Forest Ecology and Management 310 (2013) 740–746

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Short-term dynamic shifts in woody plants in a montane mixed evergreen and deciduous broadleaved forest in central China

Jielin Ge [a,b], Gaoming Xiong [a], Changming Zhao [a], Guozhen Shen [a], Zongqiang Xie [a,*]

[a] State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing 100093, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Article history:
Received 10 June 2013
Received in revised form 10 September 2013
Accepted 11 September 2013
Available online 4 October 2013

Keywords:
Successional groups
Size distributions
Ice storm
Permanent plot
Demographics
Mortality

ABSTRACT

The composition and structure in many forests is drifting across the world, although the causes of these changes remain unclear. We studied species turnover, mortality and recruitment, and population dynamism for different successional groups based on three datasets collected between 2001 and 2010 from a permanent 120 m × 80 m plot in a *Fagus engleriana–Cyclobalanopsis multinervis* mixed forest patch in central China, to identify trends in forest change and explore the possible effects of ice storm in 2008 on forest dynamics. The majority of woody species in this forest belonged to early- and late-successional species and the proportion of evergreen species was lower than that of deciduous in terms of species richness. Floristic composition showed minor structural and compositional changes with no shift in the rank of importance value index among different successional groups, over the study periods, whereas stem density and basal area changed markedly between 2006 and 2010, probably as a consequence of the ice storm in 2008. Size distributions of living individuals were similar between census intervals for all successional groups, approximating an inverse J-shaped distribution for early- and late-successional species groups and a bell-shaped distribution for pioneer species, whereas size distributions of dead individuals varied significantly for all successional groups. Furthermore, patterns of mortality and recruitment displayed disequilibrium behaviors over the investigated period with mortality surpassing recruitment for all successional groups during the final census. Surprisingly, diameter growth rates reached a maximum during the final census interval (2006–2010) among all successional groups. All successional groups also showed size-dependent growth with maximal growth rates attained among the largest-sized classes except for pioneer species, which exhibited the highest growth rates at mid-sized classes. Moreover, ice-storm in 2008 also accelerated dynamisms among successional groups to different extents. The dynamism gauged by stem density was significantly lower than that based on basal area among successional groups during 2001–2006 but the reverse situation was observed in the later census interval, demonstrating the divergence in diameter growth rate but not in recruitment individuals between the two census intervals made large contribution to this observation. Taken together, these results indicate that despite the 2008 ice-storm this forest was generally resilient, undergoing only minor structural and compositional shifts, although an accelerated rate of forest dynamism among successional groups was linked to the period that included the ice storm. Therefore, long-term observation is needed to further reveal direct evidence of relationships between disturbance and forest dynamics.

1. Introduction

The understanding of forest dynamics or turnover is based on measurements of mortality, recruitment and growth rates of individual plants. These demographic parameters are essential for forecasting how forest ecosystem may respond to global climatic change (Phillips and Gentry, 1994; Fauset et al., 2012) and extreme climatic events (Condit et al., 1992; Lloret et al., 2012).The issue is particularly significant when conceptualizing forest conservation and management strategies (Hubbell and Foster, 1992).

Long-term vegetation monitoring has been undertaken in various forests around the world, particularly in tropical areas (Rees et al., 2001; Laurance et al., 2004; Feeley et al., 2011; Fauset et al., 2012; Holzmueller et al., 2012; Marimon et al., 2012; van den Berg et al., 2012; Weckel et al., 2006), and an increasing number of studies have shown that forests have undergone dynamic widespread directional shifts in composition and structure (Phillips et al., 2004; Lewis et al., 2009; Enquist and Enquist, 2011; Feeley et al., 2011; Peng et al. 2011; Fauset et al., 2012; Kucbel et al., 2012). In contrast, comparable ecological information for montane

* Corresponding author. Tel./fax: +86 10 62836284.
E-mail address: xie@ibcas.ac.cn (Z. Xie).

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http://dx.doi.org/10.1016/j.foreco.2013.09.019

forests is limited, especially in central China, despite well-established records of floristic composition in this region (Zhao et al., 2005).

The capacity for natural disturbances and episodic events to disrupt forest dynamics, shifting structure and community composition have become increasingly apparent in recent years (Takahashi et al., 2003; Woods, 2004; Beaudet et al., 2007; Belote et al., 2012; Holzmueller et al., 2012), with each resident species responding in different ways. Examples of such an extreme, episodic event in this region are infrequent, but often devastating ice storms (Zhou et al., 2013b). Vegetation responses vary widely, depending on both the magnitude and specific timing of these events, in relation to the forest stand structure and species composition (Hooper et al., 2001; Hopkin et al., 2003; Lafon, 2004; Takahashi et al., 2007). While pioneer species may prove most vulnerable to these effects, these events can also allow more resistant late-successional species gain a competitive advantage, in response to light gaps, accelerating forest structure and composition advancement toward later successional stages (Lemon, 1961). An alternative proposition is that if damage to the canopy is extensive, the extra light this allows to reach forest floor, permits germination and establishment of pioneer species (Du et al., 2012). Any rapid reproduction and growth of these pioneer species can then retard succession and shift the forest to an earlier successional stage (Siccama et al., 1976). It is therefore essential to try to better understand the range of outcomes associated with ice-storms and how drivers of forest composition.

Previous studies on these effects have concentrated on the immediate susceptibility of tree species to ice damage (Hooper et al., 2001; Takahashi et al., 2007). Bragg et al. (2003) and Hopkin et al. (2003); further report how elevation, and topography influence ice deposition, and the associated responses of forest understory seedling or sapling density. To our knowledge, no available studies have systematically investigated the effects of ice storms on the forest successional dynamics with reference to established permanent plots records, as we do here, reporting the impacts of an unprecedented catastrophic ice storm that hit a broad band of subtropical China from 10 January to 6 February 2008. This event caused massive mechanical damage in these natural broad-leaved forests (Stone, 2008), providing a unique opportunity to document the effects of an extreme event on forest dynamics.

The montane mixed evergreen and deciduous broadleaved forest is the zonal vegetation type in the northern subtropical zone of China. Literature on the dynamics and ecology of this forest type is scarce and inventory data are limited. This forest displays one of the highest levels of biodiversity in the world and thus is considered extremely vulnerable to global change (Myers et al., 2000). Although human pressure has probably played a major role in the disappearance and fragmentation of these montane forests, climate change is undoubtedly having a major impact on them (Zhao et al., 2005).

Our principal objective was to identify how forest dynamics changed during the period from 2001 to 2010, with particular regard to the 2008 ice-storm event. We ask: (1) How was species composition and dominance among successional groups in this forest affected by this event (2) How did the ice storm affect specimen plant size and distributions among successional groups? and (3) Is susceptibility to ice storm different among successional groups?

2. Materials and methods

2.1. Study site

The study area was located on the southern slope of the Shennongjia region (31°19′4″N, 110°29′44″E), north-west of Hubei Province, central China. This region is in the transition zone between the subtropical and warm temperate climates, and so it is an important biodiversity conservation hotspot in both China and globally (Myers et al., 2000). The annual precipitation of this area is 1306–1722 mm and the mean annual temperature is ca. 10.6 °C.

In 2008, an intense storm occurred in this region. According to weather record of National Field Research Station for Forest Ecosystem in Shennongjia, Hubei, China, located at 1290 m, the snowfall during the storms of January 2008 was 30% higher, minimum daily air temperature was 4 °C lower, and it snowed and/or was misty on twice (up to 28 days) as many days. The trees remained covered with snow and hard rime ice during the storms (Li et al., 2009).

At this site, five soil classes conform with elevation: mountain yellow brown soil (600–1500 m), mountain brown soil (1500–2200 m), mountain dark brown soil (2200–2900 m), brown coniferous forest soil (>2900 m) and mountain meadow soil (>1700 m). Vegetation type also varies along this elevational gradient, from evergreen broad-leaved forests at low elevations to mixed evergreen deciduous broad-leaved forests, mixed coniferous and broad-leaved forests, coniferous forests at higher elevations (Zhao et al., 2005). The zonal vegetation community reported here is *F. engleriana*–*C. multinervis* mixed forest, a montane mixed evergreen and deciduous broad-leaved forest.

2.2. Methods

2.2.1. Tree census

In order to monitor forest development, a 120 m × 80 m permanent plot divided into 96 contiguous 10 m × 10 m subplots was established within representative forest patch in 2001. Data were collected following the standard census protocol of the Center for Tropical Forest Science network (Condit, 1998). All woody stems equal to or greater than 4 cm diameter at breast height (dbh) were identified, labeled and mapped and their dbh were measured to the nearest centimeter.

In 2006 and 2010 all tagged individuals were re-censused for dbh and their condition determined (live or dead). For new recruits, those woody stems that had attained 4 cm were identified, tagged and their dbh was measured.

2.2.2. Data analysis

Guidance from literature reviews was used principally to classify the species into different successional groups: pioneer, early- and late-successional species (Appendix A) (Wu, 1980; Peng et al., 1998; Zhang and Chen, 2000; Xiong et al., 2002; Yu et al., 2002). Analyses included: (1) floristic changes including stem number, basal area and mean stem diameter; (2) turnover (mortality and recruitment); (3) size distributions of living and dead individuals; (4) diameter growth rate; and (5) dynamism.

Importance Value Index (IVI) for the different successional groups was calculated as followed: IVI = [relative density + relative basal area + relative frequency]/3 × 100 (Lévesque et al., 2011); the annualized rate of mortality (m) and recruitment (r) following the standard models: $m = (\ln(N0) - \ln(Ns))/t \times 100$; $r = (\ln(Nt) - \ln(Ns))/t \times 100$; where N$t$ and N0 represent the size of the successional group at time t and time 0, respectively, and Ns represents the number of survivors at time t (Laurance et al., 2004). Specific successional group dynamism (D) was calculated as the average of the recruitment (r) and mortality (m) for the study period. Half-life time ($t0.5$), the time that would take for a given successional group to lose 50% of all its individuals, was calculated as follows: $t0.5 = (\ln 0.5)/\ln(1 - m)$ (Cascante-Marín et al., 2011), and double-time ($t2$), as the time that specific successional group take to double, expressed: $t2 = \ln(2)/\ln(1 + r)$ (Saiter et al., 2011). The turnover time and stability time were obtained from the mean