



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



Yu Zhu^a, J. Aaron Hogan^b, Huiying Cai^a, Yanhan Xun^a, Feng Jiang^a, Guangze Jin^{a,*}

^a Center for Ecological Research, Northeast Forestry University, Harbin 150040, China

^b International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL 33199, USA

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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.

* Corresponding author.

E-mail addresses: orienton2006@163.com (Y. Zhu), jamesaaronhogan@gmail.com (J.A. Hogan), caihy0606@126.com (H. Cai), violet1711@sina.cn (Y. Xun), jiangf951@126.com (F. Jiang), taxus@126.com (G. Jin).

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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

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