The environmental factors that were selected for inclusion in the environment latent variable included six soil nutrients (Ca, Zn, K, Mn, Cu, Mg) and pH. None of the topographic factors were selected for inclusion in the model. The neighborhood composition variable, represented by conspecific basal area of neighbor trees, had a marginal significant ($P < 0.1$; Fig. 3b, c) or nonsignificant (Fig. 3a, d) negative and direct effect on the annual growth rates in each SEM

model, while its effect on the functional trait latent variable was much stronger and positive in all models (Fig. 3). Overall, the coefficients and relationships in the SEMs were very similar for AGR-5, AGR-2, AGR-W, and AGR-C (Fig. 3). In sum, functional traits together with neighborhood composition and environmental factors explained up to 86% of the variation in growth rates, while environmental factors and neighborhood composition explained up to 69% of the variation in functional trait (Fig. 3d).

The SEMs using the species-level trait data showed that the variation of growth rates explained by traits together with neighborhood composition and environmental factor were much less than that in the individual-level SEMs

(species-level up to 45%; Appendix S1: Fig. S2). In addition, the direct effects from neighborhood composition and environment factor to functional traits were also weaker in all four species-level SEMs than that in the individual-level SEMs (Appendix S1: Fig. S2).

Trait effects on growth rates at different levels

The results from the linear regression models showed that tree height was the trait with the strongest relationship with growth rates (Fig. 4; Appendix S1: Fig. S4, Table S2). The significant relationships between height and growth rates were stronger for species-level data ($0.07 < R^2 < 0.21$) and weaker for the individual-level
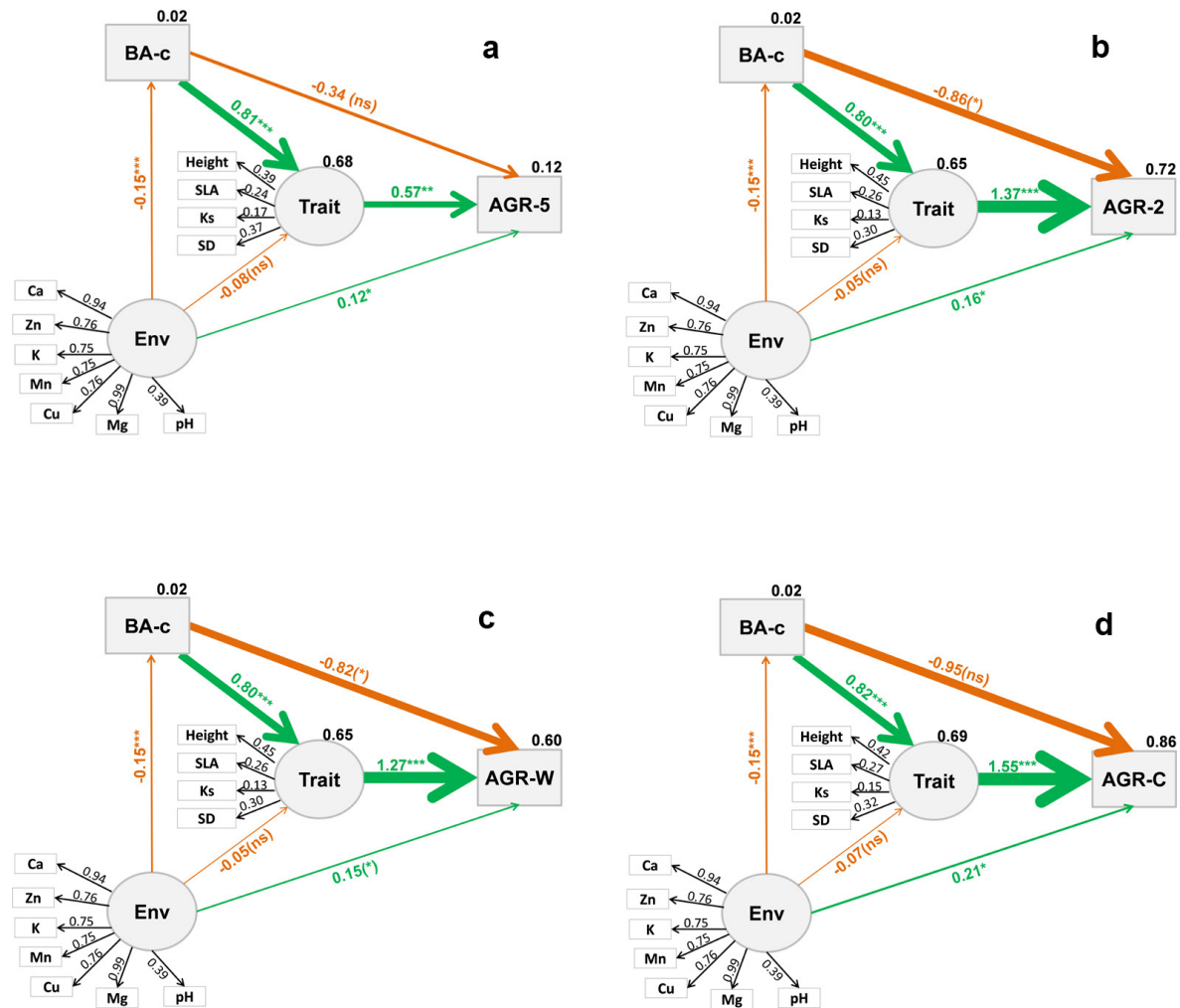

FIG. 3. The structural equation models for the effect of functional traits at individual level, environmental factors, and neighborhood composition on (a) AGR-5, (b) AGR-2, (c) AGR-W, and (d) AGR-C. Arrows represent the hypothesized causal relationships between variables. Green color indicates positive relationships. Orange color indicates negative relationships. Arrow width indicates the strength of the relationship. Values next to the arrows are path coefficients (standardized partial regression coefficients) with associated statistical significance (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; (*)$P < 0.1$; ns, non significant). Values at the upper right corner of variables represent the percentage of variance explained by the model. Variable abbreviations for growth variables are the same as in Fig. 2; Abbreviations of AGR-5, AGR-2, AGR-W, and AGR-C are the same as in Fig. 2; Env, environmental factors; BA-c, conspecific basal area; SLA, specific leaf area; Ks, specific hydraulic conductivity; SD, stomatal density.
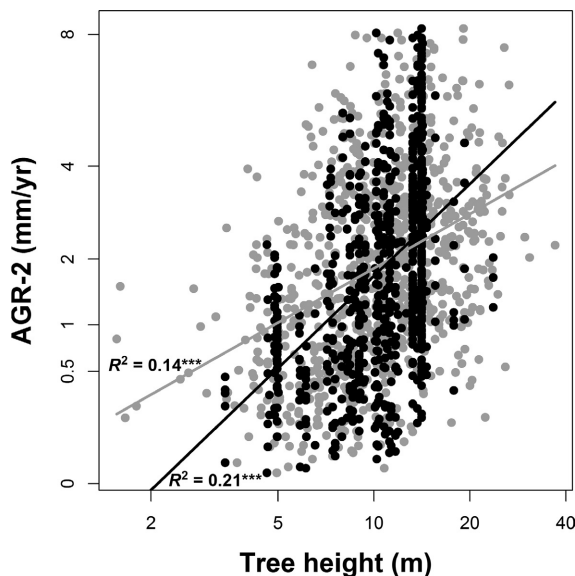
FIG. 4. Relation between tree height and individual growth rate based on two years of growth measured using dendrometers. Individual-level data are gray dots and species-level data are black dots. Abbreviation is the same as in Fig. 2. The x-axis for height in on a log scale and y-axis for AGR-2 is on a square-root scale. ***$P < 0.001$.

data ($0.03 < R^2 < 0.14$). Both specific leaf area and stomatal density were only significantly related to AGR-2 and AGR-C with slightly stronger relationships detected at the species level ($0.03 < R^2 < 0.05$ for SLA and $0.005 < R^2 < 0.03$ for SD). Although the correlations between stomatal density and AGR-2 was significant, it was quite weak ($R^2 < 0.005$; Appendix S1: Fig. S4, Table S2). Specific hydraulic conductivity was significantly but very weekly correlated with AGR-5 and AGR-2 at species level ($R^2 = 0.004$ and 0.005), but not at the individual level, while it was significantly correlated with AGR-C at both levels (Appendix S1: Fig. S4, Table S2).

DISCUSSION

A critical goal for functionally based ecology and evolution is to link individual performance to organismal function. Trait-based predictions of tree growth have often resulted in relatively little variation explained (e.g., Poorter et al. 2008, Wright et al. 2010). However, this work generally has failed to relate the growth of an individual to traits measured on that same individual while simultaneously considering the abiotic and biotic context in which that individual was found. In this study, we modeled the growth rate for 822 individual trees in a subtropical forest belonging to 59 species by combining data regarding functional traits, environmental factors, and neighborhood composition based at the individual level. We found that functional traits were the strongest direct predictors of tree growth rates, while environmental factors and neighborhood composition directly

affected growth to a lesser degree or indirectly affected growth through their direct interaction with traits. Additionally, the inconsistent results from SEMs and linear regression between species-level and individual-level traits showed that functional traits measured at the individual level are stronger predictors of individual tree growth than species-level mean values when considering the phenotypic and environmental contexts. In the following sub-sections, we discuss the results in detail.

Trait–growth relationships at the individual level with phenotypic and environmental context

The statistical relationships from the structural equation modeling (SEM) between growth rates, functional traits, environmental factors and neighborhood composition were statistically similar between AGR-2 and AGR-W (Fig. 3b, c), which strongly suggests that the average annual growth of subtropical trees was largely determined by its performance in the warm season. This is confirmed by the high correlation coefficient between AGR-2 and AGR-W (Fig. 2). The SEMs for these two growth rates showed that functional traits predict tree growth in a direct way. Here the functional trait latent variable was a combination of height, specific leaf area (SLA), xylem-specific hydraulic conductivity (Ks), and stomatal density (SD), where each was positively related to the functional trait latent variable and therefore growth. Height was the trait most strongly correlated with the functional trait latent variable. The importance of this trait is consistent with previous studies from tropical and temperate forests. In the tropics, for example, Poorter et al. (2008) has shown that tree growth rate is higher in trees with greater maximum tree height in five Neotropical forests and Herault et al. (2011) has shown that growth increases rapidly with tree height in a lowland Neotropical forest. In the temperate zone, juvenile growth in New Zealand forests and adult tree growth in Spanish forests have been linked to the maximum height of species (Martinez-Vilalta et al. 2010, Russo et al. 2010). The biological explanation proposed to underlie these relationships is that taller trees are more able to access light in a closed-canopy forest (Poorter et al. 2006). Along with height, Ks and SD were positively related to the functional traits latent variable and therefore growth (Fig. 3). High values of Ks indicate the ability to rapidly move water to the site of photosynthesis and high SD values indicate the ability of the plant to rapidly take up CO_2 for fixation. Thus, high values of all three of these traits are representative of an individual with an acquisitive resource-use strategy that should be mechanistically linked to faster growth rates and our results support this prediction.

The SEMs also showed that the environmental factors not only directly and positively affect tree performance, but also largely influenced the neighborhood composition around a target individual and that composition interacted with the latent trait variable to influence

growth, though both effects were generally weak (Fig. 3). Here the environment soil latent variable included several soil cations and pH indicating that more fertile soils tend to favor tree growth. An increased concentration and availability of soil macronutrients being correlated to faster growth is not terribly surprising. Studies from both natural ecosystems and manipulative experiments have shown that macronutrients are critical to plant health and overall tree performance (Andersen et al. 2010, Wright et al. 2011, Baribault et al. 2012). For example, potassium addition tends to increase growth rates, as potassium is a limiting nutrient in several physiological activities (e.g., phloem transport and photosynthesis; Tripler et al. 2006) and calcium shows a positive relationship with tree growth, as calcium plays an import role in the physiological processes related with stability and structural integrity of biological tissues (e.g., membrane structure and stomatal function; McLaughlin and Wimmer 1999). These taken together demonstrate a clear mechanistic positive linkage between favorable soil nutrient conditions, acquisitive resource-use strategies, and ultimately, faster growth on the individual level.

However, the effect of environmental factors on growth rates was also partly indirectly explained via a neighborhood composition effect. The neighborhood composition, represented by conspecific basal area, showed a marginal significant negative ($P < 0.1$) and direct effect on AGR-2 and AGR-W (Fig. 3b, c). In other words, the growth rate of target trees decreased as the size of surrounding conspecific trees increased, but this trend was on the boundary of statistical significance. On the other hand, conspecific basal area showed strong and positive effects on trait latent variables, while traits also showed positive and strong effect on growth rates. Combined, both results indicate that the negative competitive effect among neighbor species/trees, as they have high similarity in resource requirement, is moderated by the competitive strategies of plant functional traits, which will finally reflected on plant performance (Uriarte et al. 2010).

The SEMs for AGR-5, representing long-term growth, and AGR-2, representing short-term growth, differed in several ways (Fig. 3a, b). First, although the functional trait latent variable had a direct and positive effect on growth rate in the AGR-5 SEM as well as in the AGR-2 SEM, it tended to be much stronger for the AGR-2 SEM. Second, the effect of the neighborhood composition latent variable to tree growth rates was not significant in AGR-5 SEM. Third, AGR-2 SEM explained much more variation in growth rates than AGR-5 SEM (72% vs. 12%). This indicates short-term growth rates are largely governed by plant traits, while this effect will be moderated by other undetected variables in the longer term. It also showed that the dendrometers are providing more refined information for tree performance: It would be more reliable to use the dendrometer data.

Trait–growth models using individual vs. species-level trait data

Next we generated a new series of SEMs that were identical aside from using species-level mean trait values instead of the individual-level trait data. The results show that the SEMs using species-level trait data modeled growth worse than those original models that used individual-level data. These results highlight the value of using individual-level data and support recent work stating that the aggregation of individual-level data results in an important loss of information and it should be avoided if at all possible (e.g., Clark et al. 2011).

The SEMs we constructed utilized data for multiple traits (i.e., the phenotypic context) and soil and neighborhood compositions (i.e., the abiotic and biotic environmental context). In these models, individual-level trait data outperformed species-level data. We also wanted to quantify whether single individual-level traits were better predictors of growth than species-level traits without this contextual information. To this end, we conducted linear regressions analyses using single traits. The results showed that height was the single best predictor of growth (Fig. 4 and Appendix S1: Table S2). The averaged specific leaf area and stomatal density values explained slightly more variation in growth than individual trait values in a couple of instances, but the variation explained was very small (Appendix S1: Table S2). Specific hydraulic conductivity was not significantly related with three of four growth rates at individual level, only weekly correlated with growth rates at species level. Thus, the information and predictive ability gained by measuring individual-level trait data in our study system is only strongly realized when simultaneously taking into consideration the phenotypic and environmental context. The phenotypic context itself of an individual trait, in particular, is frequently ignored in trait–growth studies and this ignorance is problematic. Specifically, important traits are not perfectly coordinated and there is freedom to vary and explore different regions of multivariate trait space within species (e.g., Marks and Lechowicz 2006) such that an increase in one trait that might influence growth may not be related at all to the change in another key trait related to growth and without knowing how both change from one individual to the next we may never strongly model their growth upon the basis of functional traits. Thus, future work that considers multivariate phenotypes and how individual axes vary across individuals within species is greatly needed.

Conclusions

A key goal in functional and community ecology is to successfully link organismal traits to performance. Previous work in tree assemblages that has correlated average functional trait values with average growth rates has reported weak statistical relationships. It is typically argued that individual-level trait data and information

about the abiotic and biotic environment of each individual are needed to generate stronger predictions, but this has not been tested. Here we have shown that individual-level functional traits strongly predict individual tree growth in a subtropical forest. However, the strength of these predictions is facilitated by using information regarding the soil environment, identity of neighboring individuals and other trait values for the same individual. Without this contextual information, single trait values taken from an individual are often no better predictors of individual growth than an average trait value for the population or species. Furthermore, neighborhood demographic modeling analyses that utilize species mean trait values across all individuals miss a great deal of information regarding the drivers of individual demography and ultimately community structure because individual-level traits and demographic rates within species vary in relation to the abiotic and biotic environment. Given these results, we argue that individual-level trait information greatly refines our understanding of how traits link to performance and community structure, dynamics, and assembly, but it is essential that such investigations consider the context in which the individual is found otherwise the potential value of individual-level trait data will not be realized.

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