Dynamics of the Mongolian Larch Forest in Forest–Steppe Ecotone Area with Comparison to Dynamics of the Japanese Larch Forest

January 2019

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A Dissertation Submitted to

the Graduate School of Life and Environmental Sciences,

the University of Tsukuba

in Partial Fulfillment of the Requirements

for the Degree of Doctor of Philosophy in Agricultural Science

(Doctoral Program in Biosphere Resource Science and Technology)

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Chapter 1

General Introduction

1.1 Background of Research

1.1.1 Boreal forests and larch

Larch species are present in all the temperate-cold zones of the northern hemisphere, from North America to northern Siberia, passing through Europe, mountainous China, and Japan (Bonan and Shugart 1989; Gower and Richards 1990). Even at the northern and altitudinal limits for tree growth, larches are widespread and often dominate the woodland zone north of evergreen-dominated boreal forests or above subalpine forests (Richards 1985; Richards and Bliss 1986). The widespread occurrence of larches in subalpine and boreal forests has given rise to the concept that the evergreen habitat is more advantageous in harsh environments. Therefore, larches must possess physiological and morphological characteristics that enable them to survive, grow, and reproduce as deciduous conifers in environments where evergreens normally dominate. Hence, it appears that larches are successfully living in what is normally considered an evergreen world (Gower and Richards 1990).

Generally, larch forests were considered as an important biome from the following aspects: 1) Larch forests were indispensable for land surface - atmosphere energy exchange as well as climatic regulating (Kelliher et al. 1997). Also, larches in northern

hemisphere were large carbon stock of global scale (Euskirchen et al. 2006), which were important natural resources for human welfare (Gunin et al. 1999; Burton et al. 2003). 2) Habitats of larch were vulnerable and sensitively affected by global climatic change and human activity. In Siberian permafrost area, larch forests were dramatically affected by global warming (Osawa et al. 2010). In Mongolian forest – steppe ecotone, larch forests were threatened by drought and artificial destruction (Tsogtbaatar 2004; Dulamsuren et al. 2009a). As to Japanese natural larch forests, the existence of competition species, as well as warm, wet climate, might lead to more risky habitats for its regeneration (Franklin et al. 1979; Okitsu 1999). 3) Larch is also an important plantation species which widely planted in Japan and Europe (Horikawa 1972; Koike et al. 2000; Hirano et al. 2003).

The larch forest area in Mongolia is mainly located in the northern parts of the country along the Russian border, forming a transition zone between the Siberian taiga forest and the central Asian steppe zone (Mongolian Ministry of Environment and Tourism 2016), mostly dominated by *L. sibirica*. Other needle-leaved species are *Pinus sibirica*, *Pinus sylvestris,* and *Picea obovata*. *Betula platyphylla* often occurs in the forest canopy, sometimes dominating in secondary woods (van Staalduinen 2005). In more southwards, the forest-steppe zone, consisting of a mosaic of patches of forest and grassland. Due to differences in topography, there is a differentiation of the vegetation in forests on the north-facing slopes and higher altitudes, and steppes on the south-slopes, and in valleys. Stumps of larch trees, or a parachernozem soil in a meadow steppe, are indicators of a former forest site as parachernozem is typical for forest, whereas

castanozem is typical for steppe habitats (Hilbig 1995; Mongolian Ministry of Environment and Tourism 2016). A clearly defined broad-leaved forest zone as in temperate Europe does not occur in Mongolia. In northern Mongolia, the Mongolian Altai and Khyangan conifer forests directly border the steppe (Mongolian Ministry of Environment and Tourism 2016)

Unlike the dry habitat of larch forest in Mongolian forest-steppe ecotone and the cold and dry habitat of the Siberian larch forest, natural Japanese larch (*L. kaempferi*) is mainly distributed in central Honshu (Hayashi 1951; Horikawa 1972), which has a humid environment (Mt. Yatsugatake, annual precipitation more than 1400 mm; Takaku et al. 2018). *Larix kaempferi* forests are usually mixed with conifer species such as *Tsuga diversifolia*, *Abies homolepis*, *A. veitchii*, *A. mariesii* and board-leaved species such as *Fagus crenata*, *Quercus crispula*, *Betula platyphylla*, and *Betula ermanii* (Hayashi 1951; Tatewaki et al. 1965). Natural forests are commonly formed on debris of a landslide, collapsed slope, and/or river terrace (Maeda et al. 1978; Baba 1989).

1.1.2 Mongolian Larch forests

Grassland in northern Mongolia and southern central Siberia primarily border on taiga forests of *L. sibirica* (Hilbig 1995; Dulamsuren et al. 2005a). *Larix sibirica* covers 80% of the forested areas across Mongolia (Gunin et al. 1999; Tsogtbaatar 2004), and is modified by human activities (Rösch et al. 2005), but the distribution limit of this species is generally caused by drought (Gunin et al. 1999; Dulamsuren et al. 2008). As water

supply and evapotranspiration levels vary with the physiognomy of the landscape, the ecotone between forest and grassland is an aspect-dependent vegetation mosaic with forests on northern slopes and in dry valleys and grasslands on southern slopes and in moist valley bottoms (Dulamsuren et al. 2005a). The southern distribution limit of the individual tree species occurring in this ecotone and, with it, the entire forest-steppe border, migrates depending on the variation of precipitation and temperature (Dinesman et al. 1989; Gunin et al. 1999; Miehe et al. 2007). Furthermore, anthropo-zoogenic influences affect the position of the forest-steppe borderline (Hilbig 1995; Rösch et al. 2005; Sankey et al. 2006). The proportion of forests within the present vegetation pattern of forests on north-facing slopes and grassland on south-facing slopes in Mongolia's forest-steppe ecotone is not likely to increase under the present climate, but might decrease with increasing aridity due to global warming (Dulamsuren et al. 2009a).

The dynamics of the forest-steppe ecotone captured the attention of researchers. In Mongolia, Sankey et al. (2006) suggested that an abrupt decline in the Darhad Valley ecotones' larch establishment during the 20th century coincided with increased local grazing pressure and regional climate variability, affecting larch regeneration. Dulamsuren et al. (2010b) suggested that in forest-steppe ecotones, occasional growth reductions were thought to have little effect on the performance of *L. sibirica*, whereas the absence of fast-growing competitors of other tree species that are either not or only slightly affected by gypsy moth was important. Furthermore, according to Dulamsuren et al. (2010a), trees in the forest interior were more severely stressed and grow more slowly

than trees at the forest line as a result of the recent increase in aridity. The stand density and probably the trees themselves in the forest interior are adapted to more moist conditions, whereas the trees at the forest edge have always been exposed to a more extreme microclimate (Dulamsuren et al. 2010b). For this reason, future climate warming will likely decrease the productivity of Siberian larch, thus affecting its existence within the forest-steppe ecotone of Mongolia (Dulamsuren et al. 2011). Other than the ecotone in Mongolia, ecotones in other places have also aroused the interest of many researchers.

1.1.3 Siberian Larch forests

In northern Siberia, large areas are covered almost solely by larch, and the canopy is much less dense. Pine species, which can withstand a range of harsh conditions, grow in light, sandy soils, and other dry areas. As the boreal forest-tundra boundary is approached, conifers thin out to a woodland, with lichen and moss dominating the ground and trees become increasingly stunted. In the boreal ecotone, fire is a common disturbance (Rowe and Scotter 1973) and may interact with periods of favorable climate to synchronize recruitment events. In addition, one of the most influential characteristics of the environment of the boreal forest biome is the permafrost, or the perennially frozen soils of various thickness and spatial extent. Its considerable role in the formation of forests is expressed at the borderline with tundra within the West-Siberian Plain. In the taiga zone, *L. sibirica* usually only participates in the formation of mixed stands. After fires and clear cutting, this species is, as a rule, replaced by birch and other woody species (Abaimov et

al. 1998).

1.1.4 Japanese Larch forests

Japanese larch, *L. kaempferi*, is the only endemic, deciduous conifer species in Japan. The natural distribution of this species is restricted to subalpine and montane areas in central Honshu (Hayashi 1951; Horikawa 1972). Natural Japanese larch forests occur as pioneer communities on arid and immature soils in volcanic areas, flood plains, and stream banks, and they form secondary communities in climax forests that have previously been clear cut. Japanese larch is often found in open forests, together with other species such as *Salix bakko*, *A. homolepis*, *A. veitchii* and *Tsuga diversifolia*, and sometimes forms the timberline at high elevations in the species range, such as on Mt. Fuji (Tatewaki et al, 1965; Numata 1974). Since it is one of the most important silvicultural species in Japan, artificial plantations have frequently been established in upper montane zones both within and outside its natural distribution range, from Hokkaido to central Honshu, especially since the late 1880s (Toda and Mikami 1976).

1.1.5 Studies of Larch forests in Mongolia, Siberia and Japan

Siberian larch forests were intensively studied in respect of morphological and ecological features (Abaimov 2010), postfire recovery of larch forest (Zyryanova et al. 2004), forest biomass, productivity and stand structure (Kajimoto et al. 2010), dendrochronology of larch forests (Vaganov and Kirdyanov 2010), etc. In Mongolian

forest – steppe ecotone area, several studies demonstrated the vegetation composition (Dulamsuren et al. 2005a), water relation in larch forests (Dulamsuren et al. 2009a), effect of drought and climate change (Dulamsuren et al. 2010c) and species succession after forest fire (Otoda et al. 2013). However, dynamics of forests in ecotones, edge effects on forest structure and dynamics from forest edge to the interior are not fully understand. In Japanese natural larch forests, studies of natural larch forest dynamics were mainly focused on phytosociological research and volcano areas (Tatewaki et al. 1965; Maeda et al. 1978; Masuzawa 1985; Nakamura 1985; Maruta 1996) and research of mountainous area with different types of disturbance are not enough.

1.1.6 Larch species and systematics in Mongolia, Siberia and Japan

Larix tree species spread out at high latitudes after the last glacial period (LePage and Basinger 1995). *L. sibirica* and *L. gmelinii* distributed in northeastern Eurasian continent, whereas *L. kaempferi* only distributed in Honshu island (Nagamitsu and Tomaru 2015). Semerikov and Lascoux (1999) indicated *L. sibirica* is genetically close to *L. gmelinii* var. *olgensis*, that was also revealed by investigation of *Larix* phylogenies (Semerikov et al. 2003). On the other hand, *L. gmelinii* was also distributed in Hokkaido and Tohoku region during the last glacial period, but it was extinct from these areas with the warming after the last glacial period (Nagamitsu and Tomaru 2015). In addition, Japanese larch (*L. kaempferi*) was isolated at the southern limit of the distribution. Phylogeographic studies of this alpine plants have revealed the history that such a distribution pattern had been

formed in the late Pleistocene glacial, interglacial cycles (Senni 2006). Moreover, *L. kaempferi* was closest to *L. gmelinii* distributed in Sakhalin, Chishima and Korean Peninsula, which were connect to Japanese archipelago by land bridge during the glacial period (Polezhaeva et al. 2010). Therefore, *L. kaempferi* was considered to have differentiated from *L. gmelinii*.

1.2 Purpose of Research

From the above, *L. sibirica*, *L. gmelinii* and *L. kaempferi* were genetically close and important in northern hemisphere. Although each of three species had its own geographical and climatic condition, for the overall understanding, comparative research is necessary. Generally, *Larix* in Eurasian continent were continuously distributed in cold and relatively drought environment, and the main disturbance factor is forest fire. However, Japanese *Larix* showed a completely different pattern with isolated distribution and warm, humid climate. This study focused on a representative drought habitat (Mongolian forest – steppe ecotone) and a representative warm, humid habitat (central Japanese mountainous area) of *Larix*. In order to improve the comprehensive understanding of *Larix* species in Northeastern Asia, comparative study was considered effective and necessary.

My study is carried out in larch forest on the southern fringe of a Mongolian boreal forest area adjacent to steppe, as well as in the mountainous region of central Honshu which is typical natural Japanese larch habitat. Specifically, I compared the climatic

distribution of *L. sibirica*, *L. gmelinii* (Northeast Asia) and *L. kaempferi* (Japan), also estimated the climatic and topography variables which influence the distribution of *L. kaempferi* in Japan (Chapter 3); I clarified the forest dynamics of a *L. sibirica* forest and assessed the disturbance regime in forest-steppe ecotone in northern Mongolia (Chapter 4); I also studied and described the forest dynamics of a natural *L. kaempferi* forest in central Japan (Chapter 5). I conclude with a discussion on the comparison of forest dynamics, disturbance regime and regeneration of larch forests between Japan and Mongolia and additionally discuss the conservation issues of larch forests under current conditions in the two countries.

Chapter 2

Status of research area

2.1 Study site and species in Mongolia

Mongolian forest-grassland is semiarid and highly continental, with a subzero annual mean temperature and precipitation between 100 and 400 mm (Chenlemuge et al. 2013). My research areas were in Gorkhi Terelj National Park which near the capital city **(Figure 2.1**), Ulaanbaatar, the annual precipitation of the Gorkhi Terelj National Park was 270 mm (estimated using the Worldclim data set, Hijmans et al. 2005).

Northern Mongolia represents the only area where central Siberian taiga vegetation directly borders on the open steppe. This area is of special botanical interest as central Siberia has a highly diverse relief (Rylkov 1996) and because the taiga is more diverse in tree species than that of taiga vegetation in other parts of Siberia (Dulamsuren et al. 2005a). The latter is because the western Siberian dark taiga forests dominated by *Picea obovata*, *Abies sibirica*, *Pinus sibirica*, and *Larix sibirica* (Knystautas 1987) meet the eastern Siberian light taiga forests made up by *Betula platyphylla* and related species as well as by *Larix* spp. and *Pinus sylvestris* (Ermakov et al. 2002). The genus *Larix* is represented by *L. sibirica* in the Khentey Mountains and in western Siberia but is replaced by *L. gmelinii* in the ultra-continental regions east and northeast of Lake Baikal (Dulamsuren et al. 2005a). The "double" borderline situation makes the Khentey

Mountains a unique place for flora and vegetation. Here the transitional zone between western and eastern Siberian taiga forests passes into the Mongolian Daurian forest steppe within another transitional zone.

Larix sibirica (Siberian larch) is a cold-tolerant gymnosperm, coniferous, deciduous tree species in taiga forests, which serves as the main stand-forming species in montane forests and sometimes in river valleys in the lower montane belt, and is also the dominant forest species, occupying a wide range of sites stretching from the valley floor to the coniferous treeline (James 2011). In addition, *Betula platyphylla* (white birch) and *Pinus sibirica* (Siberian Pine) were also found in this study.

2.2 Study site and species in Japan

The climate of Japan is an example of a temperate monsoon region on the east coast of continents in middle latitudes (Ohsawa 1990). However, the country extends over 22 degrees of latitude, so the climate shows wide variation from region to region. In considering the distribution of plants in Japan, the climatic differences between the longitudinal variation from the Japan and Pacific sea sides cannot be ignored (Horikawa 1972). This difference has produced two groups of plants characterized phytogeographically as the Japan sea (or inner Japan) side and the Pacific (or outer Japan) zones. In winter, the dry wind blowing from the Asian continent picks up quantities of moisture when passing over the Japan sea and brings much precipitation in the form of storms and snow to the Japan sea side. In contrast, coastal areas on the Pacific side

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experience fine weather during winter, being in a rain shadow. In summer, damp monsoon winds blow across the whole of Japan from the Pacific, bringing considerable rainfall throughout the land. Particularly high precipitation is recorded in the southwestern Pacific coast areas. On the other hand, Hokkaido, the eastern half of Tohoku, and the inland sea area experience lower precipitation throughout the year. Ocean currents, both warm from the southwest and cold from the northeast, also greatly influence the distribution of plants in Japan, both climatologically and mechanically.

The Japanese islands are composed primarily of high and rugged mountains and contain many volcanoes. The highest mountains of nonvolcanic origin are found in the central part of Honshu, with many peaks over 3000 m in height. Low land areas make up only 12.5% of the total land area and they consist mostly of eroded deposits from mountainous areas (Horikawa 1972). Yatsugatake, a volcanic group of more than ten inactive volcanoes, is located across the border of Yamanashi and Nagano Prefectures in central Honshu with the highest peak named Mt. Aka (2899 m) (Tatewaki et al. 1965; Kozu and Minami 2001). Plantations of *L. kaempferi* are mainly distributed at the foot of mountain, while natural individuals are distributed in subalpine conifer forests. Research plots in this study were established in natural *L. kaempferi* forests in the southern part of Mt. Yatsugatake, Nagano, and Yamanashi prefecture (**Figure 2.2**), which have subalpine-alpine characteristics and are steeper than the more northern sections. The annual mean temperature of study area was 6.7 °C (−5.3 °C in January; 19.2 °C in August) with annual precipitation of 1426.4 mm (www.worldclim.org; Hijmans et al., 2005; Takaku et al.,

2018).

Japan has a large variety of climatic conditions and shows remarkable complexity of topographic and edaphic conditions. This situation has enabled Japan to support a diversity of vegetation and a very rich flora with complex patterns of plant distribution (Horikawa 1972). At the climax of subalpine conifer forest (*Abies-Picea* formation), the subalpine or northern regions are covered with forests consisting of evergreen conifers such as *Abies veitchii*, *A. mariesii*, *A. sachalinensis*, *Picea jezoenesis*, *Picea jezoenesis* var. *hondoensis*, and *Tsuga diversifolia*. On the forest floor, *Pyrola secunda*, *Cacalia auriculata* var. *kamtschatica*, *C. adenostyloides*, and *Dryopteris austriaca* are common. Bryophytes occur in abundance, such as *Dicranum majus*, *Mnium hornum*, *Pleurozium schreberi*, *Hylocomium splendens*, *Scapania bolanderi*, and *Nipponolejeunea subalpina*.

Larix kaempferi (Japanese larch), is a species of larch native to Japan, predominantly in the mountains of Chubu and Kanto regions in central Honshu (Hayashi 1951; Horikawa, 1972; Farjon 1990). It is a medium-sized to large deciduous, coniferous tree reaching 20–40 m tall, with a trunk of up to 1 m in diameter. The crown is broad conic; both the main branches and the side branches are level, and the side branches only rarely droop.
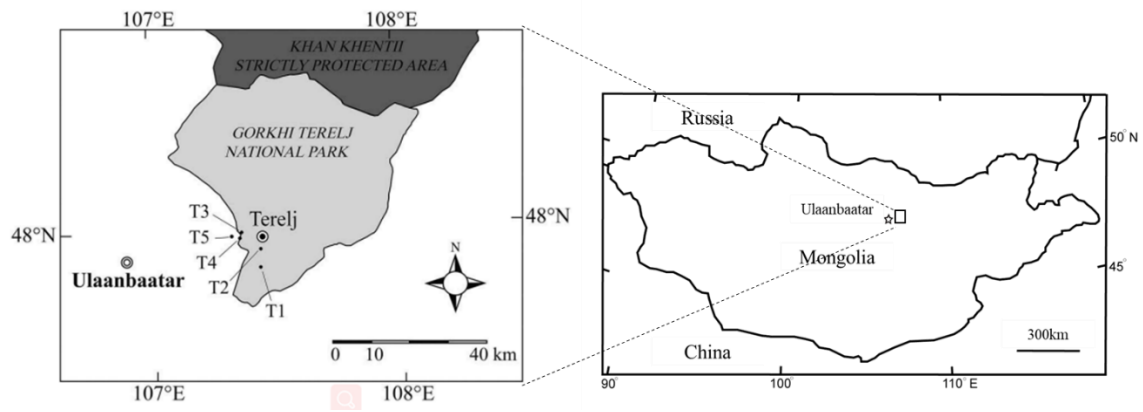
Figure 2.1 Map of research area in Mongolian forest – steppe ecotone area
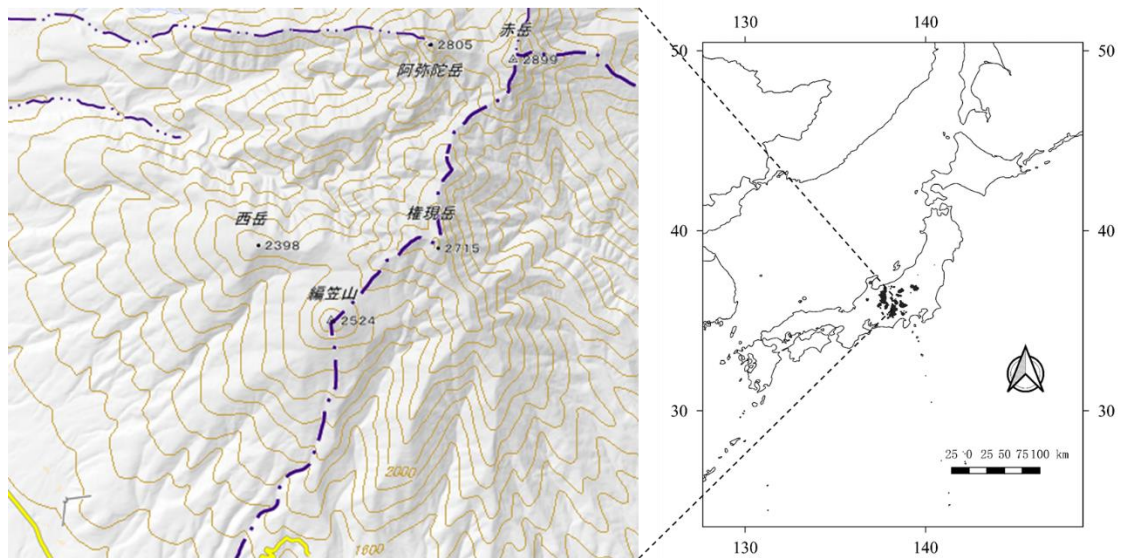
Figure 2.2 Map of research area in southern Mt. Yatsugatake, Japan.

Map was modified from the map of Geospatial Information Authority of Japan (GSI)

Chapter 4

Regeneration of *Larix sibirica* boreal forest patches in the forest - steppe ecotone in Gorkhi Terelj National Park, Mongolia

4.1 Introduction

Boreal forest, the largest terrestrial biome composed of coniferous forests, covers ca. 14 million km^2, accounting for 32% of the world forest cover (Burton et al. 2003). Intact forests still occupy a large proportion of boreal forest (Aksenov et al. 2002) and serve as an important natural resource for promoting human welfare (Zasada et al. 1997; Gunin et al. 1999; Burton et al. 2003; Tsogtbaatar 2004). In the Mongolian boreal forest area, the ecotone between the Central Asian steppe and southernmost Siberian boreal forest is mainly dominated by larch (Dulamsuren et al. 2016; Sankey et al. 2006), and this area is of great importance for the protection of water and soil quality and water flow (Tsogtbaatar 2004). According to previous estimations, Siberian larch (*Larix sibirica*) forests constitute almost 80% of the total boreal forest area and 84% of the total coniferous forest area of Mongolia (Dulamsuren et al. 2016; Tsogtbaatar 2004). Other common conifer species include *Pinus sibirica*, *Pinus sylvestris* L., *Picea obovata*, and *Abies sibirica*, coniferous forests have been replaced by *Betula platyphylla* and *Populus tremula* in disturbed areas (Dulamsuren et al. 2016).

The boreal forests area of Mongolia neighbors temperate grasslands (i.e., steppe) on

the southern border where forest distribution is limited by less precipitation (Chenlemuge et al. 2013). There are fragmented boreal forests (i.e., forest patches) surrounded by transition zones from the steppe, the forest edge, to the forest interior (i.e., forest-steppe ecotone). Typically, the forest-steppe ecotone in Mongolia consists of aspect-dependent vegetation mosaics of boreal forests at wetter sites (i.e., north-facing slopes of mountainous regions) and grasslands at drier sites (i.e., south-facing slopes and dry valleys) (Chytrý et al. 2008; de Vries et al. 1996; Dulamsuren et al. 2005a).

Based on physiological studies of water relations and the photosynthetic performance of *L. sibirica*, Dulamsuren et al. (2009a) suggested that drought serves as the major factor leading to the forest-steppe ecotone of Mongolia and that *L. sibirica* does not have the potential to encroach on the steppe under the current climate conditions. Limited reports have described differences in forest structure between the forest edge and forest interior in Mongolia (Dulamsuren et al. 2016) and Kazakhstan (Dulamsuren et al. 2013). Dulamsuren et al. (2009a) reported that at sites near the forest edge *L. sibirica* exhibited increased tree ring growth, higher stomatal conductance and higher shoot water potential than individuals in the forest interior. In addition to the topography (i.e., slope aspect), disturbance regime, such as the frequency and intensity of forest fire, is also a primary factor that forms distribution patterns in forests and affects forest structure and species composition in Mongolia (Johnson et al. 2009; Otoda et al. 2013; Tsogtbaatar 2004). Otoda et al. (2013) identified forest stand age structures in a northern Mongolian boreal forest and suggested that successional change from *L. sibirica* to *P. sibirica* forest

occurred after forest fire. For a comprehensive understanding of the maintenance mechanism of the forest-steppe ecotone in Mongolia, integrated studies on the forest dynamics and ecotone formed by topographical factors (e.g., slope aspect) seem to be effective. In the North American forest-grassland ecotone, Coop and Givnish (2007) studied the mean tree height, girth, and basal area (BA), which indicated no increasing tendency with distance into the forest from the treeline; however, tree seedling density increased strikingly in the forest interior with distance from the forest edge.

Recently, the Mongolian forest-steppe ecotone has been severely affected by climate change and human disturbance, and future declines of the forests caused by climate change have been suggested (Dulamsuren et al. 2009a, 2010c). Therefore, adequate forest management of the forest-steppe ecotone requires more knowledge about forest regeneration and forest patch vulnerability. However, studies on the dynamics of forest patches in forest-steppe ecotones and/or edge effects on forest structure and dynamics from the forest edge to the forest interior are not sufficient. In the present, I aim to clarify the dynamics of forest patches in the Mongolian forest-steppe ecotone and to examine how forest structure changes with distance from the forest edge to the forest interior on a northern slope.

4.2 Materials and methods

4.2.1 Study area

All measurements were conducted around the southwest the border of Gorkhi Terelj National Park (2,864 km^2 in area), which is located 54 km Northeast of Ulaanbaatar, Tov Province (**Figure 4.1**). The Terelj region was officially classified as a national park in 1993 (lUCN 1998). The park covers a large, diverse landscape comprising mostly mountains (i.e., the southern parts of the Khentii Range), river valleys, wetlands, forests, rocky summits and grasslands. Gorkhi Terelj National Park is mainly used for tourism, and grazing was found sporadically around the town of Terelj (Hayford 2010). The representative forest-steppe ecotone landscape is distributed in the mountainous area of Gorkhi Terelj National Park, i.e., forest patches are distributed on north-facing slopes, whereas steppe occurs on south-facing slopes and lower valleys. The Terelj area is characterized by continuous and discontinuous permafrost on the northern slopes (Battogtokh et al. 2006), which is assumed to be a water source for trees growing in forest patches (north-facing slopes) but not for trees growing in steppe (south-facing slopes) (Sugimoto et al. 2002; Etzelmüller et al. 2006) (**Figure 4.2; Figure 4.3**).

4.2.2 Climatic condition

The climate of Gorkhi Terelj National Park is classified as subarctic climate (Dwc type based on the Köppen classification), with dry winters and cold summers (Peel et al. 2007). According to the estimation from the WorldClim dataset (http://www.worldclim.org; Hijmans et al. 2005), the mean temperature in the study area is -2.3°C yr^{-1} (January: -23.1°C; July: 16.4°C). The average precipitation is 286 mm yr^{-1},

and approximately 83.6% of the precipitation is concentrated between June and September.

4.2.3 Field survey

The study sites (47°54′21.37″-47°59′44.37″ N, 107°19'49.07″-107°27′17.02″ E; 1660-2049 m a.s.l.; **Figure 4.2**) were in the forest-steppe ecotone in the mountainous area. Several burned conifer stumps indicate that forest fires have previously burned in the study area. However, historical information on forest fires or other disturbance data were not available for the study site.

Fieldwork was carried out in July and September for three consecutive years (2013, 2014 and 2015). I selected a total of five forest-steppe ecotones with a variety of structures in forest patches as the sampling sites (labeled T1-T5). T1 and T3 were composed of smaller *L. sibirica* trees, T2 and T4 were composed of larger *L. sibirica* trees, and T5 was composed of larger *P. sibirica* and *L. sibirica* trees. All sites were subject to limited anthropogenic influence, and no trees (including the dead ones) were cut, logged or removed.

To demonstrate the changes in forest structure and species composition with distance from the forest edge, I defined treeline as a borderline separating the steppe and forest edge with > 50% tree stand cover (Coop and Givnish 2007). Line transects, which crossed the treeline between forest and steppe, were established at the five sites. Additionally, 20 m × 5 m quadrats were established at 0 m, 5 m, 10 m, 25 m and 50 m on both sides of the

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treeline; thus, meaning quadrats were located equidistantly in the forest side and on the steppe side of the treeline. The long side (20 m in length) of each quadrat was perpendicular to the transect. The forest patch is represented by the stand of the line transect on the forest side. Because of the wider forest patch in T4 and T5 than in T1 – T3, I added additional quadrats to both sides at 100 m in T4 and T5 (**Figure 4.4 a, b**).

All trees were categorized into three classes: > 130 cm in height, 15-130 cm in height (i.e., saplings) and < 15 cm in height (i.e., seedlings). I measured the diameter at breast height (DBH) of trees > 130 cm in height, and the heights of the saplings were measured in each 100-m^2 quadrat. The seedlings of tall tree species (*Larix sibirica*, *Pinus sibirica* and *Betula platyphylla*) were counted in five 1-m^2 subquadrats established at regular intervals within the 5-m, 25-m, 50-m, and 100-m (only in T4 and T5) quadrats on either side of the treeline (**Figure 4.4 b**).

The number and width of tree rings of trees with DBH ≥ 5 cm were measured in all quadrats except in the quadrats at 100 m (**Figure 4.5**). The sampling numbers in each quadrat depended on the tree density (DBH ≥ 5 cm), and the largest tree in each quadrat was always sampled to estimate the stand age. (1) If the number of trees in a quadrat (20 m × 5 m) was less than 10, all trees were measured. (2) If the number of trees in a quadrat was between 10 and 30 trees, all trees were measured in the half of the evenly divided quadrat (10 × 5 m) that included the largest tree. (3) If the number of trees was greater than 30 trees, all trees were measured in one of four evenly divided quadrats (5 m × 5 m), i.e., whichever section included the largest tree. Cores were collected by using an

increment borer from each tree at 1.3 m in height. After the processes of air-drying, the cores were sanded and tree rings were counted and measured using a 0.01-mm binocular microscope with a sliding stage. Core samples were collected in September 2014 (T1, T2, T3, T4) and September 2015 (T5). I used the estimated age in 2014 for analysis.

4.2.4 Boundary – line dendroecological release criteria

I quantified the forest disturbance magnitude of each quadrats from forest edge to interior in each transect by using the boundary – line dendroecological release criteria (Black and Abrams 2003), which are considered more flexible for evaluating disturbance histories and can be used to estimate disturbance magnitude precisely and fundamentally. A feature of this approach is to analyze the relationship between tree ring release response (percent growth change) and tree ring growth prior to release (prior growth) without considering the tree age, radius or crown class (Black and Abrams 2003). The value of percent growth change was calculated according to the method of Nowacki and Abrams (1997):

$$\text{Percent growth change} = (M2 - M1) / M1 \qquad (1)$$

where M1 is the mean growth over the prior 10 years and M2 is the mean growth over the subsequent 10 years.

I used the definition of prior growth described by Black and Abrams (2003), in which prior growth is equal to mean growth over the 10 years prior to each tree ring. Both the

percent growth change and the prior growth were analyzed for each year of all sampled

cores (tree ring series) of *L. sibirica*. In this study, the percent growth change in relation

to the prior growth of tree ring series within 0 – 15 m (0 m, 5 m and 10 m quadrats), 25 –

30 m (25 m quadrat) and 50 – 55 m (50 m quadrat) from the treeline to the interior were

plotted. In this analysis, I integrated three quadrats near the forest edge (0 m, 5 m and 10

m quadrats) because the sample size (no. of trees) in the forefront of the forest edge was

too small.

In each of the transects, the percent growth change in relation to prior growth of all

tree ring series was applied to construct a boundary line, which was defined as the upper

threshold of tree ring release response through the range of prior growth (Black and

Abrams 2003). In this study, I constructed the boundary line by following the method of

Black and Abrams (2003). First, the mean value of top 10 percent growth change points

in each 0.5 mm segment of prior growth was selected. Then I determined the boundary

line using regression analysis of these selected points. In this regression analysis, I

compared liner, power, exponential and logarithmic regression and selected a regression

line with the highest R^2 value as the boundary line.

Furthermore, percent growth change values greater than 10% were reserved to

identify the growth pulse (Nowacki and Abrams 1997; Black and Abrams 2003). Only

the maximum percent growth change values among tree ring series in the same year were

selected and measured as maximum potential using the boundary line.

Similar to Black and Abrams (2003), I quantified and classified releases as "not a release", "moderate release" and "major release" based on relative value to the boundary line. I defined percent growth change values (release thresholds) no less than 50% of the boundary line as "major", those between 20% and 49.9% of the boundary line as "moderate" and those less than 20% of the boundary line as "not a release".

4.2.5 Data analysis

I used the generalized linear model (GLM; "glm" function) approach with a log-linkage and Poisson distribution to determine the association between the maximum tree age in each quadrat as an index value of stand age and tree basal areas of all measured trees, *L. sibirica* and *P. sibirica* in each of the quadrat. I also used the generalized linear mixed model (GLMM; "glmer" function in package "lme4") approach with Poisson distribution and log-linkage to assess the effect of distance from the treeline to the forest interior on the forest structures. I used the distance from the treeline to the forest interior as an independent variable, and the tree basal area, maximum age, number of trees per quadrat, sapling number per quadrat and seedling number per quadrat were the dependent variables; finally, the study transects were included as a random effect factor. All statistical analyses were performed using R 3.4.0 (R Development Core Team 2017).

4.3 Results

4.3.1 Overview of forest – steppe ecotone

Tree densities and basal areas (BA) were significantly lower on the steppe than on the forest patch (T4 and T5 have one more quadrat in 100 m than other plots; steppe tree density: 0-602.8 stems ha^{-1}, BA: 0-11.3 m^2 ha^{-1}; forest tree density: 1117-3164 stems ha^{-1}, BA: 17.2-59.4 m^2 ha^{-1}; P < 0.01, Mann-Whitney U test). Overall, *L. sibirica* was the single dominant species (87.0%-100.0% of total tree density and 95.0%-100.0% of total BA) in forest patches, with the exception of T5, where *L. sibirica* was mixed with *P. sibirica* (relative density: 61.9%, relative BA: 43.7%) (**Table 4.1**). Living *Betula platyphylla* trees were rarely found in only T1 and T4. The maximum tree ages (an indicator value of stand age) were 48, 156, 185, 222, and 244 years in T3, T1, T2, T5 and T4, respectively (Table S1).

4.3.2 Tree size distribution

DBH size distributions in each of the forest patches were sorted by the increasing order of maximum age (**Figure 4.6**). In all transects, the DBH values of living trees were significantly larger than those of dead trees (P < 0.05, Mann-Whitney U test). In T3, which had the lowest maximum age (48 years), only *L. sibirica* was present, and both living and dead trees showed unimodal size distributions (**Figure 4a, f**); additionally, the peak living tree distribution was in the 8-10-cm class and was larger than that of dead trees. All dead trees were smaller than 8 cm DBH. Similar left-leaning unimodal size distributions of both living and dead trees were found in T1 (maximum age: 156 years, **Figure 4.6 b, g**). Additionally, 89.8% of the dead *L. sibirica* trees were concentrated

under 10 cm DBH, and the peak occurred in the 2-4-cm class, which was much higher

than the peak density of living trees (4-6-cm class). In the transects with higher maximum

ages (T2: 185 years, T5: 222 years and T4: 244 years), the living trees had a bimodal

distribution (**Figure 4.6 c, d, e**). In T2, *L. sibirica* was the only living tree species with

the peak in the 2-4-cm class, which was larger than that of dead trees. *P. sibirica* occurred

in the oldest two transects (i.e., T4 and T5, **Figure 4.6 d, e, i, j**).

4.3.3 Relationship between tree quadrat age and tree size

The relationships between the maximum core age and the BA of *L. sibirica* and *P.*

sibirica in each quadrat are shown in **Figure 4.7**. *L. sibirica* occurred in all quadrats, but

P. sibirica only occurred in quadrats that had maximum core ages over 100 years old. In

addition, the basal areas of *P. sibirica* (0.0-25.1 m^2 ha^{-1}) were lower than those of *L.*

sibirica (5.0-95.5 m^2 ha^{-1}) in all quadrats. For *L. sibirica* and *P. sibirica*, the basal area of

trees increased with the increase in maximum quadrat age (**Table 4.2**).

4.3.4 Spatial distribution of tree age

The spatial distribution of sampled trees' age is shown in **Figure 4.8**. In transects

with a relative younger maximum age (T3 and T1), the ages of *L. sibirica* showed

concentrated distribution like cohorts. The ranges of ages in T3 and in T1 were 26 -48

and 56 - 156, respectively. In T2, cohort - like age distributions of *L. sibirica* were present

in quadrats from 0 to 25 m, whereas age distribution was divided into two sections

(younger and older individuals) in 50 m quadrats. The range of ages in quadrats from 0 to 25 m in T2 was 32 - 58. The ranges of lower age sections and those of higher age sections in 50 m quadrat of T2 were 45 - 64 and 180 - 185, respectively. In T5, age distributions of trees were generally distributed in two sections. The range of the lower age section and that of the higher age section from 0 to 50 m quadrats in T5 was 35 - 76 and 126 - 222, respectively. In addition, *P. sibirica* was more abundant in the lower age section of T5. In transects with the oldest maximum age (T4), unimodal age distributions of *L. sibirica* were present in quadrats from 0 to 10 m (42 - 80 in range of ages). However, quadrats in 25 and 50m in T4 did not present younger cohort of *L. sibirica* (section of younger individuals). Two younger *P. sibirica* individuals (age of 66 and 64) were found in 25 and 50 m quadrats. Age distributions of *L. sibirica* in 25 m and 50m quadrats were 201 - 244 in range of ages. Moreover, the growth curve of all sampled trees also showed cohort like regeneration of *L. sibirica* individuals in all five transects (**Figure 4.9**).

4.3.5 Results of Boundary – line dendroecological release criteria

The total percent growth change and prior growth of *L. sibirica* in 5 transects, included 10594 years of growth and were used to construct the boundary line of each transect (**Figure 4.12**). For all transects, a negative exponential regression curve was calculated with the highest R^2 value to be selected as the boundary line.

To distinguish severe disturbance events from mild events, I subdivided releases into "moderate" and "major" categories based on percent distance to the boundary line (see

methods). Major releases would lie closest to the boundary line and represent those events intense enough to elicit the largest possible growth pulses (**Figure 4.10**).

Generally, the proportion of release (moderate and major) was lower in T5 and T4 than in the other three transects with younger maximum ages (**Figure 4.11**). The proportion of release decreased with increasing distance from forest edge to the interior in T2 and T4. Additionally, major release percentages in T1 and T2 decreased with distance. However, lower proportion of major release in near the forest edge was observed in T3 (**Figure 4.11**).

4.3.6 Change in forest structure with distance

Based on the GLMM results (**Table 4.3**, **Figure 4.13**) and distribution from edge to the forest interior (data in steppe sides were not included in the GLMM results), the basal area and maximum age of both *L. sibirica* and *P. sibirica* increased with the increase in distance from the forest edge. The number of *L. sibirica* trees also increased with distance from the forest edge. Saplings of *L. sibirica* only occurred in T1, and I found no association between the number of saplings and distance from the forest edge. In contrast, saplings of *P. sibirica* occurred only in the older quadrats in T5 and T4 and increased with the increase in distance from the forest edge. Seedlings of *L. sibirica* occurred in all transects except T5, and they generally increased with the increase in distance from the forest edge; however, seedlings of *P. sibirica* were found only in T5 and T4 and had no relationship with distance.

4.4 Discussion

4.4.1 Dynamics of forest patches in the Mongolian forest-steppe ecotone

The age and DBH distribution in each of the quadrats in the younger transects (T1, T2, T3) suggest that most of the *L. sibirica* of younger cohorts regenerated after the recent disturbance (**Figures 4.6**, **Figure 4.8**). However, ages of younger cohorts varied among transects (**Figure 4.8**). This suggested that forest fires had occurred continuously in this study area and small or moderate scale (quadrat or transect scale) regeneration occurred after each disturbance. Many standing dead trees of smaller sizes (**Figure 4.6**) suggested effects of density on the tree community, which seems to be caused by an intensive stand-replacing disturbance. Angelstam and Kuuluvainen (2004) reported that severe self – thinning and competition occurred in young boreal forests. In addition, the bimodal size distribution and discontinuous age distribution in the older stands (T4, T5) indicated multiple regeneration, including recent regeneration (**Figures 4.6**, **Figure 4.8**). The recent regeneration of young trees may have been caused by forest fire (Otoda. et al 2013; Tsogtbaatar 2004). Fire disturbance frequently occurs in Mongolian boreal forests (Tsogtbaatar 2004; Nyamjav et al. 2007; Johnson et al. 2009). In my transects, many dead stumps with remnants of fire were observed (Li et al. 2019). Frequent fire disturbances seem to have important roles in boreal forest regeneration (Lavoie and Sirois 1998; Harper et al. 2002; Johnstone et al. 2004; Angelstam and Kuuluvainen 2004; Johnstone et al. 2006) and in the Mongolian forest-steppe ecotone (Johnson et al. 2009; Otoda et al.

2013). A multi-aged stand structure is also common in Siberian larch forests (Bondarev 1997). Bondarev (1997) noted that a multi-aged pattern reflected severe previous forest fire disturbances within a stand. The older age sections of T5 and T4 (**Figure 4.8**) showed wider range of age than T2. This age structure does not support simultaneous regeneration after an intensive disturbance. In addition, the results of boundary line criteria (**Figure 4.11**) showed a lower contribution of intensive disturbances (moderate and major release) in T5 and T4. Angelstam and Kuuluvainen (2004) suggested that intensive and large-scale disturbance, and low intensive and small-scale disturbance, such as gap creation in the canopy layer, might have complementary effects in European boreal forests. As in European boreal forests, the *L. sibirica* boreal forest patches in Gorkhi Terelj National Park seems to be maintained by both the high and low intensive disturbances.

Our results indicated that *P. sibirica* was more common on transects where the oldest trees were found (T4, T5) and that the BA values of *L. sibirica* and *P. sibirica* were positively correlated with the maximum age of the quadrat (**Figures 4.8, Figure 4.13, Table 4.2**); these results demonstrated that *P. sibirica* regenerated only in relatively mature stands with long large - scale disturbance intervals, such as those caused by forest fire, which was similar to the conclusions of Otoda et al. (2013). In the boreal forests of Mongolia and Siberia, *L. sibirica* and *P. sibirica* are considered as pioneer and late successional species, respectively (Otoda et al. 2013; Schulze et al. 2005; Shorohova et al. 2009). Our results suggested that succession from *L. sibirica* to *P. sibirica* occurred in the Mongolian forest-steppe ecotone. This change seems to be owing to differences in

seedling shade tolerance and soil condition. *Larix sibirica* was initially established after disturbance, as *Larix* species prefer disturbed areas with high light and less soil organic matter, as well as lower competition conditions (Tanaka et al. 2008; Zhu et al. 2008). On the forest floor in T1, T2, and T3 (**Figure 4.13**), *L. sibirica* seedlings were found; however, few saplings were found. It is possible that the seedlings cannot develop to saplings because of shade intolerance even if they can germinate under a closed canopy. In contrast, late successional species, such as *Pinus* species, can regenerate under low light conditions and on soil with a thick organic layer with decayed stumps and logs (Kuuluvainen and Juntunen 1998), and the regeneration of *P. sibirica* was continuous for over 100 years (Otoda et al. 2013). Thus, differences in shade tolerance and soil conditions, i.e., the thick soil organic layer, seem to be one explanation for the observed successional change.

4.4.2 Change in forest structure from forest edge to interior

The GLMM results showed there were significant effects of distance from the forest edge on the forest structure (**Table 4.3**). In general, the total BA and the maximum age (used as an indicator value of stand age) increased with distance from the forest edge (**Figure 4.13**, **Table 4.3**). Moreover, the results of boundary line criteria (**Figure 4.10**, **Figure 4.11**) showed a generally decreasing trend of moderate and major releases from the forest edge to forest interior in T1, T2 and T4, although ratio of major release in 0 - 15m quadrat was the lowest in T3 and there was no clear tendency in T5. Therefore, the spatial pattern from forest edge to interior seems to be caused by the changes in the

disturbance regime with distance from forest edge. Unlike other transects, a lower proportion of major release near the forest edge was observed in T3 (**Figure 4.11**). Some disturbances might have occurred exceptionally in forest interior in T3.

The relationship between edge effect and disturbance regime of forest fire has been examined in several fragmented forests. In tropical Amazonian fragmented forest, forest edges were considered to exhibit dry and fire - prone conditions (Laurance and Williamson 2001). Most forest fires were associated with forest edges, and the majority of burned forests occurred near forest edges (Gascon et al. 2000; Cochrane 2001; Armenteras et al. 2013) and were less frequent with distance from the forest edge (Cochrane 2001). Additionally, in both tropical (Murcia 1995) and boreal (Harper et al. 2014) forests, forest fires near the forest edge led to higher tree mortality than in the forest interior. According to these studies, the undeveloped forest structure with smaller BA and younger maximum age near the forest edge in our study site may be owing to more frequent and/or intensive disturbance caused by forest fires.

Abiotic environmental conditions also varied in the forest-steppe ecotone. Lower air and soil moisture (Kapos 1989; Matlack 1993), and higher vapor pressure deficit (VPD), air temperature, and light conditions (photosynthetically active radiation) (Kapos 1989; Williams-Linera 1990; Matlack 1993) at the forest edge were reported. The drier conditions (Kapos 1989; Matlack 1993) at the forest edge, combined with the south-facing slopes being drier than the north-facing slopes owing to lower exposure to solar radiation (Murcia 1995; Matlack 1993), may cause more frequent forest fires at the forest

edge. However, the physiological stress experienced by tree individuals does not simply change with distance from the forest edge. Dulamsuren et al. (2009a) reported that trees of *L. sibirica* in forest-steppe ecotone frequently suffered from drought stress, whereas *L. sibirica* trees grew better at the forest edge than in the forest interior. This decline in growth in the forest interior is possibly owing to a higher tree density in the forest interior that was related to both light and water stress induced by competition among tree individuals.

The increase in BA and number of *P. sibirica* saplings (**Table 4.3, Figure 4.13**) suggested that succession from *L. sibirica* to *P. sibirica* was more advanced in the forest interior than forest edge. This also seemed to reflect more sufficient recovery times for the seed dispersal and establishment of the late successional *P. sibirica* after disturbance in the forest interior. Furthermore, the density of seedlings and saplings of *P. sibirica* and the density of seedlings of *L. sibirica* increased with increasing distance from the forest edge to the forest interior. These results might be caused by the gradient of environmental conditions on the forest floor from the forest edge to the forest interior. Drought stress is more likely to affect the seedlings of late successional conifers (Calvo et al. 2008), especially in early spring (Berg and Chapin 1994). To examine the effects of environmental conditions, such as light and soil water on seedling establishment of *L. sibirica* and *P. sibirica*, further study is necessary.

Our study suggested multiple regeneration induced by high and low intensive disturbances and the changes in forest structure and species composition with distance

from the forest edge in the *L. sibirica* boreal forest patches in the forest-steppe ecotone in Gorkhi Terelj National Park by analyzing two spatial scales: transects and quadrats within transects. The diverse forest structure in the forest-steppe ecotone is possibly maintained by severe climatic conditions for trees (Dulamsuren et al. 2009b); topographical factors (Dulamsuren et al. 2005b); and disturbance regimes including intensive disturbances, such as fire (Otoda et al. 2013) and the higher susceptibility to disturbance at the forest edge.
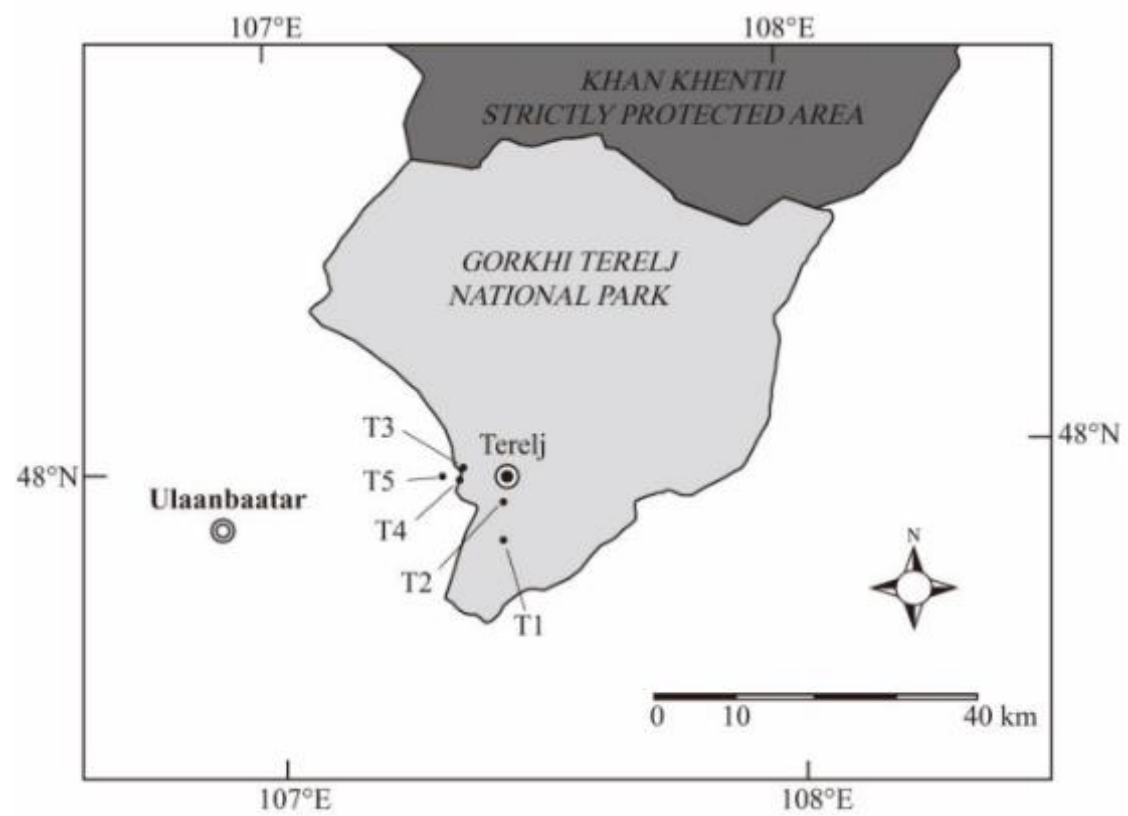
Figure 4.1 The location of Gorkhi Terelj National Park and the five transects established in this study.
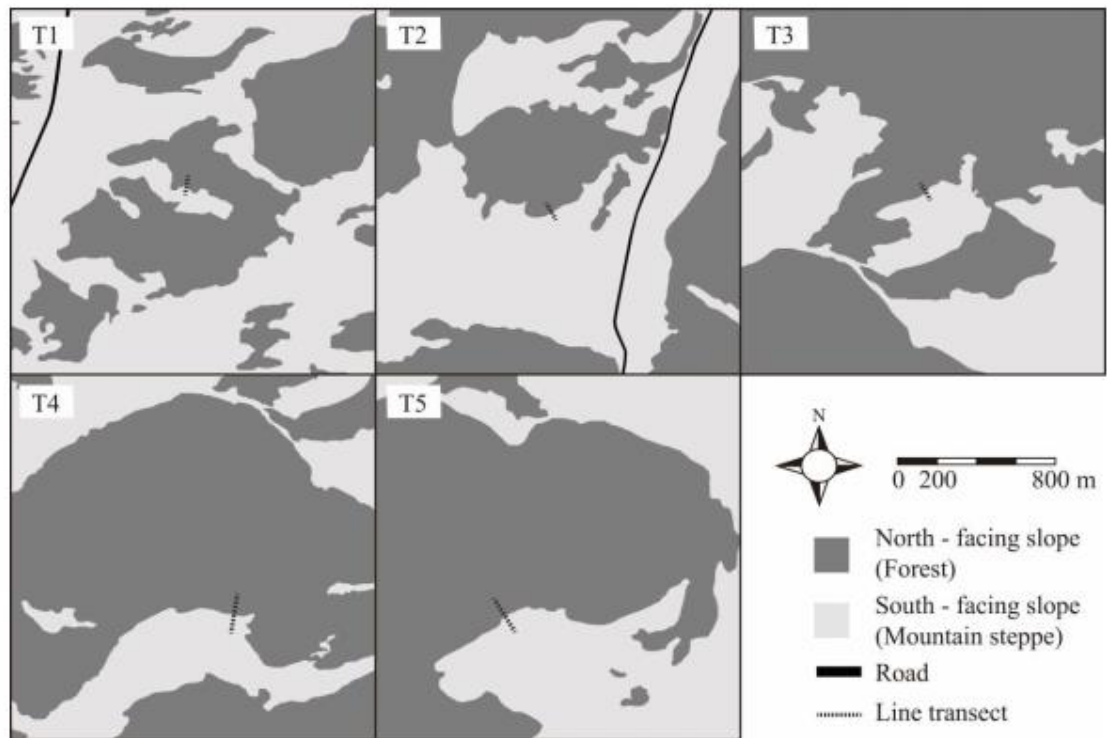
Figure 4.2 Slope aspect-dependent forest-steppe ecotone and transects applied in this study

Figure 4.3 Typical landscape of *Larix* forest – steppe ecotone in Terelj National Park, Mongolia
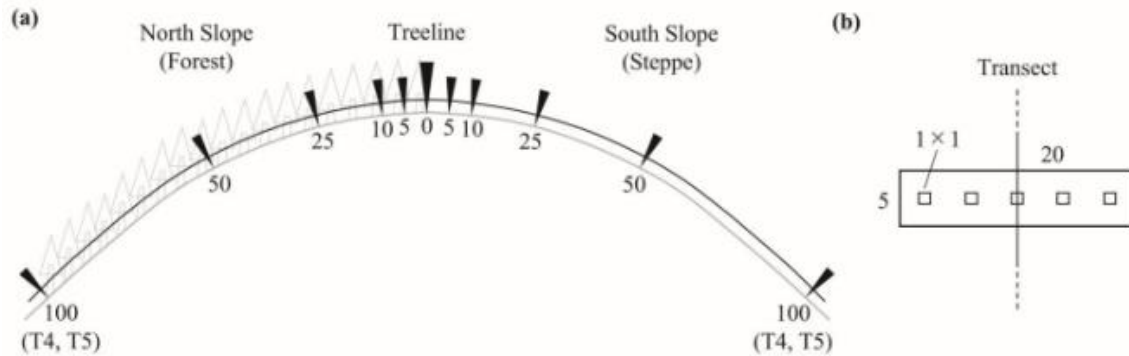
Figure 4.4 General view of each transect (unit: m)

(a) Transects were established across the treeline and extended to both forest and steppe slope; 100-m^2 quadrats (5 m × 20 m) were established on forest and steppe sides at 0 m, 5 m, 10 m, 25 m, 50 m and 100 m (only T4 and T5).

(b) The long side of each quadrat was perpendicularly bisected by the transect; thus, five 1-m^2 sub-quadrats were evenly distributed in one quadrat.

Figure 4.5 Main tree species in forest – steppe ecotone area, *Larix sibirica* and *Pinus sibirica*
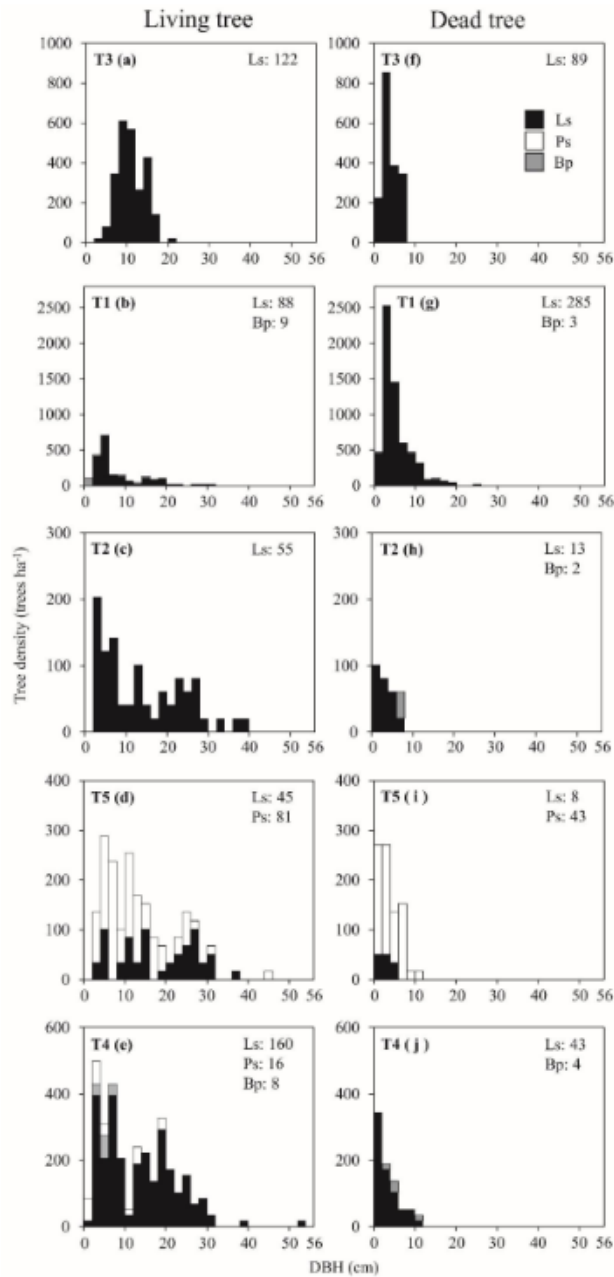
Figure 4.6 DBH size distributions of all tree species (> 130 cm in height) in each of the five forest patches (living trees: a-e, dead trees: f-j) with 2-cm classes sorted in increasing order of maximum age of quadrat.

Ls: *Larix sibirica*, Ps: *Pinus sibirica*, Bp: *Betula platyphylla*. Number of trees is shown beside tree species name. T4 and T5 have one more quadrat in 100 m than other transects.
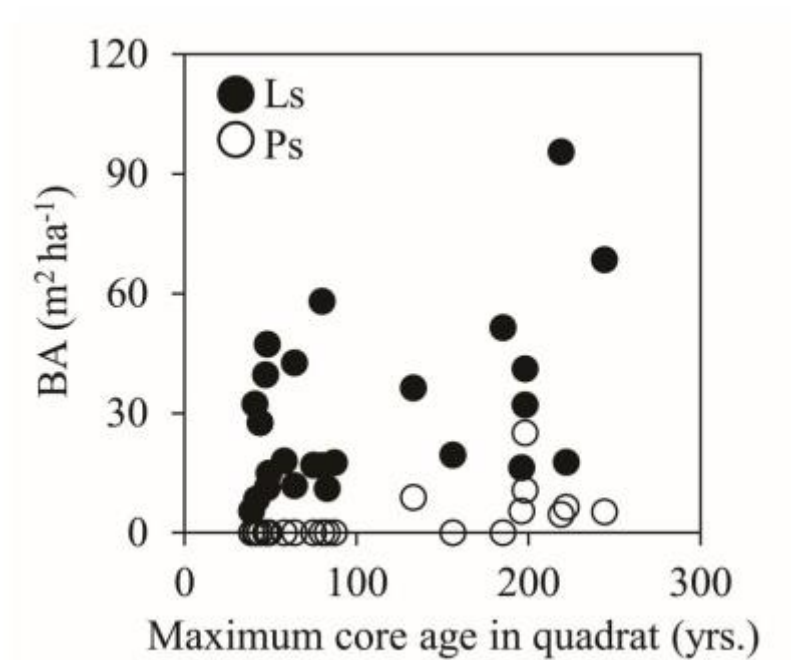
Figure 4.7 Relatinship between maximum core age and basal area (BA) for the two main tree species, *Larix sibirica* (Ls) and *Pinus sibirica* (Ps), in each quadrat.
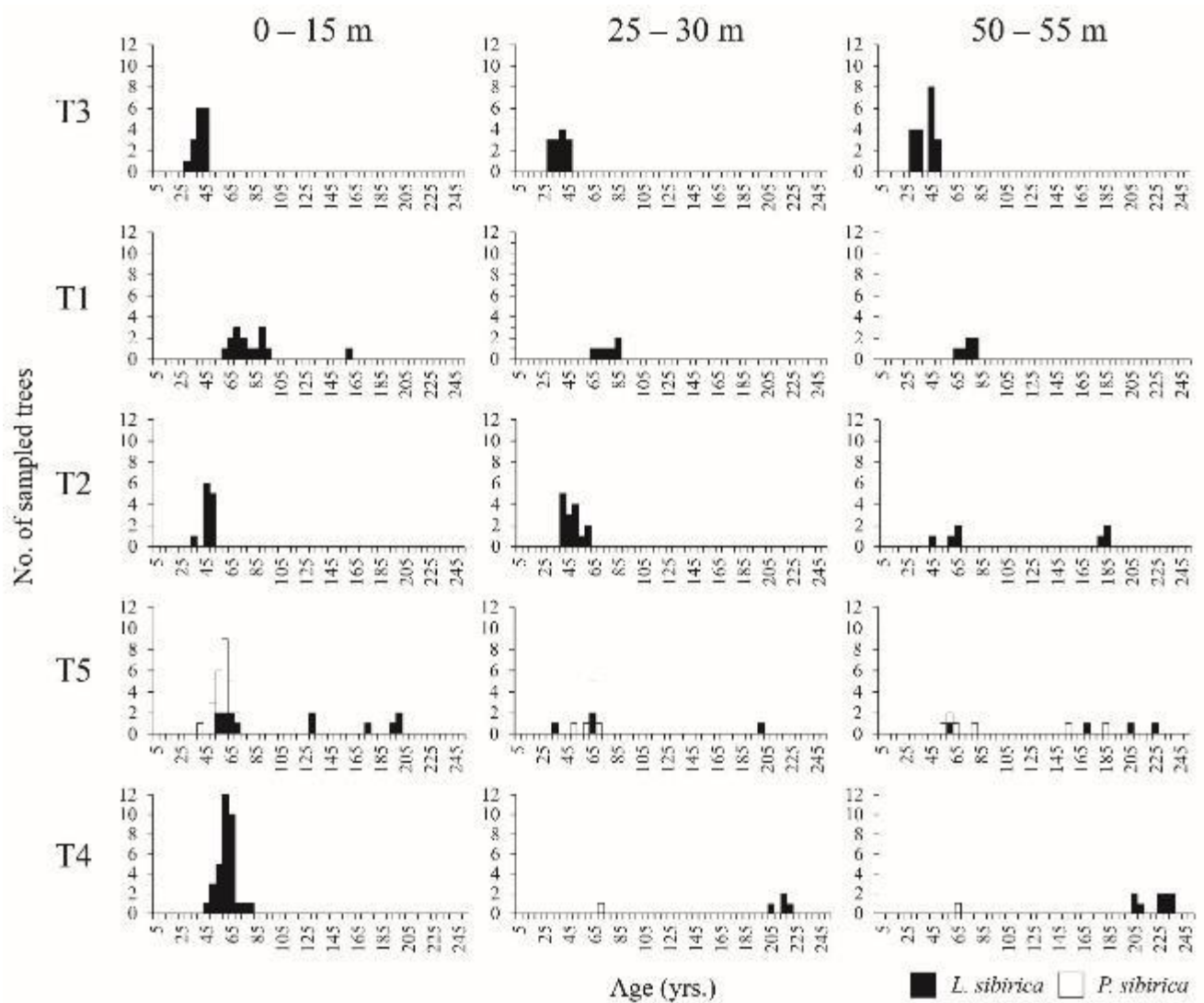
Figure 4.8 Core age distributions *of L. sibirica* and *P. sibirica* (> 130 cm in height) in each of the five forest patches with 10-year classes sorted in increasing order of maximum age of quadrat.
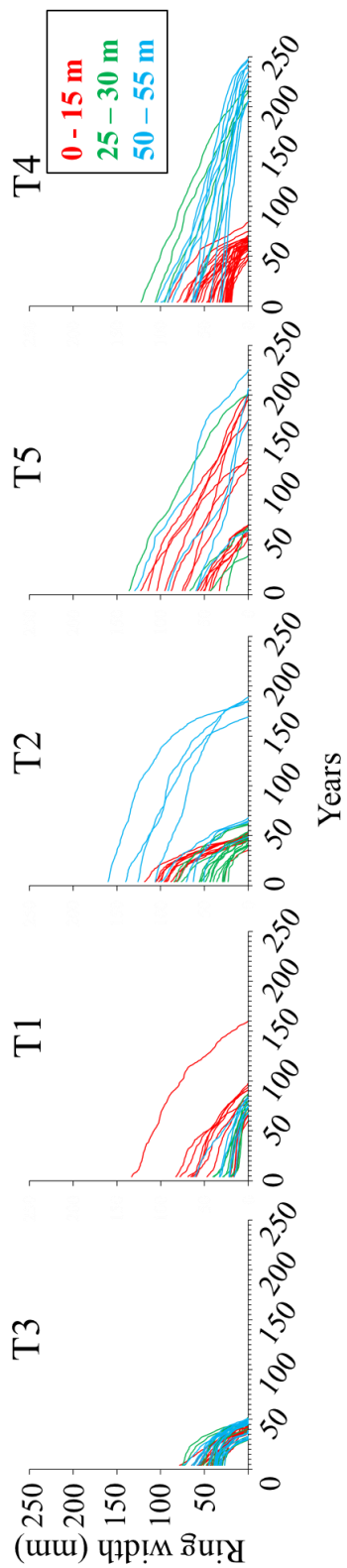
Figure 4.9 Growth curve of *Larix sibirica* in Mongolian forest – ecotone area. Tree cores in 0 – 15m quadrat were shown in

red curve, cores in 25 – 30m were shown in green curve, cores in 50 – 55m were shown in blue curve.
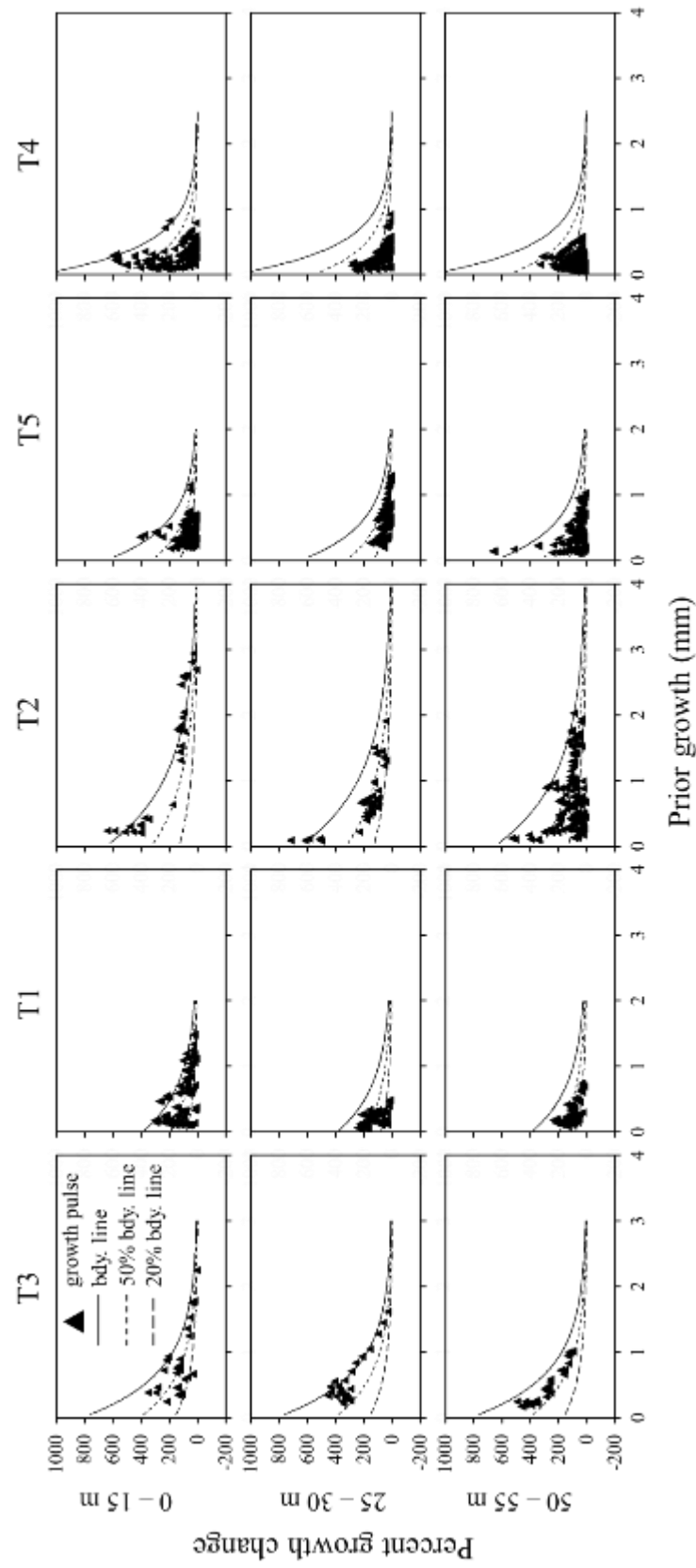
Figure 4.10 Maximum percent-growth-change values in radial growth pulses that exceed 10%. Data are shown for *Larix sibirica* in each of the five transects. Growth pulse no less than 50% boundary line are considered as major releases. Growth pulses between 20% and 49.9% are moderate releases. Growth pulses less than 20% are not considered as releases.
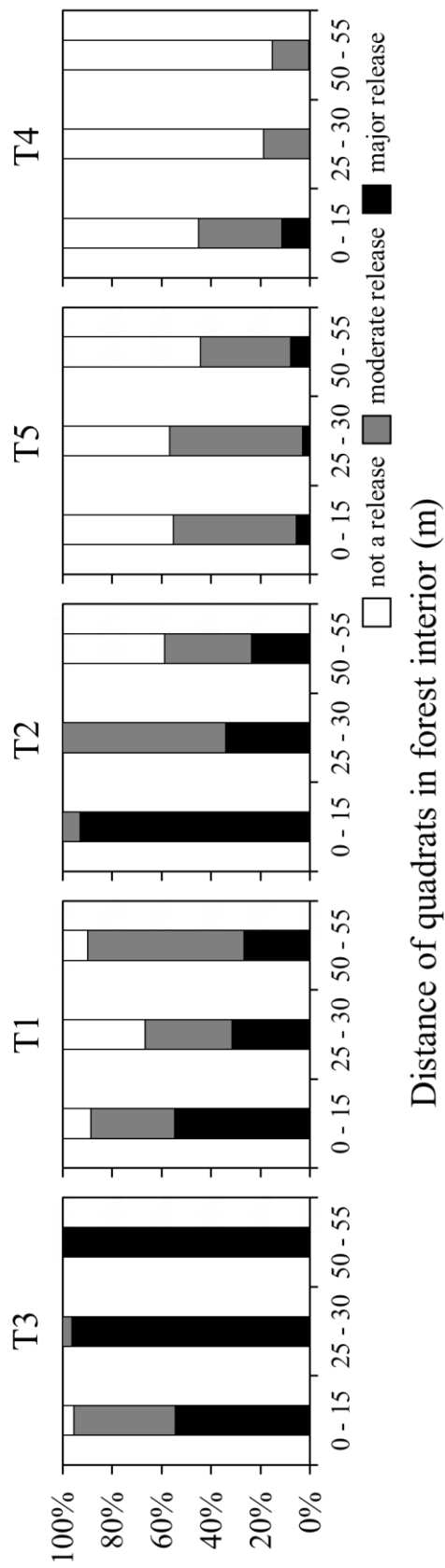
Figure 4.11 Proportion of major release, moderate release and not a release at different distance from forest edge to forest interior. Results are shown in all transects. Three quadrats near the forest edge (0 m, 5 m and 10 m quadrats) are integrated.
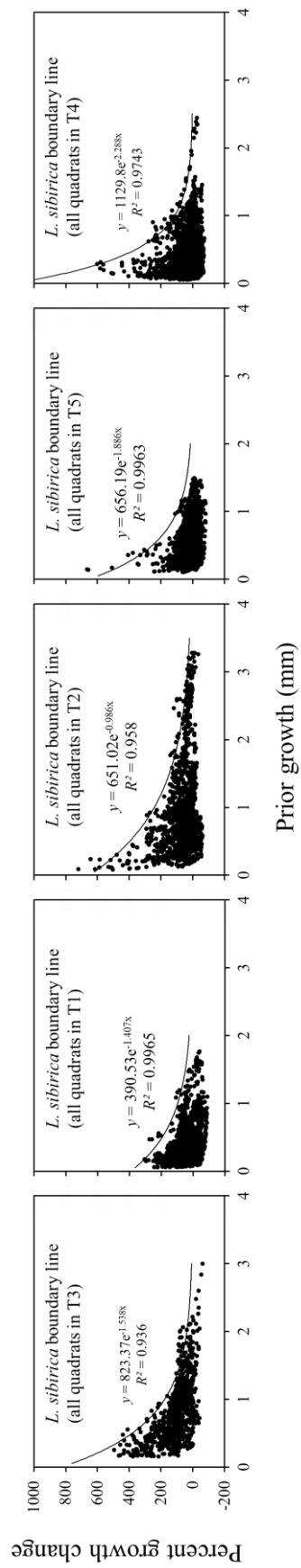
Figure 4.12 Plot of percent growth change in relation to prior growth for all sampled *Larix sibirica* tree rings cored in all five

transects. *Larix sibirica* boundary line is shown respectively.
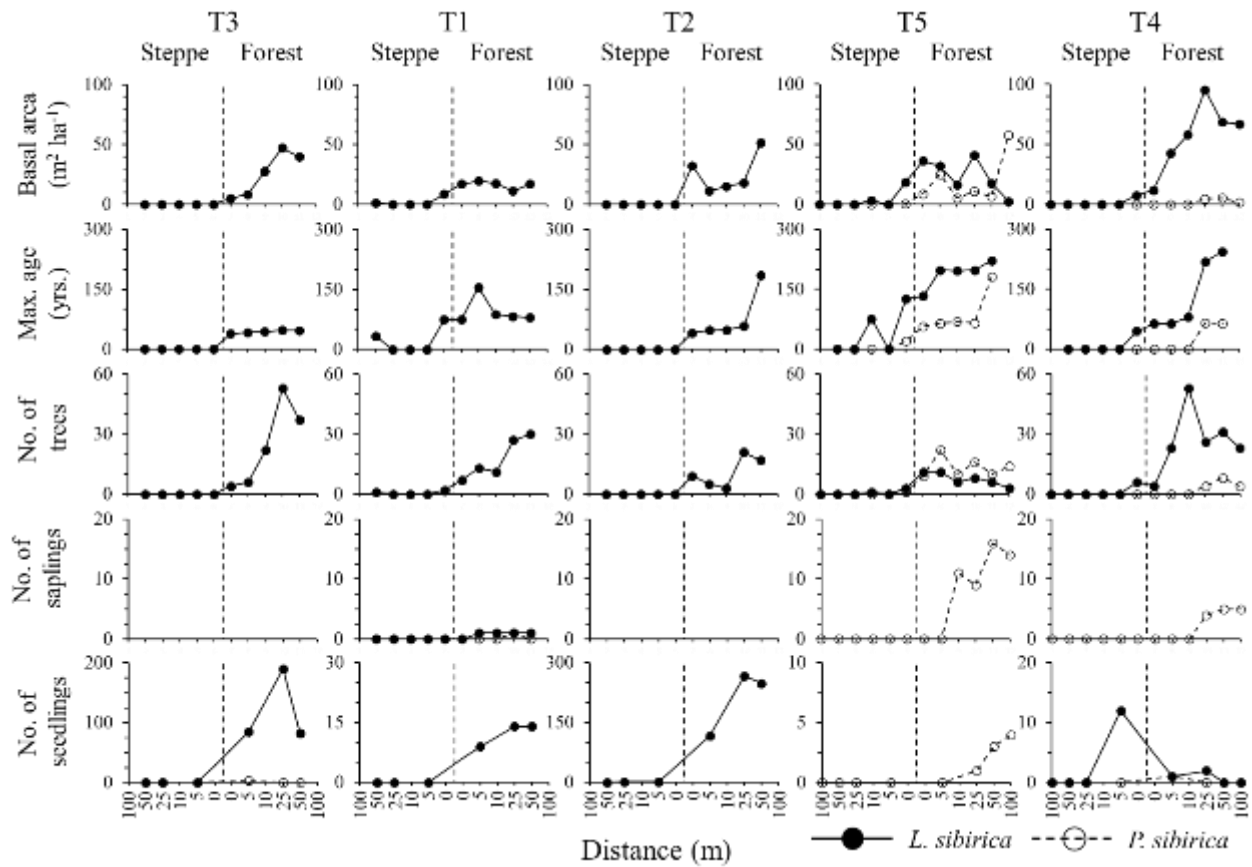
Figure 4.13 Relationship between distance and basal area, maximum age, number of trees, saplings and seedlings of the two main tree species, *Larix sibirica* (Ls) and *Pinus sibirica* (Ps), in each quadrat.

The dashed lines in the figure indicate the boundary between forest and steppe in all transects. The y-axis indicates the quadrats established at 0 m, 5 m, 10 m, 25 m, 50 m and 100 m (only in T4 and T5) in north slope (forest patches, right side of dashed line) and south slope (steppe, left side of dashed line). Trees and saplings were measured in each quadrat, seedlings were counted in 5 m, 25 m, 50 m and 100 m (only in T4 and T5) quadrats. Tree ring samples were cored in each quadrat except in the 100 m quadrats.

Table 4.1 Tree species composition, density, basal area (BA), diameter at breast height (DBH) and maximum tree age in the five transects.

"Relative tree density" and "Relative basal area" indicate the fraction of particular species in overall trees number and basal area. T4 and T5 have one more quadrat in 100 m than other plots.

Transects No. (Max. tree age)	Species	Tree density (stems ha^{-1})	Relative tree density	Basal area (m^2 ha^{-1})	Relative basal area	Mean DBH ± SD (cm)	Max. DBH (cm)
T1 (156)							
	Living trees						
	L. sibirica	1891	0.907	16.3	0.950	8.3 ± 6.5	31.0
	B. platyphylla	193	0.093	0.9	0.050	5.0 ± 5.5	14.3
	Total	2084		17.2		8.0 ± 6.5	31.0
	Dead trees						
	L. sibirica	6124	0.990	18.5	0.974	5.1 ± 3.5	25.6
	B. platyphylla	65	0.010	0.5	0.026	8.2 ± 6.7	14.0
	Total	6188		19.0		5.1 ± 3.6	25.6
T2 (185)							
	Living trees						
	L. sibirica	1117	1.000	25.7	1.000	13.9 ± 10.0	38.7
	Total	1117		25.7		13.9 ± 10.0	38.7
	Dead trees						
	L. sibirica	264	0.867	0.2	0.579	2.9 ± 1.6	6.1
	B. platyphylla	41	0.133	0.2	0.421	7.0 ± 0.1	7.1
	Total	305		0.4		3.4 ± 2.1	7.1
T3 (48)							
	Living trees						
	L. sibirica	2485	1.000	25.4	1.000	10.9 ± 3.3	21.5
	Total	2485		25.4		10.9 ± 3.3	21.5
	Dead trees						
	L. sibirica	1813	1.000	2.6	1.000	3.9 ± 1.8	7.3
	Total	1813		2.6		3.9 ± 1.8	7.3
T4 (244)							
	Living trees						
	L. sibirica	2751	0.870	57.1	0.961	13.6 ± 8.9	52.6
	P. sibirica	275	0.087	1.9	0.032	7.1 ± 6.3	19.3
	B. platyphylla	138	0.043	0.4	0.007	6.1 ± 2.0	8.4
	Total	3164		59.4		12.7 ± 8.8	52.6
	Dead trees						
	L. sibirica	739	0.915	1.0	0.805	3.3 ± 2.6	11.2
	B. platyphylla	69	0.085	0.2	0.195	6.1 ± 3.5	11.2
	Total	808		1.3		3.6 ± 2.8	11.2
T5 (222)							
	Living trees						
	L. sibirica	763	0.381	24.4	0.563	17.9 ± 9.4	37.8
	P. sibirica	1237	0.619	19.0	0.437	10.6 ± 8.0	44.1
	Total	2000		43.4		13.2 ± 9.2	44.1
	Dead trees						
	L. sibirica	136	0.157	0.1	0.070	2.6 ± 1.3	4.7
	P. sibirica	729	0.843	1.2	0.930	3.8 ± 2.6	10.6
	Total	864		1.3		3.6 ± 2.4	10.6

Table 4.2 Estimated using a Generalized Linear Model (GLM) approach for tree basal

areas of *L. sibirica* and *P. sibirica*.

Maximum age: maximum age of trees in each quadrat. The values of each variable

represent the regression coefficients ($\pm$ SE).

Between the two models (Null and Maximum age) for each species, the model with the

lower AIC (Akaike information criterion, shown in bold) value is suggested as more

appropriate for the data. Significance of the coefficients inferred from Wald's test: ns $P >$

0.05, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Model	Intercept	Maximum age	AIC
L. sibirica			
Null	3.326 $\pm$ 0.006 ***	-	216.9
Maximum age	2.826 $\pm$ 0.281 ***	0.004 $\pm$ 0.002 *	**213.6**
P. sibirica			
Null	-5.238 $\pm$ 7.904 ns	-	73.5
Maximum age	-4.341 $\pm$ 1.884 *	0.020 $\pm$ 0.007 **	**65.6**

Table 4.3 Results of generalized linear mixed model (GLMM) selection.

Maximum age: maximum age of trees in each quadrat. The values of each variable represent the regression coefficients (± SE).

Between the two models (Null and Distance) for each species, the model with the lower AIC (Akaike information criterion, shown in bold) value is suggested as more appropriate for the data. Significance of the coefficients inferred from Wald's test: ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Model	Intercept	Distance	AIC
Basal area			
L. sibirica			
Null	3.326 ± 0.006 ***		216.9
Distance	2.826 ± 0.281 ***	0.004 ± 0.002 *	**213.6**
P.sibirica			
Null	-5.238 ± 7.904 ns		73.5
Distance	-4.341 ± 1.884 *	0.020 ± 0.007 **	**65.6**
Maximum age			
L. sibirica			
Null	4.549 ± 0.276 ***		269.5
Distance	4.221 ± 0.292 ***	0.014 ± 0.003 ***	**260.1**
P.sibirica			
Null	-7.814 ± 4.115 ns		233.3
Distance	-8.581 ± 4.214 *	0.030 ± 0.002 ***	**221.3**
No. of trees			
L. sibirica			
Null	2.758 ± 0.215 ***		325.2
Distance	2.604 ± 0.224 ***	0.005 ± 0.002 ***	**315.8**
P.sibirica			
Null	-5.930 ± 5.944 ns		**89.0**
Distance	-5.832 ± 6.590 ns	0.008 ± 0.007 ns	89.3
No. of saplings			
L. sibirica			
Null	-7.327 ± 5.032 ns		**20.6**
Distance	-7.819 ± 5.162 ns	0.011 ± 0.025 ns	22.4
P.sibirica			
Null	-1.308 ± 1.454 ns		118.0
Distance	-1.679 ± 1.337 ns	0.015 ± 0.003 ***	**98.7**
No. of seedlings			
L. sibirica			
Null	1.827 ± 1.487 ns		231.0
Distance	1.530 ± 1.528 ns	0.007 ± 0.002 ***	**214.2**
P.sibirica			
Null	-1.019 ± 0.802 ns		**44.5**
Distance	-1.385 ± 0.845 ns	0.010 ± 0.009 ns	45.3

Acknowledgment

My deepest gratitude goes first and foremost to professor Takashi Kamijo, his extensive supervision throughout all of time in my study and invaluable supports to me not only in research but also in my life in Japan. Assistant professor Kiyokazu Kawada, for giving me encourage to do this study, field work and teaching me data analysis. I am also grateful to professor Kenji Tamura, associate professor Mitsuru Hirota and professor Yoshikiho Tsumura, who have given me generous support and helpful advice. Professor Tetsuya Matsui, for his assistance in species distribution modeling. Professor Undarmaa Jamsran, for her arrangement and assistance in Mongolian field research. I would never go so far like this without their endorsement and supervision. I gratefully acknowledge the support of Mr. Xiaoxing Hu, Mr. Xiulong Zhang and all members in laboratory of silviculture and nature conservation. No less gratitude should be given to my parents for their seven years' constant overall support. Especially, I would like to express the love and appreciation to Ms. Rui Sun, for giving me encourage.

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