Biotic and abiotic drivers of the tree growth and mortality trade-off in an old-growth temperate forest

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ABSTRACT

The tree growth and mortality trade-off is well documented and plays a key role in forests by forming the basis of many ecosystem processes and contributing to tree species coexistence. One area that requires further understanding is how the growth-mortality trade-off is influenced by biotic and abiotic interactions in the forest. In this study, we used a 5-year interval of tree growth and mortality demographic data from a 9-ha forest dynamics plot in a temperate old-growth Chinese forest to address two questions, (1) What is the nature of the growth-mortality trade-off among species in this forest? (2) Are there differences between the responses of tree growth and mortality to local neighborhood variables, both biotic and abiotic? Specifically, do these responses vary among species and with tree size? For the first question, we hypothesized that, within species, mortality rate would be negatively correlated with growth rate, whereas among species it would be positively correlated. For the second question, we expected biotic and abiotic factors to both be important for tree mortality; but expected biotic factors to be more important than abiotic factors for tree growth. The responses of tree growth and mortality to local neighborhood variables, both biotic and abiotic, varied among species. Abiotic factors were more important than biotic factors for small trees; biotic variables were stable with tree size for both small and large trees. Our results showed that there were differences between the responses of tree growth and mortality to local neighborhood variables (i.e., biotic and abiotic) in this temperate forest community. The responses of tree mortality to local neighborhood variables strongly varied across species. Abiotic factors were only important for the growth of small trees. Biotic factors were stable with tree size for growth of small and large trees, but not for mortality. Mortality was negatively correlated with growth for large trees within species; growth-mortality trade-off among species was found to be more accentuated for small trees. The responses of tree mortality to local neighborhood variables differed strongly across species, whereas the responses of tree growth to local neighborhood variables varied among size classes. Tree growth and mortality is tightly correlated both within (negatively) and among species (positively), and their relationships are both size dependent in this temperate forest. Our findings highlight that differential responses of tree growth and mortality to local neighborhood variables continue to shape the forest community well after sapling establishment in this temperate forest community.

1. Introduction

In forests, tree mortality is a complex ecological process and can determine forest dynamics and their successional trajectories, alter nutrient cycling, and create gaps for regeneration (Franklin et al., 1987; Canham et al., 2001; Uriarte et al., 2012). Understanding the controls influencing tree growth is also central to forecasting forest dynamics (Clark et al., 1999; Canham et al., 2004, 2006). Furthermore, growth-mortality trade-offs promote the coexistence of forest tree species (Iida et al., 2014b). Forest dynamics and community assembly are often explained by interspecific variation in demographic performance (Pacala et al., 1996; Rees et al., 2001; Russo et al., 2010). Moreover, the probability of tree mortality is related to tree growth efficiency (i.e., growth vigor) (Leemans, 1991). Therefore, tree growth and mortality and their trade-offs play key roles in forest demographics, since they form the basis of many ecosystem processes and contribute to tree species coexistence (Lutz and Halpern, 2006; Iida et al., 2014b). Without a proper understanding of the determinants of tree growth and mortality, as well as their relationships, our understanding of the assembly and dynamics of forest communities is limited.

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Tree growth and mortality are considered to be two of the most important vital rates of tree demography and they are the result of combined effects of biotic and abiotic factors that interact with tree ontogeny (Visser et al., 2016). Conspecific neighbor density was considered to be the most important biotic driver of seedling survival, persistence and recruitment, along with tree growth and survival in recent studies across temperate and tropical forests (Comita et al., 2010; Johnson et al., 2012; Wang et al., 2012; Zhang et al., 2016; Du et al., 2017; Lin et al., 2017). Conspecific neighbors often have strong intraspecific competition for resources and are more likely to be impacted by host-specific natural enemy attacks, supporting the "Janzen-Connell hypothesis", namely conspecific negative density dependence (NDD) (Janzen, 1970; Connell, 1971). The dissimilarities of functional traits and the phylogenetic relatedness of heterospecific neighbors on a focal individual (e.g., seedling or tree) were also deemed to be another important biotic neighborhood driver of seedling survival as well as tree survival and growth in tropical forests (Webb et al., 2006; Paine et al., 2012; Lebrija-Trejos et al., 2014; Zhu et al., 2015; Chen et al., 2016). These studies proposed that neighbors belonging to species that are phylogenetically or functionally more closely related to a focal individual have a significantly negative effects on the survival and growth of a focal individual.

Habitat variables (e.g., topography, light, moisture, and soil properties), together with biotic neighborhood variables, influenced seedling persistence, survival and tree survival and growth through abiotic environmental filtering (EF) in recent studies across temperate and tropical forests (Wang et al., 2012; Chi et al., 2015; Zhang et al., 2016; Lin et al., 2017). EF arises from habitat preference of species, or the inability of a species to persist in all local habitats, often occurs during earlier life stages (Hutchinson, 1957; Baldeck et al., 2017). Moreover, species with different life-history strategies often respond to local neighborhood variables differently (Comita and Hubbell, 2009; Gravel et al., 2010). Most previous studies have considered a single vital rate linked to their local drivers (i.e., biotic and abiotic factors) to further discuss mechanisms fostering species coexistence and community assembly (Wang et al., 2012; Piao et al., 2013; Johnson et al., 2014; Chi et al., 2015; Zhu et al., 2015; Chen et al., 2016). However, the question of whether there are some differences between the responses of tree mortality and growth to local neighborhood variables in temperate forests remains unclear.

Among species, the trade-off between growth and mortality is perhaps the best-established axis of life history variation (Grubb, 1977; Hubbell and Foster, 1992; Pacala et al., 1996; Wright et al., 2003; Stephenson et al., 2011). Variation in demographics with respect to mortality and growth are usually more easily observed in small trees and are especially apparent in tropical forests (Kitajima, 1994; Wright et al., 2003; Poorter et al., 2008; Wright et al., 2010; Iida et al., 2014a, 2014b). Moreover, there is a relationship between tree mortality and annual diameter growth increment (i.e., absolute growth rate). The annual tree diameter growth increment usually increases for small trees but decreases for large trees (i.e., growth rates slow with tree senescence). One reason may be that trees may be at increased risk of exogenous damage that can weaken them as they age (such as mechanical damage, or attack by insects and pathogens). It is hypothesized that if a tree that cannot maintain a certain minimum annual diameter growth increment has increased mortality risk (Botkin et al., 1972). Leemans (1991) suggested that the probability of tree mortality is related to the efficiency of tree growth in a mortality sub-model of a FORSKA forest dynamics model and that declines in tree growth efficiency may lead to increased risk of tree mortality. Although there have been many studies on growth-mortality relationships in recent years (Cailleret et al., 2017), there has been little research into relationships between growth and mortality within and among species simultaneously in temperate forests.

In this study, we used a 5-year interval of tree growth and mortality data from a 9-ha forest dynamics plot (FDP) located in an old-growth mixed broadleaved-Korean pine (*Pinus koraiensis*) temperate forest in China to evaluate following two questions: (1) Within and among species, what life-history related trade-offs in growth and mortality exist? And do these trade-offs vary with tree size? (2) Are there differences between the responses of tree growth and mortality to local neighborhood variables (i.e., biotic and abiotic) in this temperate forest community? Do these responses vary among species and with tree size? We hypothesized that (1) Within species, mortality rate would be negatively correlated with growth rate, whereas among species it should be positively correlated, as pioneer species that tend to grow fast usually have higher mortality rates than more late-successional species with slower growth rates. We also expected that (2) biotic and abiotic factors should both be important for tree mortality, but that biotic factors should be more important than abiotic factors for tree growth, given the demonstrated effects of tree neighborhoods on focal tree performance. Therefore, we expected that the responses of tree growth and mortality to local neighborhood variables should vary based on neighborhood species composition. Finally, we supposed that abiotic factors would be more important than biotic factors for small trees, and that biotic influences on tree growth and mortality should be consistent with tree size.

2. Methods

2.1. Study site

The study site is located in the Liangshui National Natural Reserve (47°10′50″N, 128°53′20″E), Heilongjiang Province, in the Xiaoxing'an Mountains of northeast China. The area has been spared from logging and other major human disturbances since 1952. The reserve was established in 1980 and became part of China's Man and the Biosphere Reserve Network in September 1997. It was promoted to a national nature reserve with the approval of the Chinese State Council in December 1997 to protect its old-growth, mixed broadleaved-Korean pine (*Pinus koraiensis*) forest ecosystem. The reserve is 12,133 ha and is characterized by a rolling mountainous terrain with elevations ranging from 280 m to 707 m. Mixed deciduous angiosperm and Korean pine forest is dominant vegetation type in the region in terms of species composition and stand structure. The soils are classified as dark brown forest soils, and the mean annual precipitation is 676 mm with 78% relative humidity and an annual evaporation of 805 mm. The precipitation mainly concentrates in summer (June - August). The mean annual temperature is -0.3 °C with a minimum mean of -6.6 °C and a maximum mean of 7.5 °C. The core zone of this reserve has never been logged.

2.2. Data collection

2.2.1. Demographic performance

In 2005, the 9-ha (300 m × 300 m) Liangshui FDP was established in the core zone of the reserve. The Liangshui FDP is part of the Chinese Forest Biodiversity Monitoring Network (CForBio) (Feng et al., 2016). The plot was divided into standard quadrats (10 m × 10 m, 900 total). The mean elevation of the plot is 463.3 m and ranges from 425.1 to 509.0 m. All free-standing, living trees and shrubs ≥2 cm DBH (diameter at breast height, 1.3 m) were mapped, measured, identified to the species and tagged, beginning in 2005. In a subsequent census in 2010, all free-standing, living trees and shrubs ≥1 cm DBH were mapped, measured, identified to species and tagged. The status of each tree, alive or dead, as well as the DBH were recorded in the 2015 census. In this study, we use a 5-year interval (2010–2015) of the plot demographic data. We selected 40 species (21, 504 free-standing live individuals in the 2010 census) for which we had functional trait data (i.e., wood density (WD), specific leaf area (SLA) and maximum tree height (H_{max})) to construct two smaller datasets, one for survival and one for growth, using the raw demographic data. For the growth dataset, we discarded

the cases where a tree (1) had its main stem broken and the re-sprouted stem was measured instead, (2) grew at a rate > 2 cm in diameter per year or had diameter shrinkage of more than 25% of the initial DBH, based on presumed measurement error, and (3) was dead during the interval of 2010–2015 in order to calculate absolute diameter growth rate (cm·yr^{-1}) according to previous studies (Rüger et al., 2011a; Dong et al., 2012) and the characteristic of temperate forest in study site, but we still treated these eliminated trees as neighbors in when conducting neighborhood analyses. The growth dataset contains 17, 500 individuals, and survival dataset contains 21, 504 individuals.

2.2.2. Functional traits

We measured and compiled data from 320 individuals for three functional traits, including WD, SLA and H$_{max}$, which are highly correlated with tree demographic performance (Poorter et al., 2008; Poorter et al., 2010; Iida et al., 2014a; Shen et al., 2014; Diaz et al., 2016; Gibert et al., 2016; Kunstler et al., 2016; Visser et al., 2016). Diaz et al. (2016) showed at the global scale these three traits to represent the majority of the functional trait variation along two-main axes of life-history variation among plant species, leaf-economics and plant size. Despite this, in our case, these three traits were still highly correlated and condensed them into two eigenvectors (which accounted for 95% of the total trait variability) using principal components analysis (PCA) for use in the linear models.

2.3. Model

2.3.1. Variables construction

We selected tree size, biotic and abiotic factors as independent variables in the models. Tree size is a very important intrinsic factor of trees that strongly affects survival and growth (King et al., 2006; Wang et al., 2012; Zhang et al., 2016). We treated the DBH of individual trees from the 2010 censes as the tree size variable.

Extrinsic drivers of tree growth and mortality included biotic and abiotic factors. The biotic neighborhood variables included the conspecific neighbor density index (CI) and the average trait dissimilarity index of heterospecific neighbors (TI) (Paine et al., 2012; Chen et al., 2016). We calculated these biotic variables based on neighborhood composition, initial basal area, topographic position, functional traits and the Gaussian kernel function (Pu et al., 2017). Larger values of TI indicate more dissimilar pairs of species at the neighborhood scale and vice versa.

The biotic neighborhood variables and Gaussian weight functions were defined as follows:

$$CI = \sum_i CBA_i \times W_i$$

$$TI = \sum_i (TD_i \times HBA_i \times W_i)/N$$

$$W_i = Exp\left[-\frac{1}{2}(\frac{SD_i}{R})^2\right]$$

where *CI* refers to the conspecific neighbor density index; *TI* refers to the average trait dissimilarity index of heterospecific neighbors; CBA_i and HBA_i refer to conspecific and heterospecific basal area, respectively; *i* refers to the individual; W_i refers to the Gaussian weight function;. TD_i refers to the Euclidean distance of two principal components axes between a focal individual and its heterospecific neighbors in PCA trait space; SD_i refers to the Euclidean distance between a focal individual and its neighbors in georeferenced spatial location; *R* refers to the neighborhood influence radius; and *N* refers to the number of neighbors.

We created 5 m scale raster digital elevation model (DEM) data based on 1 m elevation contours (ESRI Shapefile) in ArcGIS 10.1. Then we calculated convexity and hillshade at the 5-m scale from the DEM. We chose elevation, convexity and hillshade as the topographic

variables included in this study. We also divided the plot into 20-m quadrats, and sampled soil at each of the 256 intersections of each quadrat corner. Soils were analyzed for total phosphorus content, available phosphorus content, total nitrogen content, hydrolysable nitrogen content, organic carbon content, rapidly available potassium content, pH, bulk density, volumetric moisture content and mass moisture content. We extracted the first three principal component axes from all abiotic factors (i.e., topographic and soil variables) after a PCA to reduce the number of abiotic variables because many of these variables were highly correlated (e.g., elevation and SOC).

2.3.2. Generalized linear mixed-effects model

We modeled individual tree survival as a function of tree size, biotic neighborhood, and the first three PCA axes representing topographic and edaphic factors using logistic generalized linear mixed-effects model (GLMM). Individual survival was a binary variable (i.e., alive or dead, coded as 1 or 0, respectively). We modeled tree survival and growth for small trees and large trees separately with cut-off values of 10-, 20- and 35-cm tree sizes. Individual tree growth was modeled as a function of tree size, represented by DBH, and the abiotic and biotic factors using a Gaussian GLMM. For the growth GLMM, we chose to use absolute diameter growth rate (AGR) as the response variable to characterize tree growth. The AGR (cm·yr^{-1}) was defined as the raw change in tree diameter per year (Chen et al., 2016). For all survival and growth GLMMs, we included two crossed-random effects. First, we included species identity as a random effect because baseline species survival and growth rates can vary widely. Second, since individuals who are close to each other are likely to have similar survival and growth probabilities (i.e., spatial autocorrelation), we assigned each individual the identifier of the 20-m quadrat where it was located; the 20-m quadrat identifier was then included as a random effect (Chi et al., 2015; Zhu et al., 2015). We constructed 56 nested models with different variable combinations for all species with at least 400 individuals in the plot. The nested model with the smallest Akaike's Information Criterion (AIC) value was considered the most parsimonious. We excluded individuals located in border quadrats to eliminate the edge effects because neighbor interactions can be neglected beyond 10 m (Piao et al., 2013). The GLMMs were executed using the "lme4" package (Bates et al., 2015) in R version 3.1.3 (R Core Team, 2015).

2.4. Growth-mortality relationships test

We tested trade-offs between tree mortality and growth (i.e., RGR$_{95}$ vs. MR$_{25}$, RGR$_{90}$ vs. MR$_{50}$ and mean RGR vs. overall mortality) among species using Pearson correlations. Mortality rates (MR) equaled $100 \times [1–(N_f/N_i)]$ for N_i initial individuals and N_f survivors of every species. RGR$_{95}$ are growth rates under favorable conditions equaled 95th percentile relative-growth rates. MR$_{25}$ are mortality rates under unfavorable conditions were calculated for the 25% of individuals of each species with the smallest RGR in the previous census interval. We also calculated the average RGR, RGR$_{90}$, overall mortality, and MR$_{50}$ using the above similar calculation method (Wright et al., 2010), using a minimum sample size of at least 100 individuals per species for growth and mortality rates. Moreover, we also summarized the tree demographic performance (i.e., mortality proportion and AGR (Mean ± SE)) with the tree DBH size classes (9 DBH size classes in total) to evaluate the relationships between tree growth and mortality within species.

See Appendix S1 for further details about this section. See Table 1 for the definition of associated abbreviations.

3. Results

3.1. Correlates of tree growth and mortality

The survival model with the variables combinations of DBH, CI, TI,

Table 1
Abbreviations and their associated terms used throughout this paper.

Abbreviation	Term
FDP	Forest dynamics plot
NDD	Negative density dependence
EF	Environmental filtering
DBH	Diameter at breast height (1.3 m)
CI	Conspecific neighbor density index
TI	Average trait dissimilarity index of heterospecific neighbors
GLMMs	Generalized linear mixed-effects models
AIC	Akaike's information criterion
PCA	Principal components analysis
DEM	Digital elevation model
AGR	Absolute diameter growth rate (cm yr^{-1}); the change in raw sizes per year (Chen et al., 2016)
RGR	Relative diameter growth rate (cm cm^{-1} yr^{-1}); the change in logarithmically transformed sizes per year (Wright et al., 2010)
RGR$_{95}$	Growth rates under favorable conditions equaled 95th percentile relative-growth rates
RGR$_{90}$	Growth rates under favorable conditions equaled 90th percentile relative-growth rates
RGR$_{average}$	Average relative growth rate
MR$_{25}$	Mortality rates under unfavorable conditions were calculated for the 25% of individuals of each species with the smallest RGR in the previous census interval
MR$_{50}$	Mortality rates under unfavorable conditions were calculated for the 50% of individuals of each species with the smallest RGR in the previous census interval
MR$_{overall}$	Overall mortality rate

Table 2
Variable combinations with minimum AIC for tree survival and growth at the community level.

Demography	Survival	Growth
Variable combinations	DBH + CI + TI + PC2	DBH + CI + TI

See Table 1 for the abbreviations.

Table 3
Number of species in each of the most parsimonious generalized linear mixed models for tree survival and growth for species with ≥ 400 individuals.

Model	Number of species	
	Survival	Growth
Abiotic	1	1
Biotic	2	2
Abiotic + Biotic	2	1
DBH	2	7
DBH + Abiotic	1	0
DBH + Biotic	3	1
DBH + Abiotic + Biotic	2	1

Abiotic refers to any of the three PCA axes (PC1, PC2, or PC3) and any of their combinations. Similarly, biotic refers to CI, TI and their combination. See Table 1 for the abbreviations.

and PC2 had the lowest AIC and the growth model including DBH, CI, and TI was the most parsimonious among growth models for this temperate forest community (Table 2). The number of species that best fit each of the nested survival models were almost equal. The number of species that best fit each of the nested growth models with the combination of only DBH and abiotic variables were zero. Growth of five species were best fit by models that contained biotic variables, and the growth of three species were best fit by models that contained abiotic variables. Moreover, tree growth was best explained by tree size alone for the largest group (7) of species (Table 3). The most parsimonious growth model for small trees included both biotic and abiotic factors, but large trees only included biotic factors (Table 4; size cut-offs at 10 and 20 cm). The most parsimonious survival model for small and large trees included both biotic and abiotic factors with DBH cut-offs at 10 and 35 cm, but for small and large trees only included abiotic factors with a size cut-off of 20 cm (Table 4).

3.2. Tree growth-mortality relationships

Initial DBH had a significantly positive effect on survival for small trees and an insignificant effect for large trees. However, for tree growth, the initial DBH had a significantly positive effect for small trees and a significantly negative effect for large trees (Table 5). The mean AGR of trees increased, leveled off and then declined with increasing DBH size class (Fig. 1). The tree mortality proportion decreased then leveled off and even rose with increasing tree size: the mortality proportion of trees in the 60–70 cm size class was higher than the 50–60 cm size class. Given our analyses, a DBH of 35 cm may be an ontogenetic turning point where growth and mortality both asymptote (Fig. 1). Trade-off between RGR$_{90}$ and MR$_{50}$ was significant for small trees and for all individuals but was not significant for large trees; insignificant trade-offs existed between RGR$_{Average}$ and MR$_{Overall}$ and RGR$_{95}$ and MR$_{25}$ for all individuals and for small and large trees (Table 6).

4. Discussion

4.1. Determinants of tree growth and mortality

Our results are consistent with a recent study that showed that tree size and biotic and abiotic factors all have significant effects on tree mortality in Changbaishan temperate forest in northeast China (Wang et al., 2012). We show that local biotic neighborhood interactions (e.g., CI and TI) may be more important than the abiotic environment for tree growth. One reason may be because plant growth is highly related to photosynthesis and light availability and photosynthetically active radiation (Rüger et al., 2011a). Competition for light among forest trees is strong and highly dependent on forest structure, specifically the spatial arrangement of trees and their canopies. To this effect, a recent study showed that light is the most important resource for growth in the temperate forests of America (McMahon et al., 2011). Generally the negative effects of neighbors on focal tree individuals can be classified into two categories: direct light resource competition between a focal tree and its neighbors and light shading and extinction effects on focal tree individuals from the canopy of larger neighbors emphasized by the

Table 4
Generalized Linear mixed model explanatory variable combinations for the most parsimonious survival and growth models (i.e., minimum AIC) for small and large trees with DBH size cut-offs of 10, 20 and 35 cm.

Size classes	Small trees			Large trees		
Cut-off	10 cm	20 cm	35 cm	10 cm	20 cm	35 cm
Survival	DBH + CI + TI + PC2	PC2 + PC3	DBH + CI + TI + PC2	DBH + CI + TI + PC2	PC3	CI + PC1
Growth	CI + PC2	DBH + CI + TI + PC1 + PC2 + PC3	DBH + CI	CI	DBH + CI	DBH + CI

See Table 1 for the abbreviations.

Table 5
The effects of tree size, biotic and abiotic variables on tree survival and growth for small and large trees (i.e., DBH size cut-off of 35 cm) and all trees.

Variable	Survival			Growth		
	Small trees	Large trees	All trees	Small trees	Large trees	All trees
DBH	0.3881[***]	0.4469 NS	0.2722[*]	0.0326[***]	−0.0596[***]	0.0153[***]
CI	−0.1117[**]	0.5066 NS	−0.0904[*]	−0.0119[***]	−0.0476[***]	−0.0129[***]
TI	0.0381 NS	0.0791 NS	0.0447 NS	0.0034[**]	0.0063 NS	0.0034[*]
PC1	0.0118 NS	0.4903[#]	0.0146 NS	0.0006 NS	−0.0069 NS	0.0010 NS
PC2	−0.1389[***]	−0.1359 NS	−0.1345[***]	−0.0042[**]	0.0075 NS	−0.0012 NS
PC3	−0.0342 NS	0.1961 NS	−0.0318 NS	−0.0035[**]	−0.0065 NS	−0.0033[*]

Significant codes for survival model: [***]$P < 0.001$; [**]$0.001 \leq P < 0.01$; [*]$0.01 \leq P < 0.05$; [#]$0.05 \leq P < 0.1$; NS, not significant. Significant codes for growth model: $|t| < 1.65$, no significant (NS); $1.65 \leq |t| < 1.96$, marginal significant at 0.1 level (#); $1.96 \leq |t| < 2.58$, significant at 0.05 level ([*]); $2.58 \leq |t| < 3.29$, significant at 0.01 level ([**]); $|t| \geq 3.29$, significant at 0.001 level ([***]).
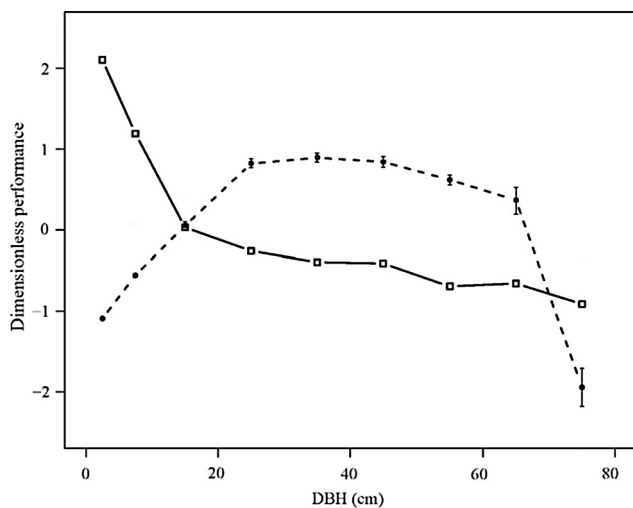See Table 1 for the abbreviations.

Fig. 1. Dimensionless tree mortality proportion (solid line with squares) and absolute diameter growth rate (Mean ± SE) (dashed line with circles) within each DBH (cm) size classes (9 size classes in total; cut-offs of each size classes: 5, 10, 20, 30, 40, 50, 60 and 70).

Table 6
Relationship between tree growth and mortality of tree species with cut-off of 35 cm.

RGR-MR	Small trees	Large trees	All trees
RGR$_{95}$-MR$_{25}$	0.33 (0.15)	0.59 (0.07)	0.37 (0.10)
RGR$_{90}$-MR$_{50}$	**0.49 (0.03)**	0.23 (0.51)	**0.50 (0.02)**
RGR$_{average}$-MR$_{overall}$	0.29 (0.19)	0.02 (0.95)	0.33 (0.14)

Note: Significant correlation indices (with *P* values) are shown in bold ($\alpha = 0.05$). See Table 1 for the abbreviations.

Beer-Lambert law (Monsi and Saeki, 1953).

The responses of tree mortality to local neighborhood variables strongly varied across species (Table 3). Species with contrasting life-history strategies often respond to extrinsic factors (i.e., biotic and abiotic) differently (Hubbell et al., 2001; Comita and Hubbell, 2009; Gravel et al., 2010). One explanation is that species leaf phenology may determine the sensitivity of a species to conspecific neighborhood density (Comita et al., 2010; Bai et al., 2012; Lu et al., 2015). Alternatively, shade tolerance should be an important determinant of a trees reaction to its local neighborhood (McCarthy-Neumann and Kobe, 2008). Our result was similar to recent studies that showed there were large differences in the best fit models for common species that were analysed individually in temperate and subtropical forests in China (Wang et al., 2012; Wu et al., 2017). However, we did not find the responses of tree growth to local neighborhood variables to vary strongly across species (Table 3). Biotic factors seem to be more important than abiotic factors for the growth of the common species in the temperate forest community; a result that is consistent with the result of community level analyses (Table 2). This is most likely due to the relatively low species richness and high dominance of a few species in this temperate forest community (i.e., several abundant species drive the community trends).

Abiotic factors were only important for growth of small trees (Table 4) and biotic factors were stable with tree size for growth, but not for mortality (Table 4). Abiotic EF often occurs during seedling to sapling establishment and growth (Baldeck et al., 2017). Small tree individuals tend to be more vulnerable to abiotic habitat impacts and large trees perform well in their preferred habitats due to EF occurring at smaller size classes (Russo et al., 2005). A previous study in this plot showed that most of the focal species exhibited habitat preference caused by large-scale habitat heterogeneity (Piao et al., 2013). This was consistent with the idea that EF at earlier life stages results in adult tree habitat associations (Comita and Engelbrecht, 2009).

In addition, we found NDD effects for both tree survival and growth of small trees in this temperate forest (Table 5). Individuals had a decreased probability of survival when surrounded by more conspecifics for small trees, due to stronger intraspecific competition for resources when compared to interspecific competition for the same resources and an increased likelihood to of the negative effects of host-specific natural enemy attacks, or pathogens at higher densities (Janzen, 1970; Connell, 1971). Tree growth increased with neighborhood richness and functionally dissimilar of neighbor trees (Table 5). Focal trees living with more-functionally similar neighbors are expected to have increased resource competition, thus inhibiting tree growth (Adler et al., 2013; Chen et al., 2016). Our results confirm those of a study in a neotropical forest that found positive effects of neighborhood complementarity on tree growth; focal tree growth increased with neighborhood trait dissimilarities (Chen et al., 2016).

4.2. Tree growth-mortality relationships

In the Liangshui temperate forest, we found that the decline in tree growth efficiency might lead to increased risk of mortality, especially for large trees (Fig. 1; Table 5). Using tree size as a surrogate for age, we can infer age-related mortality, since the physiological functioning of trees might decline as trees senesce, such as decreased photosynthesis rate (Lugo and Scatena, 1996). But a growing body of evidences suggests that trees may not physiological senesce (Mencuccini et al., 2007; Munné-Bosch, 2008, 2015; Penuelas and Munne-Bosch, 2010; Mencuccini et al., 2014). Moreover, trees may suffer exogenous damage that can weaken them as they age (i.e., xylem mechanical damage, or attack by insects and pathogens). Botkin et al. (1972) suggested that a tree that fails to maintain a certain minimum AGR cannot survive for a long time and the probability of tree mortality will increase in the JABOWA forest dynamics model. Leemans (1991) used a similar

approach and suggested that tree mortality probability is related to tree 'growth efficiency' (index of vigor), similar to the concept of net photosynthetic rate, in a FORSKA forest dynamics model. Hamilton (1986) suggested that individual tree mortality is negatively related to the annual diameter growth rate (growth vigor) in a logistic model of tree mortality constructed for forest management in a mixed conifer forest of Northern Idaho, USA. In general, dying trees showed lower radial growth rates prior to death than surviving ones (Pedersen, 1998; Bigler and Bugmann, 2004). For example, Cailleret et al. (2017) observed a decrease in radial growth before death in ca. 84% of the mortality events. Although growth efficiency usually declines with increasing tree size, increases in leaf area mean that whole-tree mass growth can still increase (Sillett et al., 2010, 2015; Stephenson et al., 2014).

An ecological trade-off occurs when higher fitness under one set of conditions causes a reduction in fitness under another set of conditions (MacArthur and Levins, 1964). We found a significant interspecific trade-off between RGR_{90} and MR_{50} for small trees with a cut-off at 35 cm, but this was insignificant for large trees (Table 6). Plant growth-mortality trade-offs are considered to be one of the most important trade-offs during plant life history, with another important trade-off being between reproduction and mortality (Stephenson et al., 2011). Plants control the timing of growth, flowering, and pollen and fruit production in order to appropriately allocate resources (Bolmgren and Cowan, 2008; Kushwaha et al., 2010). The RGR of plants usually declines with increasing size and/or age because trees accumulate respiratory costs, carry less leaves area per unit living biomass, suffer more from self-shading, and increase reproductive allocation (Ryan et al., 1997; Mencuccini et al., 2005; Rose et al., 2009).

Tree mortality may increase, decrease, or show a U-shaped curve with increasing size, probably due to differential changes in local environmental conditions (e.g., light) and the shift in resource allocation between vegetative growth and reproduction (Thomas, 1996; King et al., 2006; Rüger et al., 2011b). Our result was consistent with recent studies of tropical forests that indicated tree growth-mortality interspecific trade-offs were size dependent. Wright et al. (2010) found that there was an interspecific trade-off between rapid growth under favorable conditions and low mortality under unfavorable conditions for small trees but not for large trees in tropical forest on Barro Colorado Island (BCI), Panama. Iida et al. (2014b) found positive correlations between RGR and mortality over the whole range of stem diameters, but they were only significant for small trees in the Pasoh tropical forest, Malaysia. However, we did not find a significant U-shaped mortality curve with increasing size. Our result is similar to recent studies in a temperate and a subtropical forest of China (Wang et al., 2012; Wu et al., 2017), which found that tree mortality decreased with increasing size for all individuals at the community level and that the initial DBH had a significantly positive effect on tree survival for small trees; however, there was an insignificant effect for large trees that did not show a significant U-shaped curve and that was different from that in tropical forests (e.g., BCI and Pasoh).

5. Conclusions

The responses of tree mortality to local neighborhood variables differed strongly across species, and is likely a result of the interaction of the strength of the biotic (i.e., neighborhood NDD) interactions and the abiotic environment, whereas the responses of tree growth to local neighborhood variables varied among size classes. Tree growth and mortality is tightly correlated both within (negatively) and among species (positively), and their relationships are both size dependent in this temperate forest. Our findings highlight that differential responses of tree growth and mortality to local neighborhood variables continue to shape the forest community well after sapling establishment in this temperate forest community.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.004.

References

Adler, P.B., Fajardo, A., Kleinhesselink, A.R., Kraft, N.J., 2013. Trait-based tests of coexistence mechanisms. Ecol. Lett. 16, 1294–1306.

Bai, X., Queenborough, S.A., Wang, X., Zhang, J., Li, B., Yuan, Z., Xing, D., Lin, F., Ye, J., Hao, Z., 2012. Effects of local biotic neighbors and habitat heterogeneity on tree and shrub seedling survival in an old-growth temperate forest. Oecologia 170, 755–765.

Baldeck, C.A., Harms, K.E., Yavitt, J.B., John, R., Turner, B.L., Valencia, R., Navarrete, H., Bunyavejchewin, S., Kiratiprayoon, S., Yaacob, A., Supardi, M.N., Davies, S.J., Hubbell, S.P., Chuyong, G.B., Kenfack, D., Thomas, D.W., Dalling, J.W., 2017. Habitat filtering across tree life stages in tropical forest communities. Proc. Biol. Sci. 280, 20130548.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Bigler, C., Bugmann, H., 2004. Predicting the time of tree death using dendrochronological data. Ecol. Appl. 14, 902–914.

Bolmgren, K., Cowan, P.D., 2008. Time - size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. Oikos 117, 424–429.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–872.

Cailleret, M., Jansen, S., Robert, E.M., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Cada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Cufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Heres, A.M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., Lopez Rodriguez, R., Makinen, H., Mayr, S., Meszaros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sanguesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanovic, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martinez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. Glob. Chang. Biol. 23, 1675–1690.

Canham, C.D., Papaik, M.J., Latty, E.F., 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Can. J. For. Res. 31, 1–10.

Canham, C.D., LePage, P.T., Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can. J. For. Res. 34, 778–787.

Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol. Appl. 16, 540–554.

Chen, Y., Wright, S.J., Muller-Landau, H.C., Hubbell, S.P., Wang, Y., Yu, S., 2016. Positive effects of neighborhood complementarity on tree growth in a Neotropical forest. Ecology 97, 776–785.

Chi, X., Tang, Z., Xie, Z., Guo, Q., Zhang, M., Ge, J., Xiong, G., Fang, J., 2015. Effects of size, neighbors, and site condition on tree growth in a subtropical evergreen and deciduous broad-leaved mixed forest, China. Ecol. Evol. 5, 5149–5161.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J., Wyckoff, P., 1999. Interpreting recruitment limitation in forests. Am. J. Bot. 86, 1–16.

Comita, L.S., Engelbrecht, B.M., 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. Ecology 90, 2755–2765.

Comita, L.S., Hubbell, S.P., 2009. Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. Ecology 90, 328–334.

Comita, L.S., Muller-Landau, H.C., Aguilar, S., Hubbell, S.P., 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. Science 329, 330–332.

Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynam. Popul. 298, 298–312.

Diaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bonisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Gunther, A., Falczuk, V., Ruger, N., Mahecha, M.D., Gorne, L.D., 2016. The global spectrum of plant form and function. Nature 529,

167–171.

Dong, S.X., Davies, S.J., Ashton, P.S., Bunyavejchewin, S., Supardi, M.N., Kassim, A.R., Tan, S., Moorcroft, P.R., 2012. Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. Proc. Biol. Sci. 279, 3923–3931.

Du, Y., Queenborough, S.A., Chen, L., Wang, Y., Mi, X., Ma, K., Comita, L.S., 2017. Intraspecific and phylogenetic density-dependent seedling recruitment in a sub-tropical evergreen forest. Oecologia 184, 193–203.

Feng, G., Mi, X., Yan, H., Li, F.Y., Svenning, J.-C., Ma, K., 2016. CForBio: a network monitoring Chinese forest biodiversity. Sci. Bull. 61, 1163–1170.

Franklin, J.F., Shugart, H., Harmon, M.E., 1987. Tree death as an ecological process. Bioscience 37, 550–556.

Gibert, A., Gray, E.F., Westoby, M., Wright, I.J., Falster, D.S., Wilson, S., 2016. On the link between functional traits and growth rate: meta-analysis shows effects change with plant size, as predicted. J. Ecol. 104, 1488–1503.

Gravel, D., Canham, C.D., Beaudet, M., Messier, C., 2010. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. Oikos 119, 475–484.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145.

Hamilton, D.A., 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. For. Sci. 32, 989–1000.

Hubbell, S.P., Ahumada, J.A., Condit, R., Foster, R.B., 2001. Local neighborhood effects on long-term survival of individual trees in a neotropical forest. Ecol. Res. 16, 859–875.

Hubbell, S.P., Foster, R.B., 1992. Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. Oikos 63, 48–61.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22, 415–427.

Iida, Y., Poorter, L., Sterck, F., Kassim, A.R., Potts, M.D., Kubo, T., Kohyama, T.S., 2014b. Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. Ecology 95, 353–363.

Iida, Y., Kohyama, T.S., Swenson, N.G., Su, S.-H., Chen, C.-T., Chiang, J.-M., Sun, I.F., Zuidema, P., 2014a. Linking functional traits and demographic rates in a subtropical tree community: the importance of size dependency. J. Ecol. 102, 641–650.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104, 501–528.

Johnson, D.J., Beaulieu, W.T., Bever, J.D., Clay, K., 2012. Conspecific negative density dependence and forest diversity. Science 336, 904–907.

Johnson, D.J., Bourg, N.A., Howe, R., McShea, W.J., Wolf, A., Clay, K., 2014. Conspecific negative density-dependent mortality and the structure of temperate forests. Ecology 95, 2493–2503.

King, D.A., Davies, S.J., Noor, N.S.M., 2006. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. For. Ecol. Manage. 223, 152–158.

Kitajima, K., 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98, 419–428.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Penuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.F., Stahl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529, 204–207.

Kushwaha, C.P., Tripathi, S.K., Singh, K.P., 2010. Tree specific traits affect flowering time in Indian dry tropical forest. Plant Ecol. 212, 985–998.

Lebrija-Trejos, E., Wright, S.J., Hernandez, A., Reich, P.B., 2014. Does relatedness matter? Phylogenetic density-dependent survival of seedlings in a tropical forest. Ecology 95, 940–951.

Leemans, R., 1991. Sensitivity analysis of a forest succession model. Ecol. Model. 53, 16.

Lin, Y.-C., Comita, L.S., Johnson, D.J., Chen, M.-R., Wu, S.-H., 2017. Biotic vs abiotic drivers of seedling persistence in a tropical karst forest. J. Veg. Sci. 28, 206–217.

Lu, J., Johnson, D.J., Qiao, X., Lu, Z., Wang, Q., Jiang, M., 2015. Density dependence and habitat preference shape seedling survival in a subtropical forest in central China. J. Plant Ecol. 8, 568–577.

Lugo, A.E., Scatena, F.N., 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. Biotropica 28, 585–599.

Lutz, J.A., Halpern, C.B., 2006. Tree mortality during early forest development: a long-term study of rates, causes, and consequences. Ecol. Monogr. 76, 257–275.

MacArthur, R.H., Levins, R., 1964. Competition, habitat selection and character displacement. Proc. Natl. Acad. Sci. (USA) 51, 1207–1210.

McCarthy-Neumann, S., Kobe, R.K., 2008. Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. Ecology 89, 1883–1892.

McMahon, S.M., Metcalf, C.J.E., Woodall, C.W., 2011. High-dimensional coexistence of temperate tree species: functional traits, demographic rates, life history stages, and their physical context. PLoS One 6, e16253.

Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., Michiels, B., 2005. Size-mediated ageing reduces vigour in trees. Ecol. Lett. 8, 1183–1190.

Mencuccini, M., Martinez-Vilalta, J., Hamid, H.A., Korakaki, E., Vanderklein, D., 2007. Evidence for age- and size-mediated controls of tree growth from grafting studies. Tree Physiol. 27, 463–473.

Mencuccini, M., Oñate, M., Peñuelas, J., Rico, L., Munné-Bosch, S., Salguero-Gómez, R., 2014. No signs of meristem senescence in old Scots pine. J. Ecol. 102, 555–565.

Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion (On the Factor Light in Plant Communities and its Importance for Matter Production). Japan. J. Bot. 14, 22–52.

Munné-Bosch, S., 2008. Do perennials really senesce? Trends Plant Sci. 13, 216–220.

Munné-Bosch, S., 2015. Senescence: is it universal or not? Trends Plant Sci. 20, 713–720.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. 66, 1–43.

Paine, C.E., Norden, N., Chave, J., Forget, P.M., Fortunel, C., Dexter, K.G., Baraloto, C., 2012. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. Ecol. Lett. 15, 34–41.

Pedersen, B.S., 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. Ecology 79, 79–93.

Penuelas, J., Munne-Bosch, S., 2010. Potentially immortal? New Phytol. 187, 564–567.

Piao, T., Comita, L.S., Jin, G., Kim, J.H., 2013. Density dependence across multiple life stages in a temperate old-growth forest of northeast China. Oecologia 172, 207–217.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O., Wright, I.J., 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology 89, 1908–1920.

Poorter, L., McDonald, I., Alarcon, A., Fichtler, E., Licona, J.C., Pena-Claros, M., Sterck, F., Villegas, Z., Sass-Klaassen, U., 2010. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytol. 185, 481–492.

Pu, X., Zhu, Y., Jin, G., 2017. Effects of local biotic neighbors and habitat heterogeneity on seedling survival in a spruce-fir valley forest, northeastern China. Ecol. Evol. 7, 4582–4591.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rees, M., Condit, R., Crawley, M., Pacala, S., Tilman, D., 2001. Long-term studies of vegetation dynamics. Science 293, 650–655.

Rose, K.E., Atkinson, R.L., Turnbull, L.A., Rees, M., 2009. The costs and benefits of fast living. Ecol. Lett. 12, 1379–1384.

Rüger, N., Berger, U., Hubbell, S.P., Vieilledent, G., Condit, R., 2011a. Growth strategies of tropical tree species: disentangling light and size effects. PLoS One 6, e25330.

Rüger, N., Huth, A., Hubbell, S.P., Condit, R., 2011b. Determinants of mortality across a tropical lowland rainforest community. Oikos 120, 1047–1056.

Russo, S.E., Davies, S.J., King, D.A., Tan, S., 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. J. Ecol. 93, 879–889.

Russo, S.E., Jenkins, K.L., Wiser, S.K., Uriarte, M., Duncan, R.P., Coomes, D.A., 2010. Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand. Funct. Ecol. 24, 253–262.

Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27, 213–262.

Shen, Y., Santiago, L.S., Shen, H., Ma, L., Lian, J., Cao, H., Lu, H., Ye, W., 2014. Determinants of change in subtropical tree diameter growth with ontogenetic stage. Oecologia 175, 1315–1324.

Sillett, S.C., Van Pelt, R., Koch, G.W., Ambrose, A.R., Carroll, A.L., Antoine, M.E., Mifsud, B.M., 2010. Increasing wood production through old age in tall trees. For. Ecol. Manage. 259, 976–994.

Sillett, S.C., Pelt, R.V., Carrol, A.L., Kramer, R.D., Ambrose, A.R., Trask, D.A., 2015. How do tree structure and old age affect growth potential of California redwoods? Ecol. Monogr. 85, 181–212.

Stephenson, N.L., Mantgem, P.J.v., Bunn, A.G., Bruner, H., Harmon, M.E., O'Connell, K.B., Urban, D.L., Franklin, J.F., 2011. Causes and implications of the correlation between forest productivity and tree mortality rates. Ecol. Monogr. 81, 527–555.

Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Ruger, N., Alvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, A., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.H., Sun, I.F., Tan, S., Thomas, D., van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507, 90–93.

Thomas, S.C., 1996. Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. Oikos 76, 145–154.

Uriarte, M., Clark, J.S., Zimmerman, J.K., Comita, L.S., Forero-Montana, J., Thompson, J., 2012. Multidimensional trade-offs in species responses to disturbance: implications for diversity in a subtropical forest. Ecology 93, 191–205.

Visser, M.D., Bruijning, M., Wright, S.J., Muller-Landau, H.C., Jongejans, E., Comita, L.S., Kroon, H., 2016. Functional traits as predictors of vital rates across the life cycle of tropical trees. Funct. Ecol. 30, 168–180.

Wang, X., Comita, L.S., Hao, Z., Davies, S.J., Ye, J., Lin, F., Yuan, Z., 2012. Local-scale drivers of tree survival in a temperate forest. PLoS ONE 7, e29469.

Webb, C.O., Gilbert, G.S., Donoghue, M.J., 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. Ecology 87, S123–S131.

Wright, S.J., Muller-Landau, H.C., Condit, R., Hubbell, S.P., 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. Ecology 84, 3174–3185.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., Engelbrecht, B.M.J., Harms, K.E., Hubbell, S.P., Marks, C.O., Ruiz-Jaen, M.C., Salvador, C.M., Zanne, A.E., 2010. Functional traits and the growth-mortality trade-off in tropical trees. Ecology 91, 3664–3674.

Wu, H., Franklin, S.B., Liu, J., Lu, Z., 2017. Relative importance of density dependence and topography on tree mortality in a subtropical mountain forest. For. Ecol. Manage. 384, 169–179.

Zhang, Z., Papaik, M.J., Wang, X., Hao, Z., Ye, J., Lin, F., Yuan, Z., 2016. The effect of tree size, neighborhood competition and environment on tree growth in an old-growth temperate forest. J. Plant Ecol. rtw126.

Zhu, Y., Comita, L.S., Hubbell, S.P., Ma, K., 2015. Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. J. Ecol. 103, 957–966.