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Disturbance history and natural regeneration of an old-growth Korean pine-broadleaved forest in the Sikhote-Alin mountain range, Southeastern Russia

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ABSTRACT

We used a dendroecological approach to reconstruct the disturbance history of the old-growth Korean pine (*Pinus koraiensis* Siebold et Zucc.)-broadleaved forest in the southern part of the Sikhote-Alin mountain range (Southeastern Russia). We also performed a point pattern analysis to study the population structures of the five dominant tree species, and our findings demonstrate that there were no intense, stand-replacing disturbances from 1800 to 2000. Low- and medium-intensity disturbance events predominated, and the most probable cause of these disturbances was windthrow due to strong winds. The age structure of the coniferous species indicates recruitment continuity, so the stand is unevenly aged, but regeneration waves associated with the disturbances can be distinguished. The population structure of the dominant species is characterized by similar features, and the aggregate distribution pattern is typical of immature plants. The virginal and generative plants of most species are uniformly distributed, but the generative individuals of some species tend to be hyperdispersed over a small spatial scale. The advanced regeneration pool is mostly composed of immature plants of both shade-tolerant coniferous and light-demanding deciduous species, which confirms that immature deciduous species are characterized by significant shade tolerance, although to a lesser extent than coniferous plants. In virginal plants, light demand is greater for both coniferous and deciduous species. The populations of the dominant species are stable, so the current disturbance regime promotes the coexistence of shade-tolerant and light-demanding species but affects the abundance of the various plant species in the stand.

1. Introduction

Natural disturbances play a crucial role in the dynamics of forest communities; they affect the regeneration and growth of tree, shrub and other species as well as their coexistence, eventually influencing species diversity (Frelich and Lorimer, 1991; Abrams et al., 1999; Ishikawa et al., 1999; Kubota, 2000; Bergeron et al., 2004). Research into the disturbance history of forest communities is necessary to understand how modern stands were formed and to predict their future structure and species composition (Girardin et al., 2001; Kuuluvainen, 2002; Dang et al., 2009; Zhang et al., 2014). Various dendroecological approaches based on the dating of growth releases are used to reconstruct stand histories and disturbance regimes. Improved conditions for growth typically occur when canopy gaps are formed (Lorimer and Frelich, 1989; Frelich and Lorimer, 1991; Brisson et al., 1992; Tardif et al., 2001; Black and Abrams, 2003; Fraver and White, 2005).

In mixed forests, variations in disturbance intensity promote the coexistence of species with different life strategies and ecological characteristics (Runkle, 1985; Liu, 1997; Bergeron, 2000). In closed-canopy temperate forests, disturbances vary from small canopy gaps formed by the loss of one or several trees to large-scale, stand-replacing events (Runkle, 1985; Runkle and Yetter, 1987; Foster et al., 1998; Romme et al., 1998; Turner et al., 1998; Ilisson et al., 2005; Margolis et al., 2007). Variations in the intensity, frequency, and spatial distribution of disturbances have a spatio-temporal effect on the regeneration, growth, and survival of trees (Liu, 1997; Mori and Takeda, 2004). Regeneration of certain tree species, in turn, can affect future disturbance regimes, because tree species have differences in their life-span and resistance to various factors of disturbances (e.g. strong winds). Species with different life strategies exhibit various responses to differences in

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gap size and disturbance intensity depending on their ecological characteristics, such as shade tolerance and regeneration strategy (Runkle and Yetter, 1987; Bergeron et al., 1998; Drobyshev, 1999). Shade-tolerant species typically have an advantage due to advanced regeneration as rather small canopy gaps are sufficient for their development. In contrast, light-demanding species are characterized by more rapid growth, but they require much larger canopy gaps for establishment (Runkle and Yetter, 1987; Kobe et al., 1995; Liu, 1997). However, this pattern can be more complex because the light demand of an individual plant changes during development as it passes through different ontogenetic stages. In particular, light-demanding species can be characterized by higher shade tolerance in early ontogenetic stages, and shade-tolerant species may require a significant amount of light to sustain their growth at certain life stages (Evstigneev, 1991; Lebedev and Chumachenko, 2002). As a result, the spatiotemporal diversity of disturbance events allows species from both groups to stably coexist within forest communities.

Korean pine (*Pinus koraiensis* Siebold et Zucc.)-broadleaved forests are the main forest vegetation type in the Sikhote-Alin mountain range of the southern portion of the Russian Far East. This area is the northeastern limit of the range of Korean pine-broadleaved forests, which are also found in northeastern China (the central part of the range), on the Korean peninsula, and in Japan. The Sikhote-Alin mountains is one of the few places where significant areas of old-growth Korean pine-broadleaved forests remain. In the absence of volcanic activity, which is a source of strong natural disturbances in the central part of the range (Liu, 1997; Ishikawa et al., 1999; Dai et al., 2011), wind is the primary disturbance factor on this territory. Wind causes a wide range of disturbance events, from individual tree falls to large blowdowns (Dai et al., 2011). According to the published data, large canopy gaps are crucial for the survival of light-demanding species, such as Yellow birch (*Betula costata* (Trautv.) Regel.) and Amur linden (*Tilia amurensis* Rupr.) in Korean pine-broadleaved forests (Ishikawa et al., 1999). Smaller gaps promote the regeneration of mid-tolerant Korean pine (Ishikawa et al., 1999; Dai et al., 2011), but Yezo spruce (*Picea jezoensis* (Siebold et Zucc.) Carr.) and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim) are less dependent on canopy disturbances due to their shade tolerance (Yang et al., 1994; Okitsu et al., 1995; Liu, 1997; Ishikawa et al., 1999).

There is almost no historical information on disturbances in the Sikhote-Alin mountain range, which is a significant impediment to the analysis of data obtained from dendroecological approaches and the investigation of the dynamics of forest communities in general.

In this work, we studied the disturbance history and regeneration dynamics of old-growth Korean pine-broadleaved forest, which is the most typical vegetation type of the southern Sikhote-Alin mountain range. Our primary objectives were (1) to reconstruct the local history of the natural disturbances that have shaped the stand and controlled its dynamics over the last two centuries and (2) to understand the relationship between the disturbance history and the current species composition of the stand.

2. Materials and methods

2.1. Study area

We studied the western macroslope of the southern part of the Sikhote-Alin mountain range (Southeastern Russia) at the Verkhneussuriysky Research Station of the Institute of Biology and Soil Science, Far East Branch of the Russian Academy of Sciences (4400 ha; N 44°01′35.3″, E 134°12′59.8″, Fig. 1).

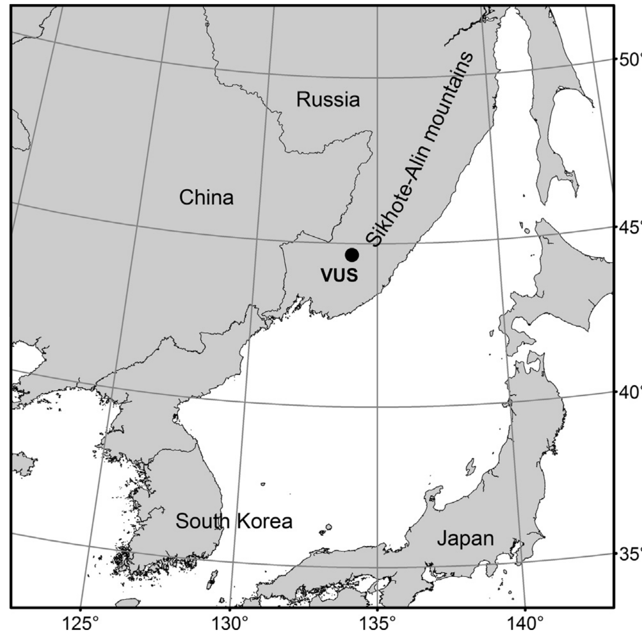

Fig. 1. Location of the study area on the Sikhote-Alin mountains, Southeastern Russia. VUS is Verkhneussyriysky Research Station.

The territory is characterized by a monsoon climate with relatively long, cold winters and warm, rainy summers. The average annual air temperature is 0.9 °C; January is the coldest month (−32 °C average temperature), and July is the warmest month (27 °C average temperature). The average annual precipitation is 832 mm (Kozhevnikova, 2009). Southerly and southeasterly winds predominate during the spring and summer, while northerly and northwesterly winds predominate in autumn and winter. Winds are typically weak, with an average speed lower than 3 m s^{-1}, and the number of stormy days with wind gusts over 20 m s^{-1} is approximately 20 per year, mostly in the spring (April) and autumn (November). The terrain includes mountain slopes with an average angle of ~20°, and the study area is characterized by brown mountain forest soils (Ivanov, 1964).

Mixed forests with Korean pine are the main vegetation type in the study area, and they form an altitudinal belt up to 800 m above sea level. They are gradually replaced by coniferous fir-spruce forests at high altitudes (Kolesnikov, 1956). Korean pine-broadleaved forests are formed by up to 30 tree species with *A. nephrolepis*, *B. costata, P. jezoensis*, *P. koraiensis*, and *T. amurensis* being dominant.

A. nephrolepis, *P. jezoensis*, and *P. koraiensis* are shade-tolerant species (Usenko, 1968). However, according to the literature, seedlings and saplings of *P. koraiensis* require a large amount of light to reach the stand canopy. Therefore, this species is considered mid-tolerant by some authors (Ge, 1994; Ishikawa et al., 1999). *T. amurensis* and *B. costata* are regarded as light-demanding species, although *T. amurensis* is sometimes classified as a mid-tolerant species (Usenko, 1968).

Approximately 60% of the Research Station area had been subjected to selective clear-cutting before the Station was established in 1972. The remaining 40% of its area has never been clear-cut and is covered by unique old-growth forest.

2.2. Discrete description of ontogenesis

In this work, the demographic and other study questions are based on the concept of the discrete description of the ontogenesis of plants. During their life, plants go through successive stages