

Enhanced sprout-regeneration offsets warming-induced forest mortality through shortening the generation time in semiarid birch forest

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ABSTRACT

Warming-induced mortality and a decline in regeneration potential have recently been observed in semiarid forests. To understand future forest dynamics, studies have begun to examine the long-term resilience of semiarid forests against climate change. Previous research has documented a relatively high resilience through seedling production for patchy coniferous forests at the arid timberline compared to continuous and arid tree line forests. However, it remains unclear whether broad-leaved forests in semiarid regions share the same pattern and how they work. In this study, we observed a similar nonlinear pattern in forest resilience along a local aridity gradient by reconstructing the regeneration history and investigating post-mortality regeneration in white birch-dominated (*Betula platyphylla*) forests in semiarid Inner Asia. Changes in regeneration modes from seedling to sprout production accelerated the white birch regeneration process and speeded up tree replacement. High competition from abundant recruits enhanced both forest resilience and resistance to climate change in arid timberline forests. However, only weak resilience was observed in birch forests at the arid tree line, which stopped regeneration and meant that old trees dominated the age structure. This might increase the risk of hydraulic failure. Our results implied that the decline in regeneration potential was not consistent in semiarid regions. Although forest mortality increased along with aridity, some broad-leaved forests at the arid timberline have a high resilience because they generate abundant sprouts to compensate for the losses from forest mortality. This study shows that a similar resilience pattern occurs under the impact of climate change and that various resilience mechanisms are affected by the different biological features of coniferous and broad-leaved forests in Inner Asia, which have important implications for future forest dynamics in semiarid regions and provide scientific background for managing this vulnerable forest and important insights into persistence of forests in semiarid Inner Asia.

1. Introduction

Semiarid forests represent the arid limit of forest vegetation (Chenlemuge et al., 2015). They are sensitive to climate change and have potentially large impacts on the local climate and the global radiation budget (Rotenberg and Yakir, 2010). Forest decline and mortality caused by elevated temperatures and water stress have been widely documented in semiarid regions (Allen et al., 2010; Anderegg et al., 2013; Kharuk et al., 2013; Liu et al., 2013; Worrall et al., 2013). Any predictions about forest dynamics under future climate change need to involve tree regeneration that compensates for forest losses following periods of increased tree mortality. The equilibrium between mortality and regeneration processes is considered to represent

semiarid forest resilience against climate change (Xu et al., 2017). Along aridity gradients, water-deficits separate continuous forests into forest patches within the arid timberline ecotone, and are followed by a further shift to a sparse savanna-like pattern beyond the aridity limits for forest vegetation, which is considered to be the arid tree line (Stevens and Fox, 1991; Xu et al., 2017). In a previous study, we observed a relatively higher resilience in arid timberline forests than in continuous forests and at the arid tree line. This resilience was co-affected by local aridity and forest patch size (Xu et al., 2017). However, the above results only focused on coniferous forests in semiarid southern Siberian areas, but the resilience to climate change of broad-leaved forests, which are widely distributed in the semiarid regions of the northern hemisphere, remains unclear.

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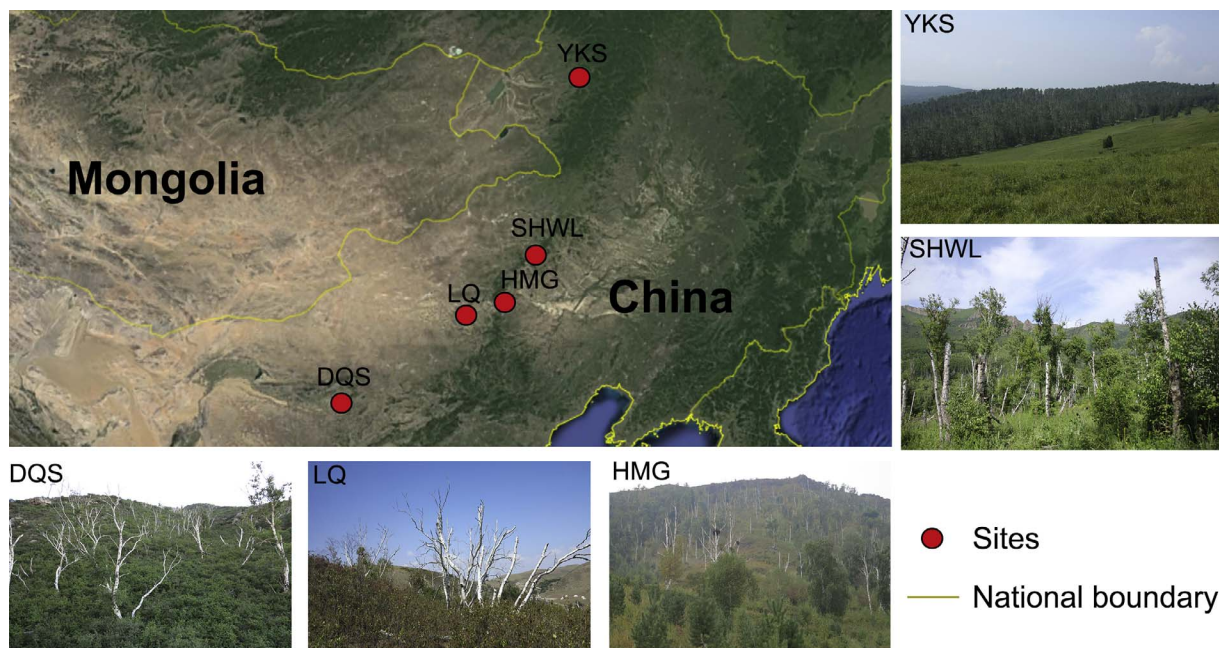


Fig. 1. Study area and locations of sampling sites (red dots). Photographs from top right corner to bottom left corner show forest mortality at each site (taken in 2014 and 2015). Site-ID were the abbreviations of the nearby places: YKS – Yakeshi; SHWL – Saihanwula; HMG – Huamugou; LQ – Lanqi; DQS – Daqingshan. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Broadleaf tree species in semiarid forests have some biological features that are different from conifers and possibly have impacts on their resilience. For instance, most broadleaf tree species can sprout vigorously in stressful sites or sites that suffer from frequent disturbances (Burrows, 1990; Bond and Midgley, 2001; Del Tredici, 2001). Compared with seed-origin seedlings, sprouts are more resistant to disturbance, can grow rapidly, and are not restricted by the local site environment (Keeley, 1992; Bellingham et al., 1994; Bellingham and Sparrow, 2000; Bond and Midgley, 2001). Therefore, sprouting ability plays an important role in the conservation and management of tree species. They can buffer regeneration failure after severe disturbance and minimize the dependence on seeds for population maintenance (Bond, 1994; Higgins et al., 2000). A previous study has shown that the clone size of the same species was much higher in arid regions than under wetter, forest conditions (Kemperman and Barnes, 1976). However, we know little about how aridity affects the shift between the two broadleaf tree species regeneration modes in semiarid regions. Furthermore, the relatively short life span of some broadleaf tree species may mean that tree age has an important effect on their mortality and regeneration in semiarid regions (Loehle, 1988). For example, the mortality of white birch (*Betula platyphylla*) and trembling aspen (*Populus tremuloides*) has been shown to be negatively affected by climate change (Allen et al., 2010; Worrall et al., 2010, 2013, 2015; Kharuk et al., 2013; Liu et al., 2013). However, the age effect on climate-induced mortality was hard to exclude in some studies because the mean age of the dead trees was near the limit of their life span (Loehle, 1988; Cameron, 1996; Kharuk et al., 2013; Perrette et al., 2014). Therefore, it is difficult to distinguish whether the severe mortality of short-life tree species was the result of climate change or natural old-age connected death. Previous studies have documented that tree age also had a close relationship with the sprouting and regeneration abilities of broadleaf tree species (Lust and Mohammady, 1973; Kays and Canham, 1991; Johansson, 2008). In some species, sprouting ability increases with size to reach a maximum during the adult stages, although in other species the sprouting capacity of a tree decreases with age (Lust and Mohammady, 1973; Bond and Midgley, 2001). Therefore, resilience evaluations of broad-leaved forests in semiarid regions need to consider the effects of local aridity and forest patch size. In addition, biological

features, such as tree age and regeneration modes, need to be taken into account.

In this study, we chose white birch, which is a representative broadleaf tree species that dominates in forests of semiarid Inner Asia. Its characteristics include rapid growth, high sprouting ability, and a short life span. We hypothesized that white birch-dominated forests in semiarid regions were resilient to climate change from a long-term perspective, and that there was effective recruitment to compensate for forest loss due to mortality. Furthermore, we hypothesized that both climatic variables and biological features co-determined the resilience pattern of white birch forests. We evaluated the resilience of white birch-dominated forests in the semiarid regions of Inner Asia by developing a chronology and investigating the regeneration status following episodes of mortality. To test the above hypothesis, we compared the differences in forest resilience, indicated by forest mortality, regeneration, and growth, at five sites that were located from the arid timberline to the arid tree line, in order to ascertain how climate, patch size, and tree age affect forest resilience in Inner Asia.

2. Materials and methods

2.1. Study area and field work

The forest–steppe ecotone in China is a representative of semiarid Inner Asia and extends from the boreal zone in northeast China, through the Inner Mongolia and Loess Plateaus, and finishes on the eastern edge of the Qinghai-Tibetan Plateau in the subtropical zone of southwest China (Department of Geography, Northwest University, 1984; Liu et al., 2015). Our study area was located in the forest-steppe ecotone that extends from the Great Hinggan Mountains to the Yinshan Mountains (Fig. 1). White birch is the dominant tree species in forests of this region. The study sites are located within elevations of about 790–1780 m a.s.l. Mean annual temperature is about -2 to 6°C , and mean annual precipitation is about 350–410 mm (Table 1).

Five sites along an aridity gradient were sampled in this region during 2014 and 2015 (Table 1). The YKS site was near continuous forest, the SHWL and HMG sites were at the arid timberline, and the LQ and DQS sites were near the arid tree line. Three plots that had similar

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