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Restoring temperate secondary forests by promoting sprout regeneration: Effects of gap size and within-gap position on the photosynthesis and growth of stump sprouts with contrasting shade tolerance

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ABSTRACT

To improve the productivity and ecological functions, it is essential to recover secondary forests, the major forest resources in the world, by promoting the regeneration of dominant tree species. Forest gaps are a dominant form of small-scale disturbances in secondary forests, and sprout regeneration commonly occur after the gap formation from logging. Within-gap position and gap size are two key characteristics affecting tree regeneration by changing micro-environments. Promoting the sprout regeneration of dominant tree species under forest gaps with various sizes and within-gap positions is a key measure to recover secondary forests. Twelve artificial gaps were created in March 2015 and the photosynthesis and growth of stump sprouts of three dominant tree species with varying levels of shade tolerance (*Quercus mongolica*, *Acer mono*, and *Tilia mandshurica*) were monitored in 2016. The results showed that within-gap position and gap size had significant effects on the photosynthetic ability of stump sprouts of *Q. mongolica*, i.e., the moderate light condition at the center parts of large gaps was more beneficial to its photosynthesis with the maximum P_{Nmax} of 26.49 μmol m^{-2} s^{-1}. Gap size significantly affected the biomass of stump sprouts of both *Q. mongolica* (shade intolerant tree species) and *A. mono* (intermediate shade tolerant tree species), e.g., the aboveground biomass of these two tree species in large gaps (178.90 g for *Q. mongolica* and 158.42 g for *A. mono*, respectively) were significantly higher than those in small gaps (50.52 g for *Q. mongolica* and 56.95 g for *A. mono*, respectively) ($P < 0.05$). It can be concluded that of the three tree species in this study, only *Q. mongolica* and *A. mono* are sensitive to the changing environments caused by the gap size and within-gap position at the early stage of gap formation, and their photosynthesis and growth can be promoted in large gaps and at the central part of gaps with moderate light conditions. Consequently, when logging trees to create gaps, forest managers can control the gap size and within-gap position where target trees are located to promote their stump sprouts regeneration. This study may provide a new insight for the directed cultivation and restoration of temperate secondary forests.

1. Introduction

Secondary forests, derived from the natural regeneration of primary forests after destructive disturbances (e.g., extreme natural disasters and human activities) (Yan et al., 2010), have become major forest resources in China, accounting for more than 50% of the total area of national forests (Zhu et al., 2007a). Compared with primary forests, several problems have been observed in broadleaved secondary forests, including unoptimizable stand structure, unsuccessful natural regeneration of dominant tree species and unsustainability in both ecosystem services and productivity (Zhu and Liu, 2004; Zhu and Liu, 2007). Moreover, secondary forests are going through a variety of disturbances; forest gaps created by the death or fall of one or more trees (Runkle, 1982) are recognized as a dominant form of small-scale disturbances playing a critical role in forest regeneration and succession in secondary forests (Zhu and Liu, 2004; Kneeshaw and Prévost, 2007; Gendreau-Berthiaume and Kneeshaw,2009; Yan et al., 2010). One principal goal of forestry development is to facilitate the regeneration of dominant tree species to recover secondary forests (Gu et al., 2005; Yan et al., 2010). Therefore, promoting natural regeneration under forest gaps is one of the key measures to achieve this development goal (van Kuijk et al., 2008).

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After gap formation in broadleaved secondary forests, there are two sources of natural regeneration: seed regeneration and sprout regeneration. Seed regeneration can be used to predict the direction of future regeneration (Bellingham, 2000); the regenerated stump sprouts after gap formation can grow much faster than seedlings germinated from seeds to quickly occupy the gap environment (Bond and Midgley, 2001). Previous studies have been concerned on the effects of gaps on seed regeneration (e.g., seed rain, soil seed bank, and seedling emergence from seeds) in forest ecosystems (e.g., Albanesi et al., 2008; Yan et al., 2010, 2012). However, restoration of gaps at the early formation stage in temperate secondary forests may mostly rely on vegetative propagation of species (e.g., sprout regeneration) rather than seed regeneration (Yan et al., 2010). Unfortunately, compared with the achievements on seed regeneration, less is known about the characteristics of sprout regeneration in forest gaps in secondary forests (Feng et al., 2011).

There are some researches on sprout regeneration of woody plants (Tredici, 2001; Mostacedo et al., 2009; Mc Carthy et al., 2014), and most of them have mainly concentrated on sprouting mechanisms (e.g., there are six hypotheses for the sprouting mechanisms of woody plants) (Zhu et al., 2007c), effects of stump traits (e.g., basal diameter and height) on sprout survival and growth (Huang, 1990; Wang et al., 2004), and sprout regeneration after a fire (Vesk and Westoby, 2004). Sprouting in many woody angiosperms is common (Wells, 1969), and the success of sprout regeneration for many woody angiosperms species is important to their regeneration. This is mainly because seedling survival and establishment phases are the key bottlenecks in the seed regeneration processes and strongly rely on both abiotic factors (e.g., the light environment) and inherent biotic factors (e.g., shade tolerance of the tree species and nutrient storage from falling trees/stumps) (Poorter and Kitajima, 2007; Bace et al., 2011). However, sprout regeneration is less restricted by site conditions (Su et al., 2012) due to the fact that sprouts can obtain enough nutrients and micronutrients from stumps or roots to maintain growth (Iwasa and Kubo, 1997; Zhu et al., 2007c).

As two key characteristics of forest gaps, gap size and within-gap position play a crucial role in the natural regeneration of tree species by affecting the gap micro-environment (e.g., Gray and Spies, 1996; Ritter et al., 2005; Albanesi et al., 2008; He et al., 2012; Čater et al., 2014). Variations in gap sizes and within-gap locations first lead to changes in light conditions in forest stands and further affect the spatial and temporal distribution features of other micro-climate factors (Ritter et al., 2005; Zhu et al., 2007b; Albanesi et al., 2008; Latif and Blackburn, 2010; He et al., 2012), and consequently, influence the regeneration in gaps. Present studies have proposed that the photosynthetic active radiance (PAR) value mostly increases and is higher at the northern parts of gaps but is lower at the southern parts of gaps in the northern hemisphere (Zhang et al., 2001; Zhu et al., 2007b). It can be indicated that gap size and within-gap position are the direct "driving forces" for natural regeneration in forest gaps. For the sprout regeneration, it has been indicated that light can facilitate the growth of plant sprouts and can especially promote three growth traits: relative growth rate (RGR), total biomass, and leaf mass per unit area (LMA) (Rydberg, 2000; Kubo et al., 2005). These growth traits can reflect plant adaptability (Reich et al., 2003; Yan et al., 2016) and consequently, enhance seedlings' adaptability in relation to environmental gradients (especially light irradiance levels) (Evans and Poorter, 2001; Jensen et al., 2012). However, little is known about the role of light in facilitating sprout regeneration in terms of photosynthesis. Photosynthesis, which is closely related to the changes in light, is one of the vital physiological processes for seedling growth (Kozlowski and Pallardy, 1997; Jensen et al., 2012). The chlorophyll concentration is an important determinant factor of the light-capturing ability of the leaf, and lower irradiance usually results in a lower chlorophyll content (Kramer and Kozlowski, 1979; Sun et al., 2016). The carotenoid content is closely correlated with light intensity and can protect chloroplasts from damage by high irradiance (He et al., 2010). To promote sprout regeneration in gaps, it is vital to discover how the photosynthesis and growth of stump sprouts respond to variations in the micro-environment caused by gap size and within-gap position.

The main objectives of this study were to: (1) quantify the responses of the sprout regeneration performance (including photosynthesis, foliage traits and growth fitness) of three broadleaved tree species with varying levels of shade tolerance to the changes in the micro-environment caused by varying gap sizes and within-gap positions and (2) determine the optimum size and within-gap position for promoting stump sprout regeneration of these three broadleaved species. This study may provide some scientific references for the restoration of temperate secondary forests by promoting sprout regeneration in forest gaps.

2. Materials and methods

2.1. Study site

The study was carried out at Daxicha (41°50′N, 124°47′E, elevation 600–800 m a.s.l.), 20 km away from Qingyuan Forest CERN, Chinese Academy of Sciences in Liaoning Province, Northeast China. The climate of this area is a continental monsoon type with a strong windy spring, a hot and humid summer and a dry and cold winter. The mean annual air temperature is 4.7 °C, and the extreme temperatures are 36.5 °C in July and −37.6 °C in January. The annual precipitation is 810.9 mm, of which 80% falls during summer from June to August. The frost-free period is approximately 130 days, and the growing season lasts from early April to late October (Yan et al., 2010).

2.2. Gap description

The twelve artificial gaps used in this study were created randomly in typical secondary forests (dominated by *Q. mongolica*, *A. mono* and *Fraxinus rhynchophylla*). Gaps were created on snow-covered ground in March 2015 to reduce the disturbances on the forest floor during logging. We harvested all trees, including saplings and shrubs higher than 2 m to create gaps. All logging materials were removed from the gaps to create a uniform forest floor that only consisted of grasses. There were similar site conditions for these artificial gaps with similar soil types (brown forest soil containing 25.6% sand, 51.2% silt and 23.2% clay (Yang et al., 2013)), topographies (mountains with slope of 18–28°, slope aspect of 158–228°, and mid-slope position), and vegetation compositions, as well as the same history of forest management. The diameter at breast height (DBH) of border trees ranged from 20 to 35 cm. According to the size of each gap, the gap size was classified as: large gap of the size > 600 m^2, medium gap of the size 300–600 m^2, and small gap of the size < 300 m^2. Four gaps for each size category, and the basic description of these twelve experimental gaps was shown in Table 1.

2.3. Experimental design

A preliminary investigation of all tree stumps within gaps was conducted in 2015 after logging to ascertain the basic information (e.g., tree species, stump diameter and height, within-gap location). According to this investigation, we selected three tree species with varying levels of shade tolerance (shade intolerant species: *Q. mongolica*; intermediate shade tolerant species: *A. mono*; shade tolerant species: *T. mandshurica*) as subjects in the present study (Shi et al., 2006; Wu et al., 2013; Yan et al., 2016). Because of the limitation on the inherent positions of these tree stumps in gaps, our experimental stumps with sprouts of the three tree species were only chosen from five within-gap positions (subareas) (north, south, east, west and center) (Fig. 1) in large-medium gaps (476–984 m^2) to test the effects of the within-gap position on sprout regeneration. To determine the within-