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Effects of gap size and within-gap position on seedling growth and biomass allocation: Is the gap partitioning hypothesis applicable to the temperate secondary forest ecosystems in Northeast China?

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ABSTRACT

Forest gaps can change stand structure and affect forest regeneration dynamics. The gap partitioning hypothesis claims that tree species would regenerate along gap environmental gradients owing to their different resource demands. However, many studies that examined this hypothesis in uncontrolled gap conditions have yielded inconsistent conclusions and there are limited studies testing the hypothesis taking into account biomass allocation. In this study, we examined the gap partitioning hypothesis in a temperate secondary forest ecosystem where gap formation drives forest regeneration. We created gaps with different sizes and planted two commercially important native tree species with contrasting shade tolerance in nine positions along four cardinal directions within the gaps. We found that shade tolerance was the main factor affecting seedling regeneration performance within gaps. For the light-demanding Manchurian walnut (*Juglans mandshurica* Maxim.), seedling growth varied significantly along the light intensity gradients, which indicated that seedlings could greatly benefit from high light areas within gaps, especially when the gap size increased. Seedling biomass in gap centers and transitions (54.0 g) were much higher than in gap edges (13.7 g) and forest understories (8.6 g). High light environments contributed to higher biomass allocation to the leaves and accelerated carbon assimilation. Low light conditions resulted in increasing proportions of stem biomass, which might promote seedling height growth, although the promotion effects were relatively limited. However, for the shade-tolerant Korean spruce (*Picea koraiensis* Nakai), little evidence of seedling divergence was found within gaps. Mostly, seedlings only showed growth and biomass allocation differences between gaps and forest understories. Korean spruce showed high adaptability to various gap environments and might be a generalist species rather than being limited to small gaps. The performance of Manchurian walnut strongly supported the gap partitioning hypothesis, but Korean spruce provided little evidence for gap partitioning. Therefore, planting scenarios in silvicultural practices could be suitably designed, with Manchurian walnut in high light gap areas and Korean spruce in most positions within gaps, during the early stage after competition elimination.

1. Introduction

Forest gaps, openings in the canopy caused by the death of one or more trees, are common small-scale disturbances and play important roles in forest dynamics (Watt, 1947; White, 1979; Runkle, 1981; Brokaw, 1985, Whitmore, 1989). The effects of gaps on species diversity and tree regeneration have been widely reported in various climatic zones (Denslow, 1980b; Runkle and Yetter, 1987; Hubbell et al., 1999). According to the gap partitioning hypothesis, gaps alter the physical structure of forest stands and create a gradient of resource conditions between the gap center and forest understory (Ricklefs, 1977; Denslow, 1980a). The gap partitioning hypothesis suggested that different tree species would regenerate along the resource gradient within gaps based on their ecological requirements, creating the possibility of species coexistence within gaps (Denslow, 1980a; Zhang et al., 2013). In natural conditions, light-demanding species would

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generally regenerate in large gaps, and shade-tolerant species would regenerate in small gaps and forest understories (Denslow, 1980a; Zhu et al., 2014a).

Examinations of the gap partitioning hypothesis mainly focused on natural gaps owing to their wide distribution in forests, and such gaps with different characteristics are easy to come by (Foster and Reiners, 1986; Yamamoto, 2000; Blackburn et al., 2014). However, mixed results were found from such studies. Seedling establishment of different tree species were correlated to gaps with different sizes (Runkle, 1982; Van Couwenberghe et al., 2010), but this phenomenon often occurred among light-demanding species (Busing and White, 1997; Schnitzer and Carson, 2001; Obiri and Lawes, 2004). Other studies suggested that regeneration in gaps followed a chance event and gaps played a neutral role in diversity maintenance (Hubbell et al., 1999; Coates, 2002). For example, Hubbell et al. (1999) monitored more than 1200 gaps and found that species composition was not predictable and gap effects might be masked by recruitment limitation. Different findings in natural gap regeneration probably resulted from uncertain environmental conditions (Sipe and Bazzaz, 1994; Kern et al., 2017). Gaps caused by different forms of disturbances may be significantly different from each other (Miura et al., 2001; Zhu et al., 2017). For example, windstorms mainly created gaps in high altitude forests with steep slopes, whereas floods could lead to large openings with severely eroded soil layers (Zhu et al., 2017). The microenvironments of gaps with uprooted trees, snapped trees, and standing dead trees are different (Schliemann and Bockheim, 2011). Therefore, natural gaps without additional artificial control may not be optimum for testing the gap partitioning hypothesis (Sipe and Bazzaz, 1994), and findings among studies are sometimes difficult to compare because of environmental heterogeneity, such as stand structure and soil types (Van Couwenberghe et al., 2010).

Silvicultural practices based on gap creation have been increasingly suggested to promote forest regeneration and restoration (Coates and Burton, 1997; Schutz, 1999; York et al., 2004; Adamic et al., 2016), which also provides opportunities to test gap partitioning under controlled environmental conditions (Sipe and Bazzaz, 1995; Gray and Spies, 1996; Kern et al., 2013). For example, Kern et al. (2013) established a well-replicated experiment and monitored the natural regeneration in artificial gaps, with a wide size range, for 13 years. They found differences in species composition among gap sizes and along the center-to-edge gradient within large gaps (Kern et al., 2013). However, some artificial regeneration experiments focusing on seed sowing or seedling planting reported that almost all species had positive growth trends (Gray and Spies, 1996; Coates, 2000; York et al., 2004; Walters et al., 2014), although light-demanding species had higher mortality in the shaded portions of the gaps (Coates, 2000). For example, Walters et al. (2014) monitored the height growth of 14 planted species in expanded gaps ranging from 120 to 950 m^2 and found that the relative growth rates increased with gap canopy openness, although the responses of shade-tolerant species were much weaker. Compared with natural regeneration, artificial regeneration could minimize the interference of advance regeneration (Uhl et al., 1988; Forrester et al., 2014), soil seed bank (Yan et al., 2012), and seed trees (Brokaw and Busing, 2000). Thus, controlled experiments are critical for the examination of the gap partitioning hypothesis (Sipe and Bazzaz, 1994).

Previous studies tested the gap partitioning hypothesis by evaluating plant diversity and density (Hubbell et al., 1999; Coates, 2002; Wang and Liu, 2011) or seedling survival and growth (Clarke, 2004; Van Couwenberghe et al., 2010), but few studied seedling biomass and its allocation. Compared with height and diameter, seedling biomass can better reflect the difference between treatments in the field (Weber et al., 2017) or greenhouses (Sevillano et al., 2016). However, the resource gradient within a gap may not be as apparent as the difference in resources between gaps and forest understories, especially when the gap size is not large enough (Powers et al., 2008). Thus, seedlings may not perform differently when the gap size is below some lower limit (de Montigny and Smith, 2017; Lu et al., 2018). Moreover, seedlings are considered to allocate more biomass to organs that can most efficiently acquire light, water, or nutrient resources according to the adaptive strategy (Garnier, 1991). For example, Modrzynski et al. (2015) reported that seedlings growing in high resource conditions increased root biomass at the cost of leaf biomass, regardless of shade tolerance. However, a meta-analysis quantified the patterns of biomass allocation and reported that plants were less able to adjust biomass allocation, but more likely to modify morphological traits (Poorter et al., 2012). Since most studies on the patterns of biomass allocation were conducted under controlled laboratory conditions, it remains unclear whether seedlings could re-allocate the biomass to adapt to various gap environments.

Temperate secondary forests, originating from primary forests after severe deforestation, are the largest forest ecosystems in Northeast China. The poor regeneration of dominant tree species is one of the main challenges that forest managers currently face (Zhu, 2002). Forest gaps resulting from small-scale disturbances provide opportunities for tree species regeneration and have been widely used in silvicultural practices (Coates and Burton, 1997; Schliemann and Bockheim, 2011; Kern et al., 2017). However, studies are needed to further detect the effects of within-gap position on seedling regeneration, which could improve the efficiency of gap usage and seedling planting during forest restoration (York et al., 2004; Knapp et al., 2013). In this study we aim to examine whether the gap partitioning hypothesis can be used in the restoration of secondary forests. The light-demanding Manchurian walnut (*Juglans mandshurica* Maxim.) and shade-tolerant Korean spruce (*Picea koraiensis* Nakai) were selected for the study. Both species are dominant tree species in Northeast China and have important ecological and commercial values. We monitored the growth and biomass allocation of tree seedlings across the resource gradients of gaps by creating gaps of different sizes and planting seedlings in nine positions along four cardinal directions within gaps. Advanced regeneration and herb competition were eliminated to reduce uncertain influences. If the gap partitioning hypothesis was supported, the light-demanding species should have better growth in areas such as the gap centers and northern transitions, and the shade-tolerant species should thrive in shaded areas, such as in the southern edges within gaps. Otherwise, seedlings would perform randomly as the chance event hypothesis (Brokaw and Busing, 2000; Obiri and Lawes, 2004) claims or similarly which indicates limited effects of within-gap positions on seedling regeneration.

2. Methods

2.1. Study area

The study was carried out in Qingyuan Forest CERN, a Chinese Ecosystem Research Network site established by the Chinese Academy of Sciences. The study area is located in a mountainous region of Liaoning Province, Northeast China (41°51′N, 124°54′E), with elevations from 500 to 1100 m above sea level. The climate is a typical temperate continental climate, with a warm and humid summer and dry and cold winter. The mean annual air temperature is 4.7 °C with the coldest month in January (−12.1 °C) and the warmest month in July (21.0 °C). The mean annual precipitation is 811 mm, 80% of which falls during the summer. The growing season begins in April and ends in September (Zhu et al., 2006). The area was dominated by natural broadleaved-Korean pine (*Pinus koraiensis* Sieb. et Zucc.) forests before the 20th century (Zhu et al., 2008). However, most original forests have severely degraded after decades of exploitive timber harvesting (Mason and Zhu, 2014). Currently, the forests are dominated by naturally-regenerated secondary forests (Zhu et al., 2008). The primary natural tree species are painted maple (*Acer mono* Maxim.), ash (*Fraxinus rhynchophylla* Hance), Manchurian walnut (*Juglans mandshurica* Maxim.), Mongolian oak (*Quercus mongolica* Fisch.), *etc.* (Zhu et al., 2014b). There is also a small part of coniferous plantations for timer production. The main plantation species are larches, Korean pine, and Korean