

Chapter 5

Forest Vegetation and Ecological Studies



Satoshi N. Suzuki and Susumu Goto

Abstract The University of Tokyo Hokkaido Forest (UTHF) is located in a hemiboreal mixed forest zone and is predominantly characterized by boreal conifers such as *Abies sachalinensis*, *Picea jezoensis*, and *Picea glehnii* and cool-temperate deciduous broadleaves such as *Tilia japonica*, *Acer pictum*, *Betula* spp., and *Quercus crispula*. As an ecotone, the forest composition within the UTHF varies with elevation, transitioning from a cool temperate deciduous broadleaf-dominant forest at lower elevations to an alpine dwarf pine (*Pinus pumila*) forest at the highest point. The vegetation associated with specific disturbances, topography, or geography serves as a habitat for diverse species. Over the span of more than 60 years, the UTHF has conducted long-term measurements of forest trees. In addition to numerous small forest plots (typically smaller than 1 hectare), there are two large-scale long-term ecological research (LTER) plots: Maeyama LTER (36.25 hectares) and Iwanazawa LTER (18.75 hectares). These extensive monitoring efforts have elucidated the dynamics and environmental changes in hemiboreal forests. The UTHF has established several experimentally designed study plots utilized for assessing biodiversity-ecosystem functional relationships and the genetic local adaptations of trees to elevational gradients. Long-term observations of plant phenology have also been conducted, providing robust evidence for plant responses to climate change. The comprehensive research conducted at the UTHF contributes significantly to our understanding of hemiboreal forest ecosystems.

Keywords Hemiboreal mixed forest · Elevational gradient · Forest dynamics · Long-term ecological research

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T. Owari et al. (eds.), *Integrative Forest Management and Silviculture*,

Ecological Research Monographs, https://doi.org/10.1007/978-981-95-1017-7_5

5.1 Vegetation of the UTHF

5.1.1 Vegetation Zone: Hemiboreal Mixed Forest Zone

The UTHF is in a hemiboreal mixed forest zone that is primarily composed of boreal conifers and cool-temperate deciduous broadleaves. This type of forest is widespread globally in transitional vegetation zones between cool temperate and boreal forests. Tatewaki (1955, 1958) named this type of forest zone the “pan-mixed forest zone.” The major species constituting the hemiboreal forests in Europe, North America, and East Asia, such as spruce (*Picea*), fir (*Abies*), oak (*Quercus*), birch (*Betula*), linden (*Tilia*), maple (*Acer*), and ash (*Fraxinus*), are largely similar at the genus level. In Hokkaido, the mixed forest was composed of evergreen conifers such as *Abies sachalinensis*, *Picea jezoensis*, and *Picea glehnii* and deciduous broadleaves such as *Tilia japonica*, *Acer pictum*, *Betula* spp., and *Quercus crispula*.

In the UTHF, 894 species/subspecies/varieties of vascular plants, including 169 tree species and 78 fern species, have been recorded (Horie et al. 2013). A total of 9.8% of them are endemic to Japan, and 10.6% are alien species. The vegetation is composed of a mix of northern (boreal) and southern (temperate) components of plant communities. The northern components are species that have migrated from the north through Sakhalin and Kuril Islands and are characterized by species such as *Picea jezoensis*, *P. glehnii*, *Urtica angustifolia*, *Crataegus chlorosarca*, *Lonicera alpigena* subsp. *glehnii*, and *Rhododendron dauricum*. The southern components are species that have migrated from the southern direction, that is, mainland Japan, characterized by species such as *Styrax obassia*, *Daphniphyllum macropodum* subsp. *humile*, *Symplocos sawafutagi*, *Vaccinium oldhamii*, and *Arachniodes standishii* (Horie et al. 2013).

5.1.2 Vertical Distribution of Vegetation

As the hemiboreal mixed forest zone is an ecotone, the forest composition changes with elevation even within the UTHF (Kato 1952; Irikura et al. 1979, Figs. 5.1, 5.2, and 5.3). In the lower area (approximately lower than 650 m a.s.l. in elevation), cool-temperate deciduous broadleaves are dominant, but their dominance decreases with elevation. Instead, the dominance of boreal evergreen conifers increases with elevation and reaches a maximum at approximately 800–900 m a.s.l. in elevation. The abundance of *Betula ermanii*, a boreal deciduous broadleaf species, also increases with elevation and should become more dominant in the higher part of the forest zone (Fig. 5.1). Soon below the tree line, sparse *Betula ermanii* forest is dominant. Above the tree line, at approximately 1250 m a.s.l. in the UTHF, dwarf stone pine *Pinus pumila* shrubs are dominant. This elevation of the tree line is ca. 300 m lower than that of the surrounding mountains, such as the Daisetu Mountains, probably due to harsh environments and shallow soils due to mountain ridge

Fig. 5.1 Elevational patterns of the stand basal area of major subalpine species at the University of Tokyo Hokkaido Forest. (Modified after Irikura et al. 1979 by Satoshi N. Suzuki, with the publisher's permission)

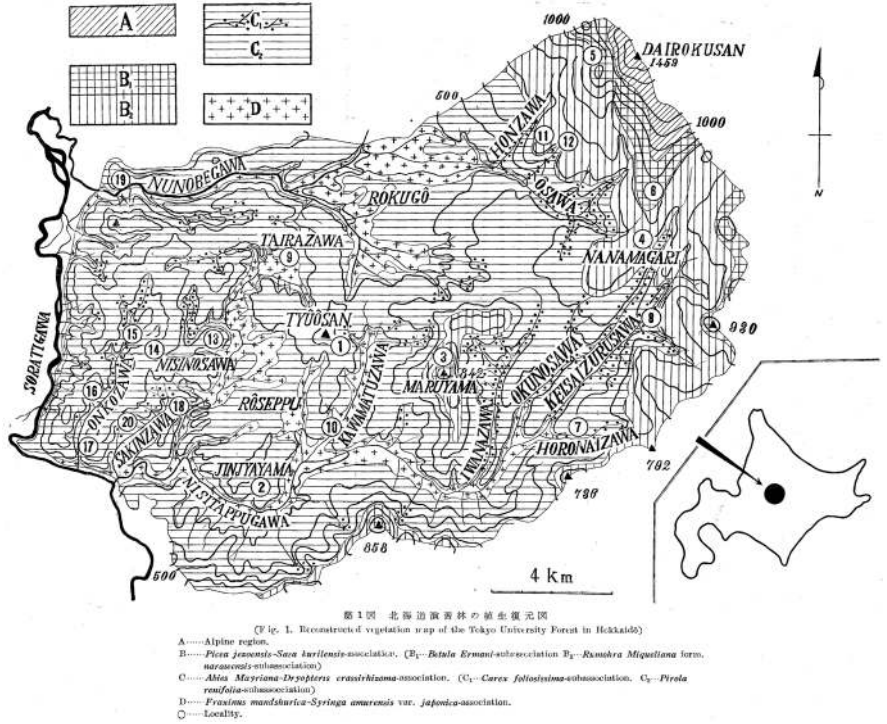
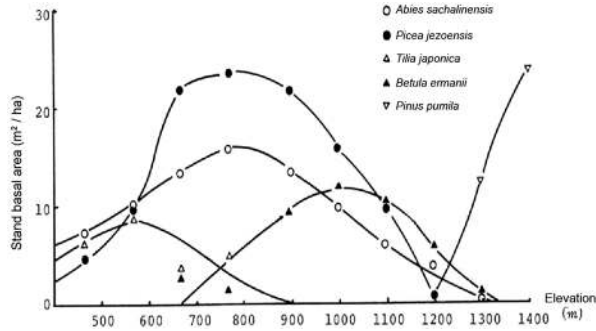


Fig. 5.2 Reconstructed vegetation map of the University of Tokyo Hokkaido Forest. (Reproduced from Kato 1952, with the publisher's permission)

topography (Irikura 1979, Nakata et al. 1994). Above the tree line, there are a variety of alpine plant species, such as *Vaccinium ovalifolium*, *Vaccinium smallii*, *Vaccinium vitis-idaea* (cowberry), *Gaultheria adenotheix*, and *Linnaea borealis*.

The forest floor is mostly covered by *Sasa* dwarf bamboos, primarily *Sasa senanensis* (Fig. 5.4), but *Sasa kurilensis* occurs at higher elevations (above ca. 700–800 m asl.). As *Sasa* dwarf bamboos densely cover forest floors, tree



Fig. 5.3 (a) Alpine vegetation (1450 m a.s.l., SEP 7, 2022), (b) upper subalpine forest (1230 m a.s.l., JUN 8, 2020), (c) lower subalpine forest (700 m a.s.l., AUG 30, 2021), (d) conifer-broadleaf mixed forest (340 m a.s.l., Oct. 17, 2009). (a–c, photo by Satoshi N. Suzuki; d, photo by the UTHF for d, licensed under CC BY-NC-ND 4.0)

regeneration is often greatly restricted by them in cool temperate and boreal forests in Japan (Nakashizuka and Numata 1982, Nakashizuka 1988, Kubota and Hara 1996). In these forests, fallen logs or stumps, called nursery logs, play important roles as regeneration sites for some tree species (Kubota and Hara 1996, Narukawa et al. 2003). Additionally, *Sasa* density is relatively low in moderately shaded environments under evergreen conifers (Tatsumi and Owari 2013), providing opportunities for the regeneration of shade-tolerant species.

5.1.3 *Vegetation Related to Disturbance, Topography, and Geography*

Pioneer species such as birches (*Betula* spp.) often dominate in disturbed areas. The stands that regenerated naturally after fires in the 1910s are now dominated by *Betula maximowicziana* and *Betula platyphylla* var. *japonica*, as well as *Quercus crispula* (Fig. 5.5, see also Chap. 13). On the other hand, the stands that regenerated naturally after severe typhoons, such as those in 1954 and 1981, were dominated by not only *Betula* but also *Abies sachalinensis* and a variety of broadleaves (Fig. 5.6).

a



b



Fig. 5.4 Forest floor covered with *Sasa senanensis* (a, August 30, 2021) and seedlings of conifers on a nursery log (b, May 29, 2024). (Photo by Satoshi N. Suzuki)

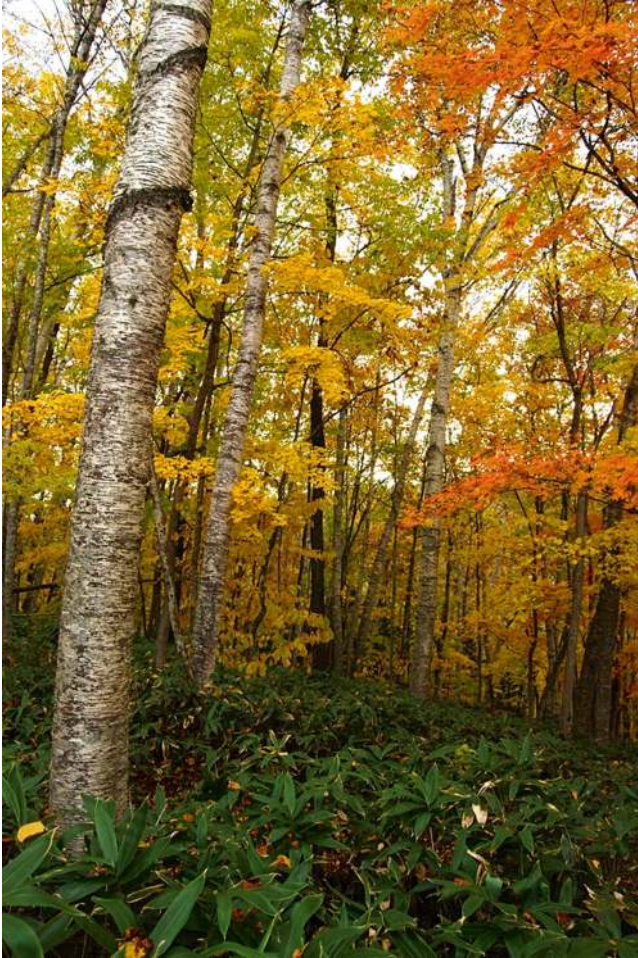


Fig. 5.5 Secondary postfire broadleaf forest dominated by *Betula maximowicziana* after the fire in 1911. (Photo by the UTHF, licensed under CC BY-NC-ND 4.0)

This is likely because advanced regeneration or sprouting from stumps or downed trees contributed to the recovery of the canopy (refer to Chap. 13).

In lowland areas, wetland forests are dominated by species such as *Fraxinus mandshurica* var. *japonica*, *Alnus japonica*, and *Ulmus davidiana* var. *japonica*. Before the colonization of Japanese people from mainland Japan, it is believed that lowland wet forests, characterized by alder trees, were widely distributed in the Furano Basin and the lowlands of the original UTHF area (Fig. 5.2). However, following the colonization, most of the lowland area was replaced by farmlands, leaving only small remnants in Furano. The largest remnant in Furano was found within the UTHF, where it is now conserved as the Tairazawa Forest Reserve (Fig. 5.7).



Fig. 5.6 A secondary forest regenerated after the typhoon in 1981. (Photo by Satoshi N. Suzuki)



Fig. 5.7 Lowland wet forest in the Tairazawa Forest Reserve. (Photo by Satoshi N. Suzuki, July 1, 2024)



Fig. 5.8 Sakhalin spruce wetland forest in the Maeyama Forest Reserve. (Photo by Satoshi N Suzuki, July 6, 2020)

Some endangered wetland shrubs and trees, such as *Crataegus chlorosarca* and *Padus avium*, grow in the reserved forest.

Picea glehnii often predominates in wetlands at high elevations, approximately 600 m a.s.l. (Fig. 5.8). In such a cold wetland forest, no tree species other than *P. glehnii* can invade the environment because of the overhumidity and unstable nature of the soil (Matsuda 1989).

As limestones are found in the southern part of the UTHF (refer to Chap. 3), limestone vegetation has developed in some limited areas. In the Fujimori Special Plant Community Protection Area, where limestone is exposed to the surface (Fig. 5.9a), limestone plants such as *Berberis amurensis*, *Cortusa matthioli* subsp. *pekinensis* (Fig. 5.9b), *Thalictrum foetidum* var. *glabrescens*, and *Asplenium viride* have been found.

The Chikushimori Special Plant Community Protection Area is on a rocky peak (584 m a.s.l.) of Quarts diabase and is located in the westernmost part of the UTHF. Here, several rocky habitat species, such as *Juniperus chinensis* var. *sargentii*, *Spiraea media* var. *sericea* and *Alnus maximowiczii*, were found. A relatively large population of *Rhododendron albrechtii* was found on a rocky steep slope in the Iwaya Special Plant Community Protection Area.

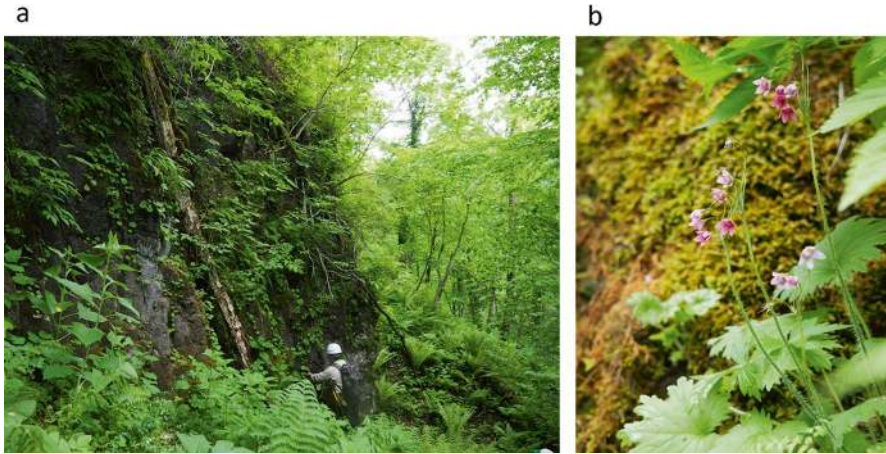


Fig. 5.9 Exposure of limestone (a) and *Cortusa matthioli* subsp. *pekinensis* (b) in the Fujimori Special Plant Community Protection Area. (Photo by Kota Kimura, July 3, 2019. Used with permission from the UTHF, licensed under CC BY-NC-ND 4.0)

There are also serpentine areas in the western parts of the UTHF. However, as most of the areas had been mined to extract asbestos, the original vegetation had already been lost. Only a few serpentine species, such as *Viola sachalinensis* var. *alpina* and *Picris hieracioides* subsp. *japonica*, can be found within the UTHF.

Several blowing caves with cold and warm air vents have been found in the UTHF. In these caves, winds blow directionally due to differences in temperature and air pressure, producing air currents that flow in or out of the cave. In the UTHF caves, winds warmer than the ambient air temperature blow out from the vents in the upper positions of slopes in winter, while winds cooler than the ambient air temperature blow out from the vents in the lower positions in summer. Due to the cool winds in summer, several alpine plant species, such as *Vaccinium vitis-idaea* (cowberry), grow around the lower vents even at lower elevations (Matsui and Iguchi 2001, Fig. 5.10).

5.2 Long-Term Research Plots

The UTHF has established forest plots for monitoring the dynamics of natural forests. Most representatives are the Maeyama long-term ecological research (LTER) plot and the Iwanazawa LTER plot.



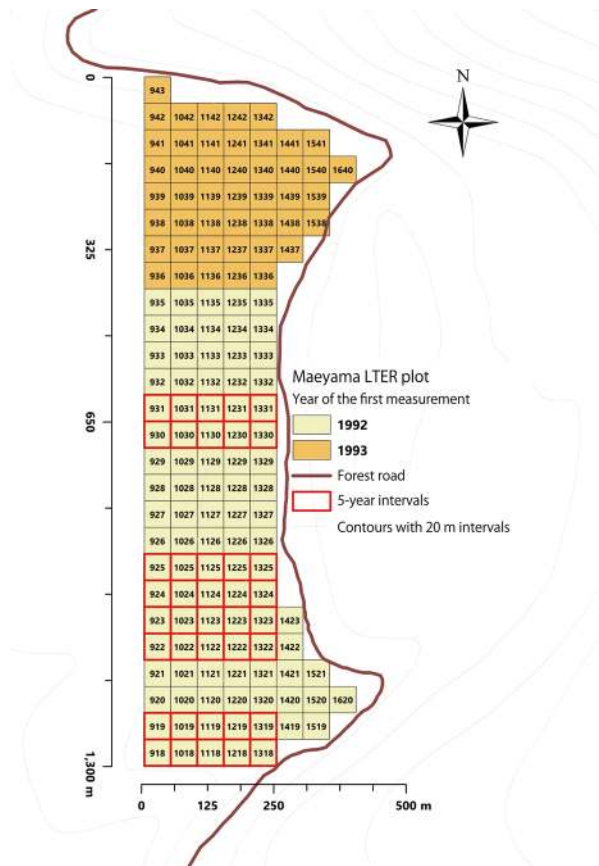
Fig. 5.10 *Vaccinium vitis-idaea* population around the lower vents of the blowing cave in the Nunobe Special Plant Community Protection Area (340 m a.s.l.). (Photo by Satoshi N. Suzuki, September 6, 2024)

5.2.1 Maeyama LTER Plot

The Maeyama LTER plot spans an area of 36.25 hectares (ha) and is situated on the western slope of Mt. Dairoku, ranging between 620 and 680 meters a. s. l. It is located within the Maeyama Forest Reserve, where light selection cutting was carried out once or twice by 1937. However, since then, no logging or human disturbances have taken place, allowing the forest to reach the state of an old-growth natural forest. The plot was established in 1992 and divided into 145 quadrats measuring 50 m by 50 m (Fig. 5.11, Shibano et al. 1996). Measurements of tree diameter at breast height (DBH) have been conducted at 5- or 10-year intervals for trees with a DBH of 5 cm or more (Ogawa et al. 2021a). These measurements were carried out for all quadrats in 1992–1993, 1997–1998, 2007–2008, and 2017–2018 and for 40 of 145 quadrats (10 ha) in 2002, 2012, and 2022. This plot is the largest among those where trees with a DBH of 5 cm or larger have been consistently measured in natural forests in Japan.

The canopy is dominated by boreal conifers, *A. sachalinensis* and *P. jezoensis*, mixed with deciduous broadleaves such as *Tilia japonica*, *Betula ermanii*, and *Ulmus laciniata* (Fig. 5.12). The understory is predominantly occupied by *Sasa senanensis*, with a few patches of mosses and sedges (*Carex* spp.).

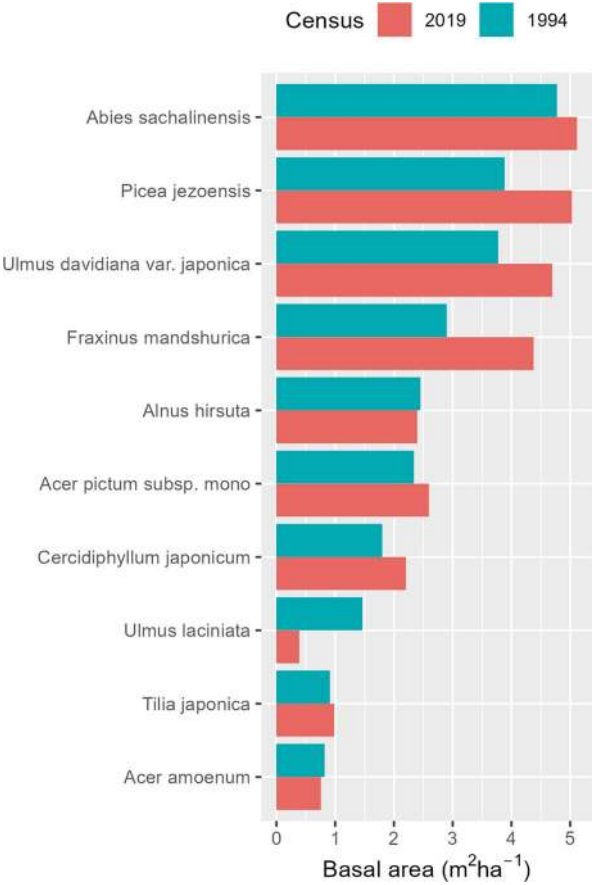
Fig. 5.11 The layout of the Maeyama LTER plot. The number of each square indicates the quadrat ID. (Redrawn from Ogawa et al. 2021a, with the publisher's permission)



The relative dominance of deciduous broadleaves has increased in the plot since the beginning of observation (Fig. 5.13a, Ogawa et al. 2021b). This is mainly because deciduous broadleaves has increased, while conifers have not decreased (Fig. 5.13b). In particular, the relative dominance of deciduous broadleaves was more likely to increase in stands with greater biomass (Fig. 5.13b). A similar increase in deciduous broadleaves has also been reported in other boreal forests in Japan (Suzuki et al. 2015, Hiura et al. 2019) and Canada (Searle & Chen 2017, Hisano et al. 2021). These previous studies suggested that disturbances such as windstorms, climate changes and atmospheric CO₂ enrichment contributed to the increase in deciduous broadleaves (Hiura et al. 2019, Searle & Chen 2017).

The contribution of downed logs to the biodiversity of understory vegetation has been evaluated in the Maeyama LTER (Okada et al. 2019). Not only seedlings of tree species such as *Abies sachalinensis*, *Picea jezoensis*, and *Ulmus laciniata* but also herbaceous species such as *Oxalis acetosella*, *Circaea alpine*, *Dryopteris crassirhizoma*, and *Tiarella polyphylla* were predominantly found on the downed logs. The species compositions of the tree seedlings and herbaceous plants

Fig. 5.12 Basal area of major species at the initial (1992–1993) and most recent (2017–2018) measurements in the Maeyama LTER plot. (Redrawn from Ogawa et al. 2021b, with the publisher’s permission)

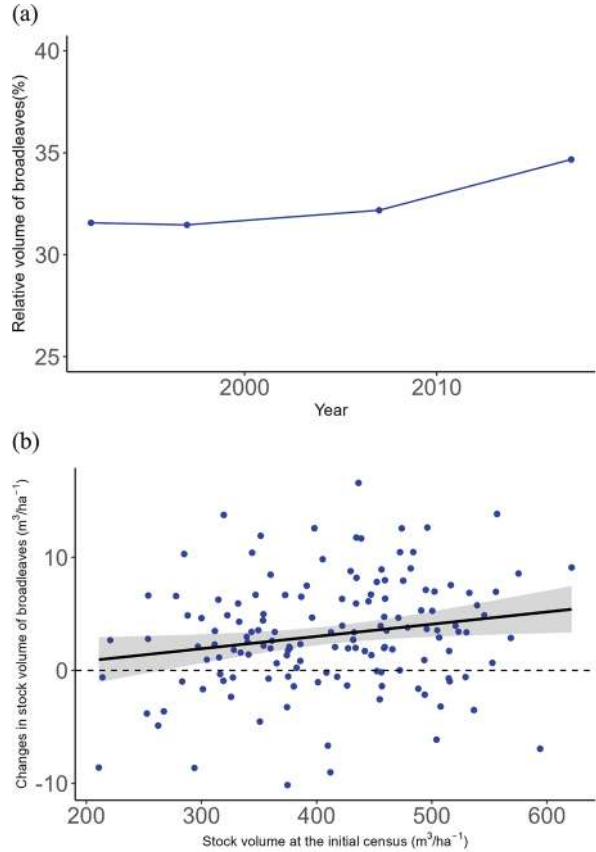


significantly differed between the forest floor and fallen logs and significantly differed between the study quadrats within the habitats (forest floor or downed logs), which contributed to the diversity of the understory in the forest.

5.2.2 Iwanazawa LTER Plot

The Iwanazawa LTER plot is in a riparian forest along the Iwanazawa River. It spans 18.75 ha, is 3200 m from south to north, and ranges from 348 to 411 m a. s. l. In this area, a forest tramway was used until the 1950s, during which time weak selection cutting was carried out. The plot was established in 1994 and divided into 75 quadrats measuring 50 m by 50 m (Fig. 5.14). Measurements of the DBH of trees were carried out for all quadrats in 1994, 1999, 2009, and 2019 and for 21 of the 75 quadrats in 2004 and 2014 (Ogawa et al. 2022a). Therefore, the survey was performed every five years for the 5.25-ha subsamples and every 10 years for the remaining subsamples.

Fig. 5.13 Changes in the relative stock volume of broadleaves (a) and the relationship between changes in the stock volume of broadleaves and the total stock volume at the initial census in each quadrat (b) in the Maeyama LTER. (Redrawn from Ogawa et al. 2021b, with the publisher’s permission)

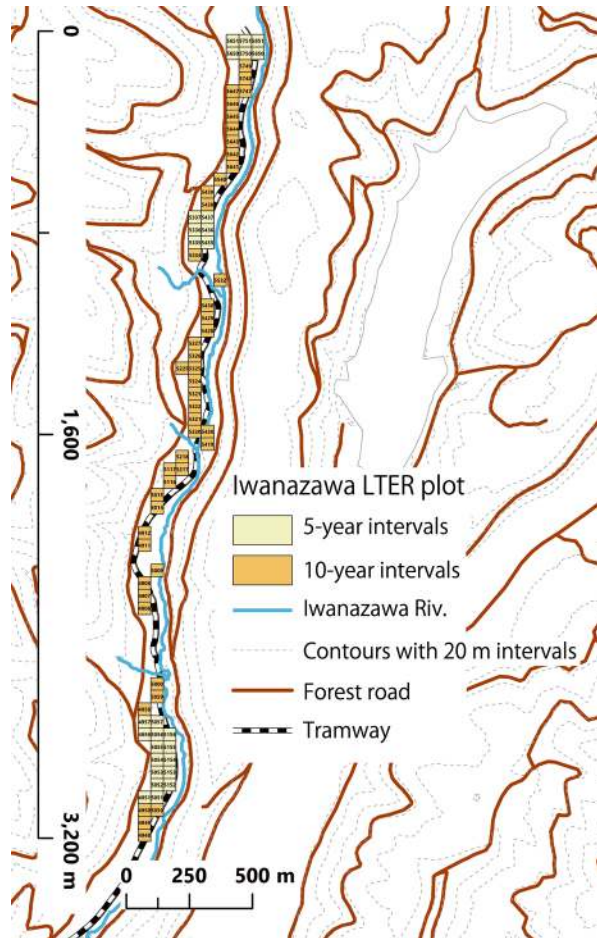


The canopy is dominated by boreal conifers, *A. sachalinensis* and *P. jezoensis* (10.3%), and riparian broadleaved species such as *U. davidiana* var. *japonica*, *F. mandshurica* var. *japonica*, and *Alnus hirtus* (Fig. 5.15, Ogawa et al. 2022b). In particular, light-demanding species such as *U. davidiana* var. *japonica* and *A. hirtus* were more abundant in areas where forest tramway was installed than in intact areas (Ogawa et al. 2022b).

Some tree species in this riparian area, such as *Ulmus laciniata*, *Hydrangea paniculata*, and *Taxus cuspidata*, have been severely damaged by deer (Ogawa et al. 2022b, refer to also Chap. 14). The frequency of stems damaged by deer was greatest in the period between 1999 and 2009, when more than half of the stems of *U. laciniata*, *H. paniculata*, and *T. cuspidata* were bark-stripped. Due to deer damage, the numbers of live stems of *U. laciniata* and *H. paniculata* steeply decreased until 2009 (Fig. 5.16). Although deer abundance in the UTHF did not decrease (refer to Chap. 14), the frequency of deer damage greatly decreased in the following period between 2009 and 2019 (Fig. 5.17). This can be partly attributed to the decrease in the density of these species palatable to deer and may also be due to changes in the behavior and habitat of deer.

In the Iwanazawa Forest Reserve, which includes the Iwanazawa LTER plot, researches on the dispersal patterns of pollen and seeds of species such as *F.*

Fig. 5.14 The layout of the Iwanazawa Long-Term Ecological Research Plot. The number in each square represents the quadrat ID. The term “tramway” indicates the rail trace detected in the digital elevation model computed from aircraft LiDAR. The tramway was removed in the 1950s. (Redrawn from Ogawa et al. 2022a, with the publisher’s permission)



mandshurica var. *japonica* (Goto et al. 2006), *Cercidiphyllum japonicum* (Nakanishi et al. 2021), Todo fir *A. sachariensis* and *P. jezoensis* (Lian et al. 2008), *Juglans mandshurica* var. *sachalinensis* (Kimura et al. 2012), as well as studies on the genetic structure of species such as *F. mandshurica* var. *Japonica* (Goto et al. 2006), *C. japonicum* (Sato et al. 2006), and *P. jezoensis* (Kitamura et al. 2018), have been actively conducted using a molecular ecological approach. These studies revealed that long-distance dispersal, exceeding 1 km, frequently occurs among these riparian tree species (Fig. 5.18) and that landscape-scale genetic exchange between riparian and adjacent nonriparian forests occurs, indicating that gene flow from external sources plays an important role in maintaining genetic diversity. Considering these points, to conserve riparian forests effectively, it is essential to protect not only the riparian forests themselves but also the surrounding forests.

Based on 6 years of observations of the survival of *P. jezoensis* and *A. sachalinensis* plants, Okada et al. (2015) reported that genetic diversity significantly affected the survival of plants on the forest floor in the Iwanazawa Forest Reserve. They

Fig. 5.15 Basal area of major species at the initial (1994) and latest (2019) measurements in the Iwanazawa LTER plot. (Redrawn from Ogawa et al. 2022b, with the publisher’s permission)

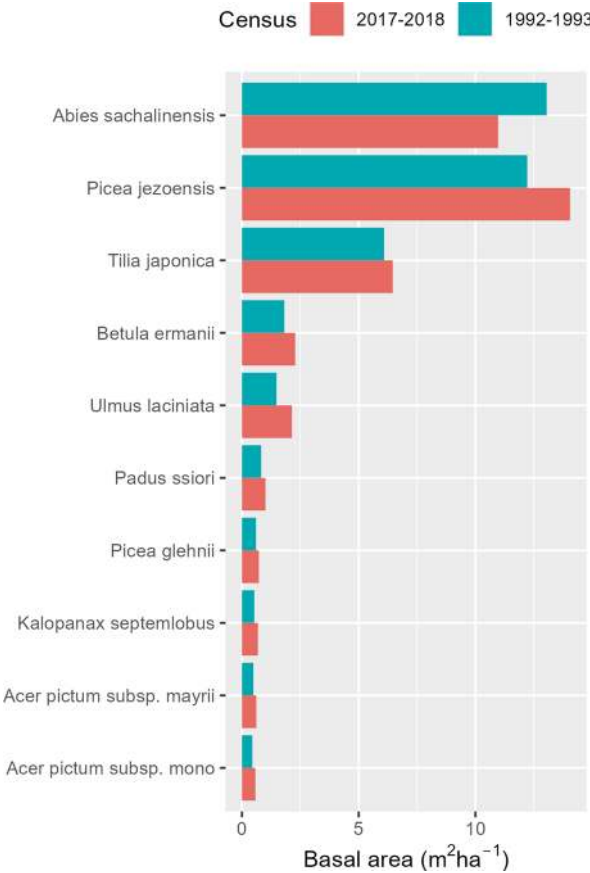
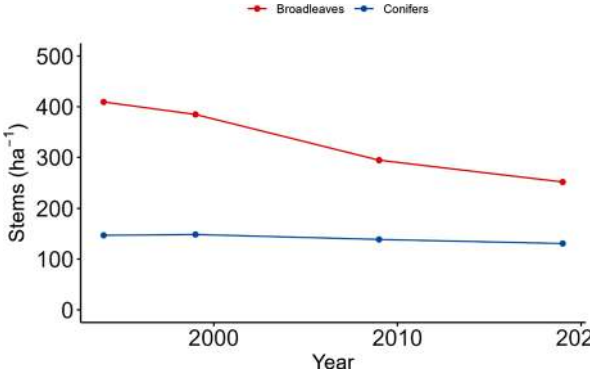


Fig. 5.16 Changes in stem density of conifers (blue) and broadleaves (red) in the Iwanazawa LTER plot. (Data source: UTHF)



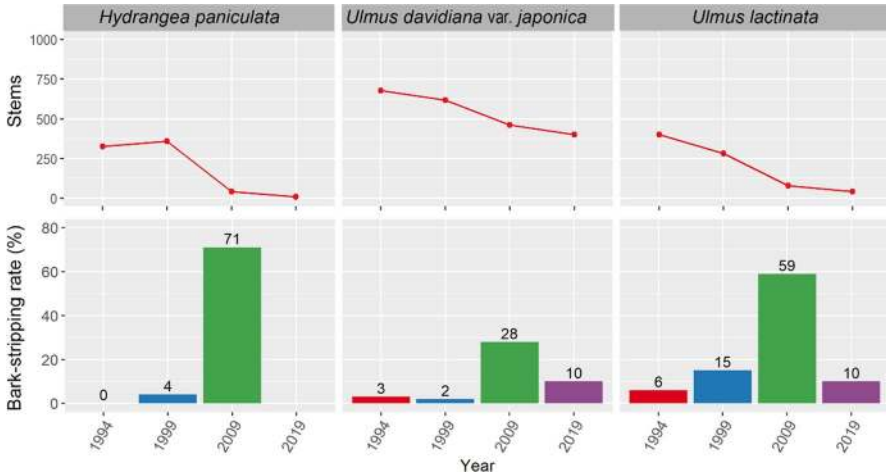


Fig. 5.17 Changes in stem density (upper) and bark-stripping rate (lower) of the deer-favoring species *Hydrangea paniculata*, *Ulmus davidiana* var. *japonica*, and *Ulmus laciniata* in the Iwanazawa LTER. The bark-stripping rate was calculated as the proportion of newly debarked stems that had not been recorded as debarked at previous census, relative to the total number of live stems at each census. (Redrawn from Ogawa et al. 2022b, with the publisher’s permission)

evaluated multilocus heterozygosity (MLH) of seedlings and found that heterozygous individuals lived longer than homozygous individuals for *P. jezoensis* (Fig. 5.19); this was the first study to directly quantify the effects of the MLH on the survival rate of forest tree seedlings.

5.2.3 Natural Forest Management Experimental Plots

Since 1955, the UTHF has also established multiple smaller long-term research plots, currently referred to as Natural Forest Management Experimental Plots. The plot size is typically 0.25 ha but ranges from 0.04 to 2.25 ha. These plots were established for the purpose of evaluating the effects of harvesting and estimating the growth rates of forest stands (see also Chap. 8) and have been utilized for a variety of studies. The stand growth, stem growth, and size structure of natural forests under the selection system have been evaluated (Ishibashi and Hirokawa 1986, Ishibashi 1986, Hirata et al. 1987, Hirata and Ishibashi 1987, Tatsuhara et al. 1995, Fig. 5.20). Kitabatake et al. (2003) evaluated the effects of selection cutting on the population dynamics of *A. sachalinensis* and reported that the number of small stems decreased and that the turnover rates of stems decreased during 30 years of dynamics under the selection system. Tatsumi and Owari (2013) and Tatsumi et al. (2016) developed individual-based growth modeling considering the effects of neighborhood competition for predicting long-term effects of selection cutting on forest structure.

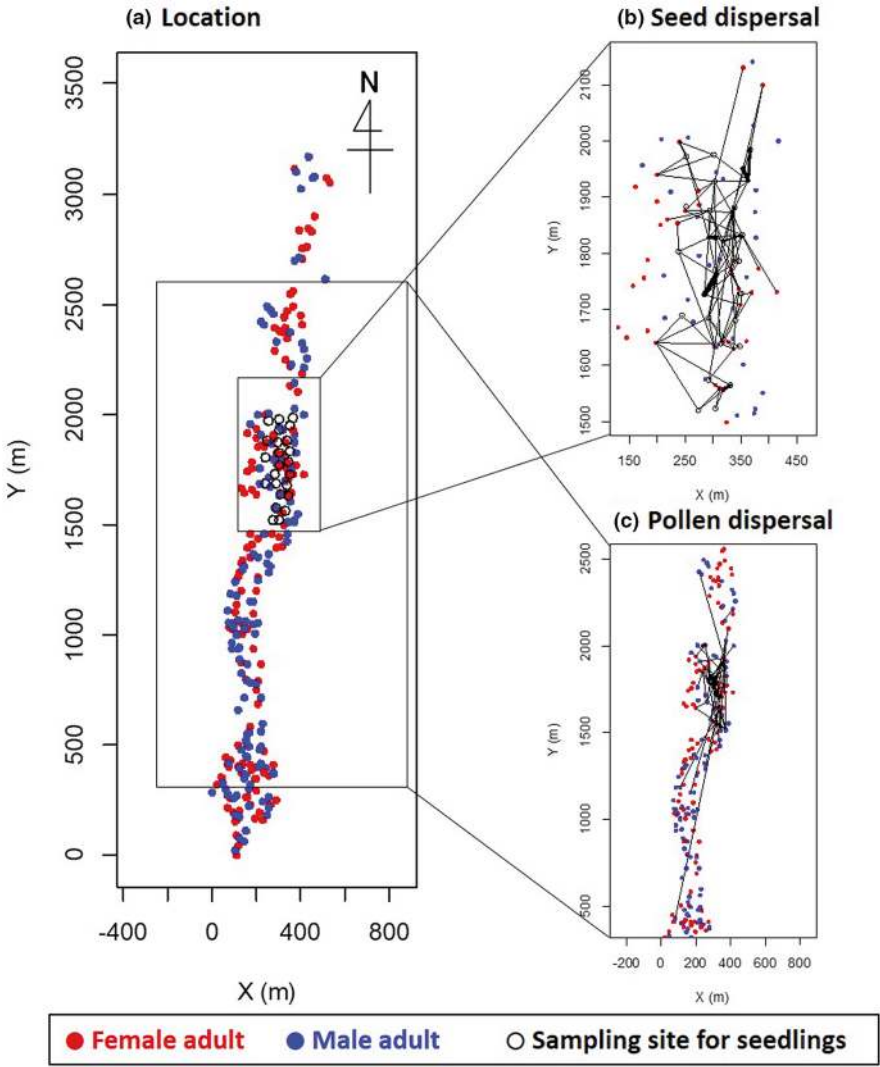


Fig. 5.18 Pollen and seed dispersal of *Cercidiphyllum japonicum* in the Iwanazawa Forest Reserve. (a) Locations of the female (blue dots) and male (red dots) adults surveyed and sampling sites for the seedlings (open circles). (b) Seed and (c) pollen dispersal estimated by genetic analysis. The segments indicate the detected dispersals, and the thickness of each segment increases with increasing frequency of dispersal. (Reproduced from Nakanishi et al. 2021, published under CC BY 4.0)

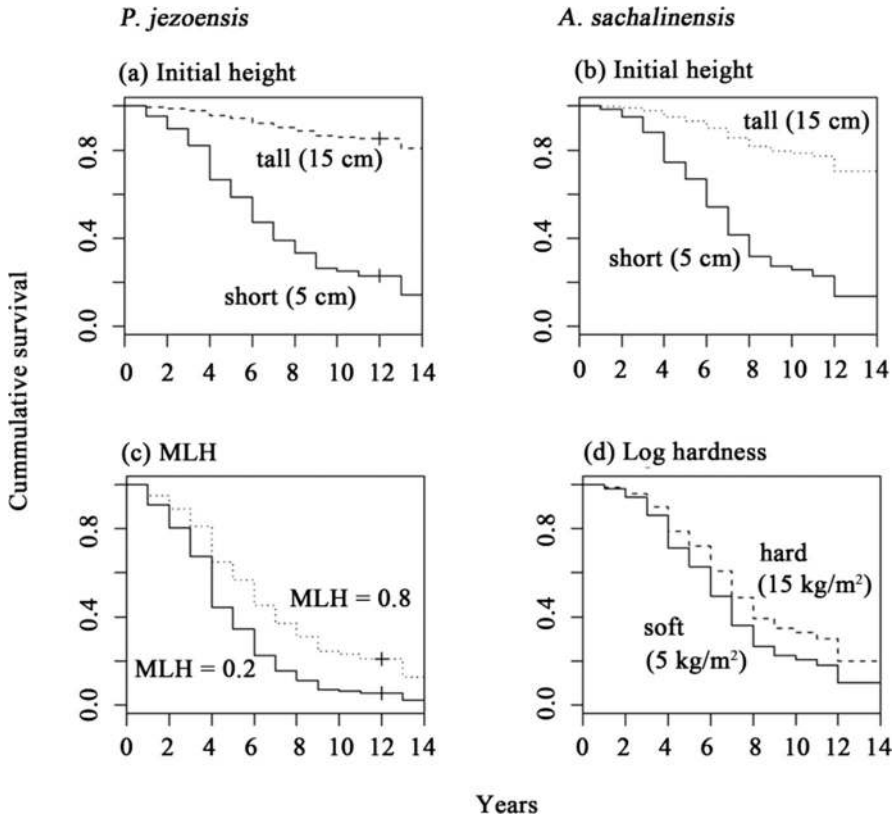


Fig. 5.19 Estimated seedling survival functions for *Picea jezoensis* (a, c) and *Abies sachalinensis* (b, d) and effects of initial height (a, b), multilocus heterozygosity (MLH, c) and hardness of logs where seedlings were present (d). Note that a higher MLH individual of *P. jezoensis* has a longer longevity in (c). (Reproduced from Okada et al. 2015, published under CC BY 4.0)

5.3 Other Ecological Studies on Forest Stands and Vegetation

5.3.1 Biodiversity Experiment

In recent decades, biodiversity-ecosystem function (BEF) has been vigorously studied worldwide via both experimental and field approaches (Ali 2023). In the typical experimental approach, ecosystem functions such as productivity are compared between study quadrats with different numbers of planted species. Initial experimental studies mostly used only herbaceous species due to the feasibility of experimental treatments, but several large-scale experimental studies using tree species started in the 2000s (<https://bef-china.com/refer> to TreeDivNet, <https://treedivnet.ugent.be/>). Prior to these studies, a small-scale biodiversity experiment was initiated

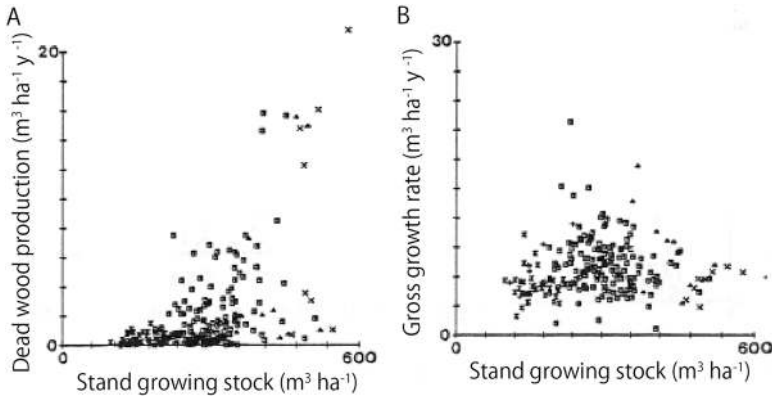


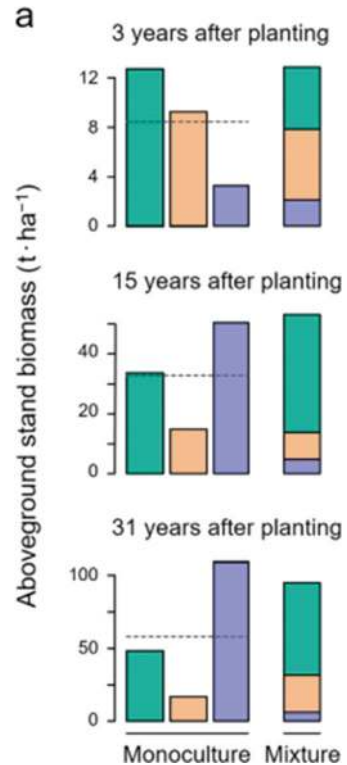
Fig. 5.20 Relationships between the stand growing stock and dead wood production (a) and between the stand growing stock and gross growth rate (b) in the Natural Forest Management Experimental plots. (Modified after Ishibashi and Hirokawa 1986 by Satoshi N. Suzuki, with the publisher's permission)

at the UTHF in 1987 (Tatsumi 2020). Mixed stands of three species (pioneer *Betula*, mid-successional *Q. crispula*, and shade tolerant, *A. sachalinensis*) and monocultures of each of the three species were set up. At 31 years after planting, the total aboveground biomass of the three-species mixed stands was significantly greater than the average biomass of the monocultures of the three species (Fig. 5.21) and increasing complementarity effects as stand development contributed to the diversity effects of the mixture (Tatsumi 2020). This finding indicates that mixed forests are more efficient at producing woods of diverse species than a combination of monocultures of multiple species. Recently, Tatsumi and Loreau (2023) developed an analytical method for partitioning biodiversity effects into “density-mediated effects” and “size-mediated effects” and found that size-mediated effects (i.e., growth of trees) contributed to net diversity effects at early stages (≤ 3 years), but density-mediated diversity effects (i.e., mortality) mostly contributed at later stages. This indicates that mixing promotes tree growth via canopy packing in the young stage and that reduced mortality via the complementary use of canopy space enhances stand growth in mixtures.

5.3.2 Elevational Adaptation Studies

Transplanting and common garden experiments are two of the most popular and effective tools for assessing the local adaptation of plant species. Especially, a reciprocal transplant experiment is a powerful tool for detecting local adaptation (Kawecki and Ebert 2004); nevertheless, very few studies have been conducted in conifers. In the UTHF, several transplanting and provenance experiments, including reciprocal transplanting, have been conducted to evaluate the genetic adaptations of

Fig. 5.21 Aboveground stand biomass in the monoculture and mixed stands of *Betula maximowicziana*, *Quercus crispula*, and *Abies sachalinensis* at 3, 15, and 31 years after planting. The horizontal dashed lines indicate the mean values across the monocultures. The difference between the mixture and the mean value of monocultures can be considered the “diversity effect.” (Reproduced from Tatsumi 2020, published under CC BY 4.0)



local populations of forest tree species to elevational gradients within the UTHF. The most studied experimental system is the transplanting experiment of *A. sachalinensis*.

The environment, such as temperature, snowfall, and wind speed, changes markedly with elevation. Elevational variation in the growth and morphology of *A. sachalinensis* seedlings was of early interest to researchers. In common garden experiments in which seedlings from high- and low-elevation populations were grown simultaneously in a mild (low-elevation) environment, individuals from high-elevation populations often ceased growing earlier, resulting in smaller seedlings (Oleksyn et al. 1998). While such patterns are commonly reported for conifers, these results alone might suggest that seedlings from lower elevations grow better in any environment. To determine whether this was due to the local adaptation, the UTHF initiated a reciprocal transplant experiment in the 1970s. Open-pollinated seeds of *A. sachalinensis* were collected from eight elevational populations (230 m, 340 m, 420 m, 530 m, 730 m, 930 m, 1100 m, and 1200 m) in 1973. After growing in the nursery, seedlings derived from these populations were planted at six sites (230 m, 420 m, 530 m, 730 m, 930 m, and 1100 m) in 1976 (Kurahashi and Hamaya 1981). Then, the effects of population and site on the phenology, mortality, and growth of 1- to 7-year-old plants were evaluated. Seedlings derived from low-elevation populations exhibited better growth at several sites near the native altitude, whereas high-elevation populations exhibited a low growth rate across all sites (Fig. 5.22).

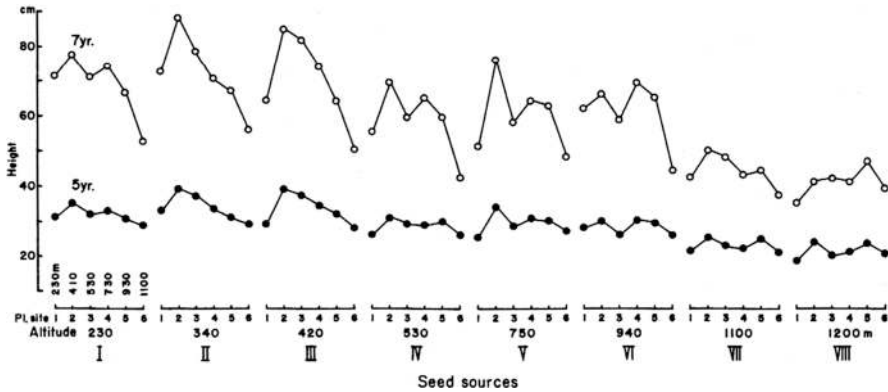


Fig. 5.22 Tree height of 5-year-old (closed circles) and 7-year-old (open circles) *Abies sachalinensis* seedlings in all combinations of seed source elevation (Roman number) and planted site elevation (Arabic number). (Reproduced from Kurahashi and Hamaya 1981, with the publisher's permission)

Furthermore, a mathematical model using data on survival rate and tree height from the early to 36th years at the experimental site confirmed that the average tree height $\times$ survival rate decreased with elevational distance from the native site, indicating a native site advantage (Fig. 5.23, Ishizuka and Goto 2012). The results of the 36-year study showed that the low-elevation populations had good growth and survival at low elevations but very low survival at high elevations and that the high-elevation populations had better growth and survival at high elevations but less growth at low elevations than did the low-elevation species. These findings on elevational adaptation in conifers were the result of long-term, large-scale reciprocal transplant experiments conducted in this study.

A high-elevation (1200 m) $\times$ low-elevation (530 m) interelevation crossbreeding test site was also created (Kurahashi and Hamaya 1981). The experiment revealed that tree height followed the pattern: high $\times$ high $<$ high $\times$ low $\approx$ low $\times$ high $<$ low $\times$ low, indicating that the reduced growth at high elevations was inherited. For DBH, the results suggested that a reduced vigor, known as distant-cross weakness, occurred in offspring of distantly related crosses, resulting in values lower than the parents' average. (Goto et al. 2011). The number of cones in the study area was counted using an elevated vehicle over a 4-year period, and the results showed that high $\times$ high $>$ high $\times$ low $>$ low $\times$ low $>$ low $\times$ high in the fertile years. In other words, reproduction clearly differed between the forward and reverse modes of the cross type, suggesting that there may be a mother-tree effect or epigenetic influence (Hisamoto and Goto 2017). These F_1 individuals are suitable materials for mapping individuals for linkage analysis. Therefore, a mapping population was made by artificial pollination in 2011 using two high $\times$ low individuals. The study also examined the genotyping, seedling phenology, and initial growth of the mapping population in the nursery and performed QTL analysis using a linkage map of *A. sachalinensis* with SNP markers via RAD-seq on a next-generation sequencer to identify QTLs

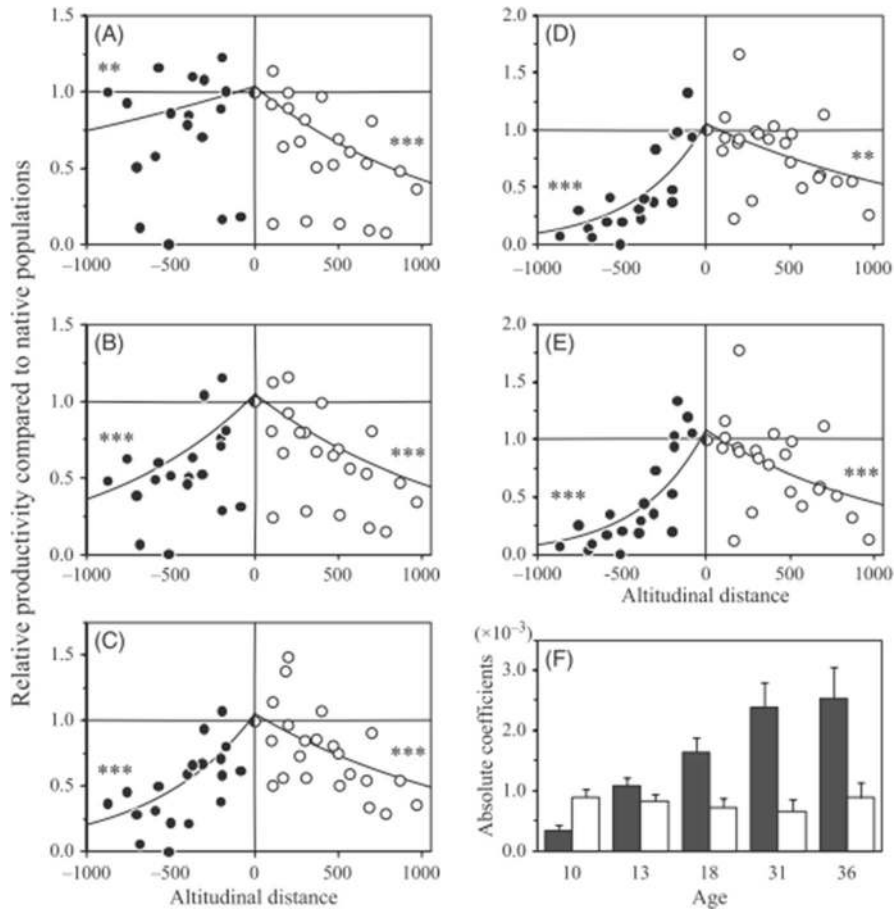


Fig. 5.23 The magnitude of the home-site advantage across the altitudinal range for trees of different ages (a–e) and its behavior over time (f) in the transplant experiments between different elevation sites. Relative productivities were calculated based on the performance of the transplanted population relative to that of the local population at a given planting site. The plots were arranged in order of the altitudinal distance, DIST, that is, the difference between the elevation of the seed source and the elevation of the planting site, to determine whether the local plants (DIST = 0) outperformed the transplants. The letters a to e refer to the different testing ages, that is, 10, 13, 18, 31, and 36 years, respectively. A negative DIST value (closed circle) indicates upward translocation, and positive DIST value (open circle) indicates downward translocation. Lines indicate the results of regression analyses with the associated significance level, *** $P < 0.001$, ** $P < 0.01$. The variation in the magnitude of the home-site advantage over time (f) is shown in terms of the absolute coefficient of DIST in the regression analysis for trees transplanted upslope (closed bar) and downslope (open bar). The error bars indicate the standard error. A steeper slope reflected more severe transfer effects. (Reproduced from the author’s original work, Ishizuka and Goto 2012, published under CC BY-NC)

linked to the trait (Goto et al. 2017). Furthermore, the obtained seedlings were transplanted into long pots, and their photosynthetic and other traits were measured; subsequently, the plants were planted and subjected to linkage analysis for growth traits, and QTLs for Φ_{NO} , one of the photosynthetic parameters, and crown area were detected (Goto et al. 2021).

A common garden experiment of *P. jezoensis* from a range of elevations was also established in 1990. Seeds were collected from 420, 530, 600, 700, 950, 1100, and 1200 m a. s. l. in the fall of 1983 (Nakagawa et al. 2003). Seven-year-old seedlings from all of the elevations were planted at 610 m a.s.l. in elevation, and seedlings from 420, 700, and 1200 m were planted at 750 m a.s.l. in September 1990. Although there was no difference in the timing of bud opening between populations from different elevations in 1997 (Nakagawa et al. 2003), tree height tended to decrease with elevation in 2004 (Fig. 5.24a). The difference was more apparent in 2017 (Fig. 5.24b). This finding implies that boreal conifers, including *A. sachalinensis* and *P. jezoensis*, are also genetically adapted to local elevational conditions, although further studies are needed to assess the nongenetic effects, such as maternal effects or epigenetic variation.

5.3.3 Long-Term Plant Phenology Observations

The UTHF has a long history of phenology observation of budburst, leaf coloration, leaf shedding, and flowering in dozens of tree species (Kamata 2019a). Phenological observations of 43 UTHF species started in 1930 (Nakayama and Kunugi 1940). Although target species have changed over time, the phenology of approximately 30–50 species has been recorded every year except in 1951 (Kamata et al. 2019; Kimura et al. 2022). Unfortunately, the original data during the period 1938–1959 were lost, and only the average values for each species were reported by Kunugi (1952) and Kunugi and Sasaki (1961). As there were some mismatches in the reported values for the same years between the two previous papers, Kamata (2019b) estimated the average values among them.

Long-term data have provided strong evidence of the phenological responses of trees to climate change. While Kimura et al. (1995) reported that the timing of budburst and flowering were significantly correlated with spring temperature, no distinct shift in phenological timing was observed from 1958 to 1993, suggesting that the effects of climate warming were not clear until 1993. However, recent data spanning the last 40 years revealed clear shifts in the phenological timing for nearly all species (Fig. 5.25).

The UTHF maintains a diverse plant community, a result likely influenced by the varied environmental conditions and the establishment of numerous conservation areas (refer also Chap. 15). This vegetational diversity helps to protect a wide range of habitats, contributing to the overall diversity of the ecosystem (refer to also Chap. 6). Furthermore, long-term ecological research at the UTHF has provided valuable insights into the fundamental dynamics of hemiboreal forests, enhancing our

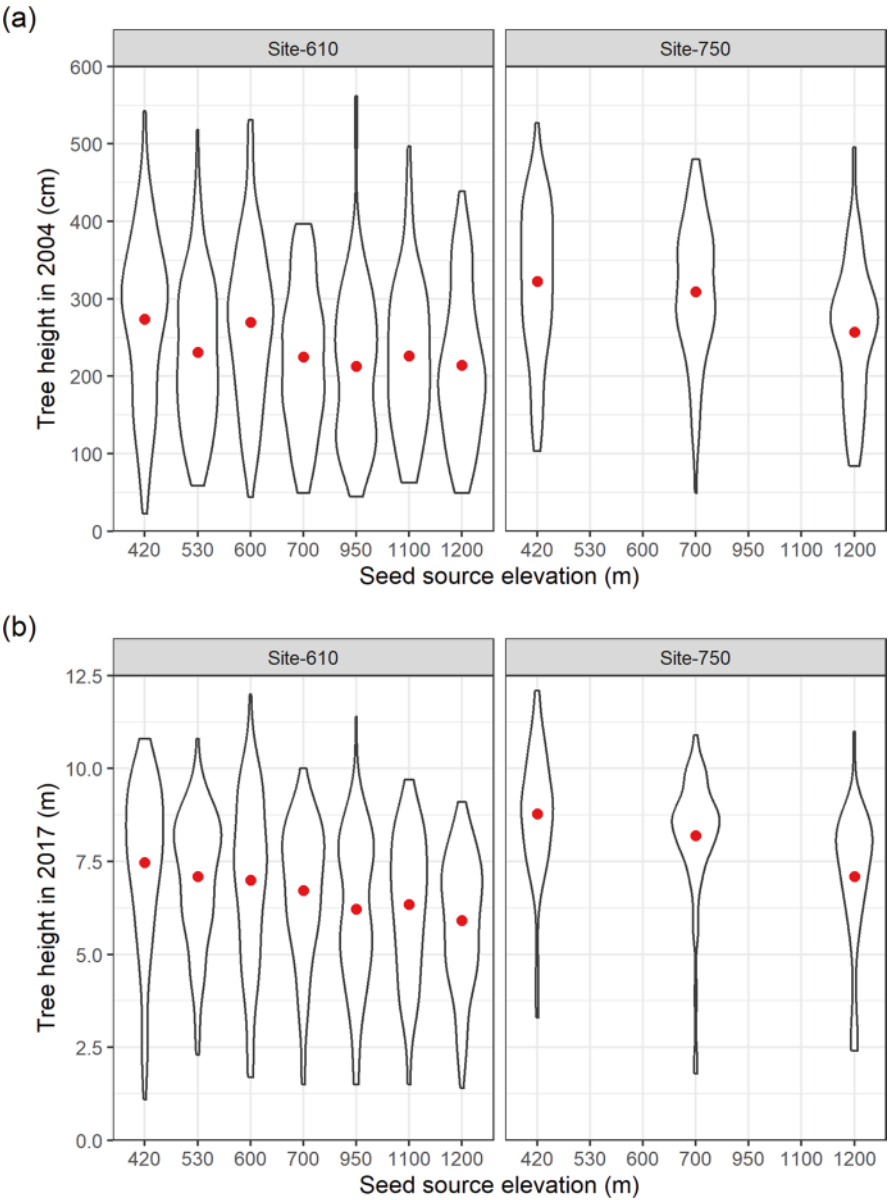


Fig. 5.24 The frequency distribution of tree height of *P. jezoensis* from different elevations at the two sites, measured at 15 years old (a) and 28 years old (b). The red closed circle indicates the average. (Data source: the UTHF)

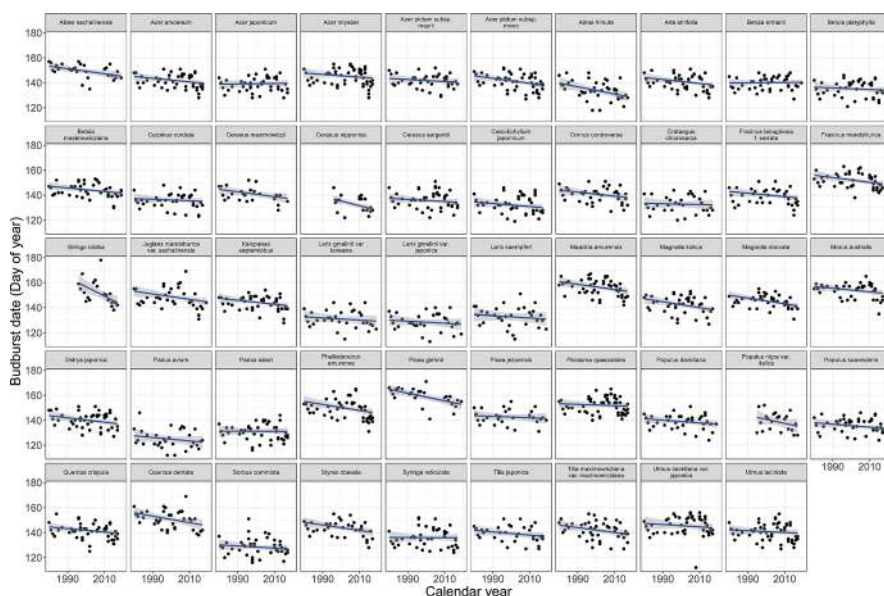


Fig. 5.25 Forty-year observations (1981–2020) of budburst timing of 49 species in the UTHF. (Data compiled from Kamata et al. 2019 and Kimura et al. 2022)

understanding of these complex systems. Based on this extensive body of knowledge, the UTHF has adopted sustainable methods of forest management practices, the Stand-based Silvicultural Management System, that promote the natural regeneration of the forest and maintain ecological balance (refer to Chap. 7). By avoiding extensive clear-cutting, the UTHF ensures that the large portion of the forest remains in a mature or old-growth natural state, which is crucial for the survival of many species and the overall health of the ecosystem.

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