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Responses of seedling performance to altered seasonal precipitation in a secondary tropical forest, southern China



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ABSTRACT

Given the intensified global climate change, understanding the responses of seedlings in tropical forests to changing precipitation patterns is critical for predicting plant community regeneration. In a field study, we investigated the potential effects of changes in seasonal precipitation on seedling establishment and growth of Cinnamomum burmanni, a dominant tree species in a secondary tropical forest, southern China. The field precipitation treatments included ambient rainfall (CT), increased precipitation (IP) in the wet season, and extended dry (ED) season without change in annual rainfall. For the IP treatment, 25% of the mean annual precipitation was added in the wet season using pumps and sprinklers. For the ED treatment, 60% of incoming throughfall was removed in March and April to extend dry season for two months using transparent roofs, and re-added back in October and November with the total annual rainfall amount not changed. The results showed that the IP treatment increased seedling height growth in June and August when extra water was applied. By the end of experiment, stem biomass was significantly greater in IP plots than in ED plots. Precipitation treatments also affected biomass allocation. Seedlings in ED plots had a lower root/shoot ratio and root mass to total mass ratio. Compared to the control, the IP treatment significantly increased leaf and stem nitrogen concentrations of the seedlings. Nitrogen and phosphorus contents in stems and roots were much higher in IP plots than in ED plots, which might be explained by the increased NO3⁻-N and available phosphorus concentrations in soil. Our findings indicate that extended dry season without change in annual rainfall or increased precipitation in the wet season induced by climate change, is likely to affect soil nutrients, seedling biomass accumulation and partitioning, and nutrient uptake, and thereby impact regeneration dynamics and future community structure in tropical forests.

1. Introduction

During plant recruitment, seedling establishment and growth are affected by many biotic and abiotic factors such as climate, soil conditions, and interspecific competition (Olano and Palmer, 2003; Wang et al., 2009). Among the climatic factors, precipitation and soil water availability greatly affect seedling survival, height, biomass production and nutrient uptake (Knapp et al., 2002; Wullschleger and Hanson, 2006; Achten et al., 2010; Chaturvedi et al., 2013; February et al., 2013). Because their root systems are limited, seedlings are always drought-sensitive, and seedling establishment process is vulnerable to long dry periods (Fortini et al., 2010). Seedlings may adapt to variations in water availability through morphological and physiological responses (Joslin and Wolfe, 1998; Achten et al., 2010). The functional equilibrium theory suggests that plants are preferentially allocated more biomass towards roots when belowground resources such as soil nutrient and water are in low status (Brouwer 1962). For example, plants can tolerate drought by reducing leaf area and maintaining a high root/stem biomass ratio (Li et al., 2008).

With global warming, precipitation regimes (e.g., precipitation amount, intensity and timing) are expected to change worldwide because of alterations in global air circulation and hydrologic cycle patterns (Easterling et al., 2000). In many regions including most tropical areas, some climate-change models or observations have indicated that durations of dry seasons may increase in the coming decades (Huntington, 2006; Durack et al., 2012). Researches have also predicted

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increases in mean annual precipitation and in heavy rainfall events in the tropics (Dore, 2005; Meehl et al., 2005; May, 2008; Mailhot et al., 2010). Change in precipitation regimes was found have profound influences on terrestrial ecosystems. For example, repeated drought conditions would lead the functional composition of tropical forests to smaller and denser-wooded trees (Phillips et al. 2010). In a review paper, Wu et al. (2011) indicated that reduced precipitation could inhibit plant growth and ecosystem carbon fluxes, and suppress aboveground net primary production and net ecosystem change.

Given the importance of tropical forests for local and global climate regulation, carbon storage, air and water purification (Brown and Lugo, 1990; Dixon et al., 1994), researches have evaluated the effects of altered precipitation on tropical vegetation (e.g., Nepstad et al. 2007; Hiltner et al., 2016; Souza et al., 2016). Some of this research has focused on seedlings because seedling recruitments greatly affect forest regeneration and determine community composition in the future. In both Panamanian and Amazonian tropical forests, for example, irrigation during the dry season enhanced seedling growth and diversity, indicating that variation in precipitation and related water availability can affect seedling community structure (Bunker and Carson 2005; Paine et al., 2009). Similarly, Song et al. (2016) reported that the seedling community and soil moisture varied seasonally, with seedling abundance and species richness dramatically lower during the dry season period than in the wet season in tropical montane forests. In a recent study in tropical Asia, simulated drought inhibited seedling growth, but some species compensated for the slow growth during the drought with faster growth after the drought, suggesting that seedling communities may be able to adapt to the predicted scenario of frequent drought conditions (O'Brien et al., 2017). Although researchers have studied the effects of drought stress on seedling performance, our understanding of how tropical seedlings respond to changes in seasonal precipitation patterns is still limited.

Tropical forests in Asia have distinct ecosystem functions and provide distinct ecological services (Corlett and Primack, 2006). In southern China, most of the existing tropical forests are secondary forests that developed on degraded land (Ren et al., 2007). Within this region, long-term field observations have shown that, since around 1980, the total annual precipitation has changed little but the number of days with no rain or less than expected rain has increased in the dry season occurred (Zhou et al., 2011), suggesting that forests may be increasingly subjected to drought conditions for longer prolonged durations than in the past. How a change in the intra-annual seasonal precipitation pattern, including an extended dry season and an increased precipitation induced by the occurrence of extreme rainfall events during the wet season, affects seedling performance during the regenerative phases is still not clear.

In this study, we conducted a manipulative experiment with altered seasonal precipitation (i.e. extended dry season without change in annual rainfall amount, and increased precipitation in the wet season) in a secondary tropical forest in southern China, with the aim to evaluate their potential effects on seedling establishment and growth of Cinnamomum burmanni, a shade-tolerant and widely distributed dominant tree species. The main objective of this study was to improve our understanding of how the seedlings of a tropical forest species would respond to seasonal precipitation changes. During plant recruitment, seedling survival, height, biomass production and partitioning, nutrient uptake were important determinants for seedling establishment. In response to variations in water availability, seedlings may alter their morphological characteristics to adapt these environmental changes. Specifically, we addressed the following questions: (1) Do the responses of seedling height growths differ between the altered seasonal precipitation treatments? (2) How do the changed precipitation patterns affect biomass accumulation and allocation, morphology and nutrient uptake of transplanted seedlings?

2. Materials and methods

2.1. Study site and target species

This study was carried out at the Xiaoliang Research Station for Tropical Coastal Ecosystem, Chinese Academy of Sciences (110°54'E, 21°27'N), Maoming City, Guangdong Province, South China. This area is characterized by a tropical monsoon climate with a mean annual temperature of 23 °C. Annual rainfall ranges from 1400 mm to 1700 mm with a distinct variation of dry and wet seasons, and most rainfall occurs from March to September. The soil is latosol that developed from granite. The original top soils were mostly eroded due to long-term anthropogenic disturbances. By 1959, the study area had deteriorated into barren land. Our experiment was conducted in a restored mixednative evergreen broad-leaved forest. The forest started as Eucalyptus exserta plantation in 1959 from the barren land, and native tree species were introduced between 1964 and 1975 (Ren et al., 2007). Currently, the dominant tree species are C. burmanni, Schefflera octophylla, Carallia brachiata and Symplocos chunii. The understory is dominated by the fern Dicranopteris dichotoma. In this study, we focused on the seedling establishment and growth of the dominant tree species, C. burmanni. Cinnamomum burmanni, which belongs to the Lauraceae family, is a shade-tolerant and long-lived tree species that can reach the height of 14 m. It grows well on acidic soil and in humid microhabitats, and is widely distributed in the secondary tropical forests in southern China. In the experimental forest, C. burmanni had the greatest important value among the existing plant species.

2.2. Experimental design

The experiment had a randomized complete block design with four replicate blocks in the experimental forest. In each block, three 12×12 m plots were established with at least a 4-m buffer zone between each two plots. The seasonal precipitation treatments including three levels: extended dry season without change in annual rainfall amount (ED), increased precipitation in the wet season (IP), and ambient precipitation as the control (CT). The simulated precipitation patterns were selected based on ongoing climatic change in the study region (Zhou et al., 2011) and climate model simulations (Meehl et al., 2005) that predict an extended drought period for the dry season and increased precipitation during the wet season. In the ED treatment, the dry season was extended two months (to late April) by preventing 60% of the throughfall from reaching the understory; the quantity of throughfall removed in spring was applied as irrigation at the start of the dry season during October and November as described later in this section. In the IP treatment, extremely heavy precipitation events were simulated in the wet season (between June and August) by irrigation as described later in this section. The CT plots received the ambient rainfall inputs. Within each block, the three precipitation treatments were randomly assigned to one of the three plots.

In each ED plot, a partial throughfall exclusion infrastructure was used throughout the first two months of the wet season (from March 1 to April 30). The structure consisted of a suspended, movable, transparent plastic roof and plastic-lined rain gutters in the understory. The transparent roofs intercepted 60% of incoming throughfall but allowed ambient light to penetrate to the forest floor. Twelve polyurethane panels ($0.6 \text{ m} \times 12 \text{ m}$) as throughfall intercepted roofs were suspended in rows and mounted on a steel frame approximately 2.5 m above the ground. The gutters were located on the edges of the plot where they collected the water that ran off the panels. During the ED treatment period (from early March through late April), the panels were opened so that they intercepted the throughfall, which gravity then moved to the gutters and then to pipes that released the water outside of the experimental site. After April, the panels were closed so that the ED plots received ambient throughfall. Stemflow, which also contributes to the total precipitation reaching the forest floor, was not manipulated or

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