

DISTRIBUTION AND GROWTH OF *PINUS PUMILA* REGEL ALONG
THE *LARIX GMELINII* (RUPR.) RUPR. TIMBERLINE ECOTONE
OF MT. DAL'NYAYA PLOSKAYA, CENTRAL KAMCHATKA

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Abstract: Variation in distribution and growth of *Pinus pumila* REGEL was described along a timberline ecotone of *Larix gmelinu* (RUPR.) RUPR. from the closed forest margin (910 m altitude) up to the last trees of *L. gmelinu* (960 m altitude) on the western slope of Mt. Dal'nyaya Ploskaya, central Kamchatka. *P. pumila* occurs exclusively within the range of *L. gmelinu*; it never appears in a closed forest below the timberline ecotone, and stopped at ca 100 m before the last trees of *L. gmelinu* in the upper part of the ecotone. The mean annual stem elongation of *P. pumila* maintains constant value (around 5 cm/yr) at a stand along the ecotone under the protection of *L. gmelinu* trees providing wind-shelter, ameliorated temperature extremes and higher humidity. The distribution and growth pattern of *P. pumila* suggest that *P. pumila* is ecologically one of an undergrowth element of *L. gmelinu* forests. Among the distribution areas of *P. pumila*, it can make its own vegetational zone only in restricted regions with peculiar environments where the thermal regime alone potentially permits arborescent trees to establish a forest, but in practice strong wind, snow and the exposure of a rocky substrate prohibit them from forming a forest zone. Such regions include high mountains of Japan and some mountains in Far East Russia.

key words: *Larix gmelinu*, Kamchatka, *Pinus pumila*, timberline ecotone, vegetation zonation

Introduction

Pinus pumila REGEL is one of the major components of boreal and subalpine vegetation in north-eastern Eurasia including north-eastern Siberia, Far-East Russia, north-eastern China, the Korean Peninsula and Japan. It is an element of the *Larix gmelinii* (RUPR.) RUPR. forests (Nomenclature follows VOROSHILOV (1982)), as an understory dominant in Siberia and Far-East Russia within its distribution range (TIKHOMIROV, 1946; KIL'DYUSHEVSKI, 1965; GORCHAKOVSKY and SHIYATOV, 1978; GRISHIN, 1995). However, it forms a distinct vegetational zone, *P. pumila* zone, above the forest limit in the subalpine region of the high mountains of Japan (OKITSU and ITO, 1989). No arborescent trees such as *Picea jezoensis*, *Abies sachalinensis*, and *L. gmelinii* occur in the *P. pumila* zone. A similar vegetational zone of *P. pumila* appears also in some mountains in Far East Russia (GORCHAKOVSKY and SHIYATOV, 1978; HULTÉN, 1972; NESHTAYEV and NESHTAYEVA, 1975). OKITSU and ITO (1989) conclude

that the formation of the *P. pumila* zone of Hokkaido, northern Japan is due mainly to strong wind, snow and substrate conditions in the high mountains within the thermal regime of the forest zone. It may be presumed, from this conclusion, that *P. pumila* shows two different ecological relationships to *L. gmelinii*, an understory element of the *L. gmelinii* forests and the dominant plant of the vegetation zone where *L. gmelinii* is absent. Those two relationships may be related to the environmental conditions of the sites. A comparative study on the distribution and growth of those two species will be necessary to understand more clearly the ecological relationships between them in a site where they occur sympatrically.

On the Kamchatka Peninsula, Far East Russia, occurrence of *L. gmelinii* is confined to the central part of the peninsula, forming a conifer island surrounded by *Betula ermanii* forests. It forms a timberline ecotone on mountain slopes (OKITSU, 1997). *P. pumila* usually forms a shrub layer under *L. gmelinii* open forests around the timberline ecotone (GRISHIN, 1993). Mt. Dal'nyaya Ploskaya, central Kamchatka, shows such a representative occurrence of those two species.

A number of studies have described the general ecology of *P. pumila* on the Kamchatka Peninsula (e.g. NESHATAYEV and NESHATAYEVA, 1975; GRISHIN, 1994, 1996; KHOMENTOVSKY, 1994, 1995); of them KHOMENTOVSKY (1995) comprehensively reviewed the various aspects of its ecology such as species composition, community dynamics, growth, distribution and vegetation history. However, there is still no study that focuses on the ecological relationship between *P. pumila* and *L. gmelinii* occurring sympatrically in the timberline ecotone in Kamchatka. OKITSU (1997) documented the changes in the size structure, height growth and regeneration of *L. gmelinii* along the timberline ecotone of Mt. Dal'nyaya Ploskaya. He did not focus, however, on the growth and distribution of *P. pumila* along the *L. gmelinii* timberline ecotone.

This paper describes the changes in the scrub cover and height of *P. pumila* along the *L. gmelinii* timberline ecotone of Mt. Dal'nyaya Ploskaya. It also discusses the ecological relationship of *P. pumila* and *L. gmelinii*, based on the distribution and the growth patterns of these two species.

Study Site

Mt. Dal'nyaya Ploskaya is a late-pleistocene volcano (4050 m altitude), situated in the Klyuchevskaya volcano group, central Kamchatka at 56°04'N, 160°27'E (Fig. 1). The lower part of the mountain, ranging from ca. 200 m to 1200 m altitude, consists of a gently sloping lava plateau, with a slope usually less than 10° inclination.

The vegetation around the timberline ecotone consists mainly of the following types: 1) open woodland of *L. gmelinii* with undergrowth of *P. pumila* scrub, which develops on the gentle slopes and ridges covering the widest area of this ecotone, 2) forest islands of *Betula ermanii* occupying usually rather steep slopes and hollows of valley heads, 3) *Alnus maximowiczii* shrubs appearing sporadically on fairly steep slopes and hollows of valley heads, and 4) subalpine meadows dominated mainly by *Geranium erianthum*, *Calamaglostis langsdorfii*, *Epilobium angustifolium*, *Aruncus dioicus*, etc., mixing with forest islands of *B. ermanii*. The alpine tundra gradually replaces the open woodland of *L. gmelinii* (OKITSU, 1996).

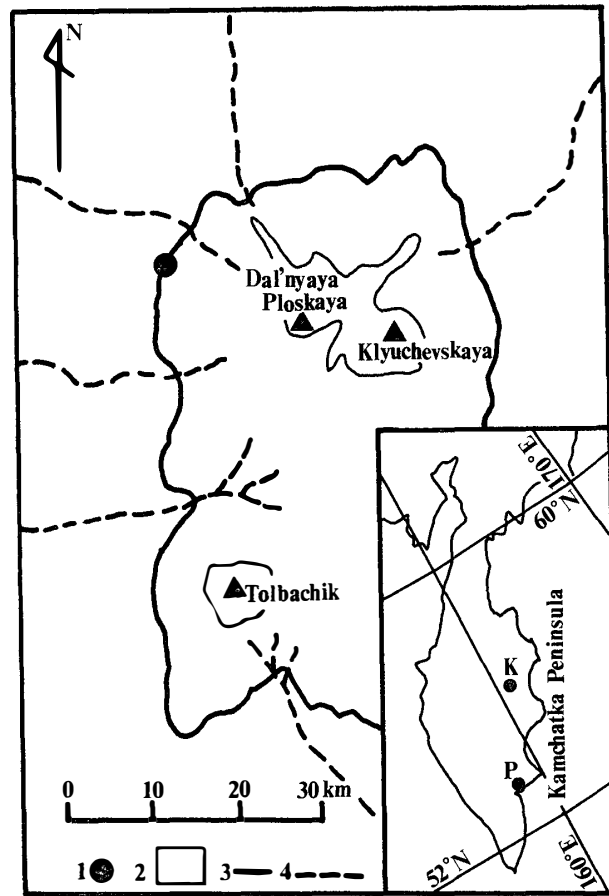


Fig. 1. Location of Mt Dal'nyaya Ploskaya in the Klyuchevskaya volcano group, central Kamchatka and approximate position of study transect (modified after GRISHIN, 1988a). The Klyuchevskaya volcano group includes Mt. Tolbachik (3624 m), Mt. Klyuchevskaya (4750 m) and Mt. Dal'nyaya Ploskaya (4050 m). Mt. Klyuchevskaya is the highest peak on the Kamchatka peninsula. The region between the closed forest limit and cold rock desert and glaciers is covered by alpine tundra vegetation.
 P: Petropavlovsk-Kamchatsky, K. Klyuchevskaya volcano group.
 1: Approximate position of study transect, 2: Cold rock desert and glaciers, 3: Closed forest limit, 4: Dry river.

The *L. gmelinii* closed forest limit is situated at 910 m altitude on the west slope of the mountain. *L. gmelinii* gradually reduces both its tree height (from 12 m to 0.3 m) and total basal area (from 40 m²/ha to less than 2 m²/ha) upward, forming a timberline ecotone (OKITSU, 1997). The last trees of *L. gmelinii* occur at 960 m altitude, 280 m distance from the closed forest margin.

Methods

A 300 m long transect was established along the timberline ecotone, from the margin of the closed forest (910 m altitude) to the uppermost trees of *L. gmelinii* (960 m altitude), on the west slope of the mountain (Fig. 1). Thirty successive stands (10 by 10 m) were set along the transect. In each stand, two crown diameters (the long axis and the short

axis) of all trees of *L. gmelinii* taller than 200 cm were measured. Naturally *L. gmelinii* trees shorter than 200 cm are also present (OKITSU, 1997), but in this paper they are not mentioned because this paper focuses chiefly on the relationship between high trees of *L. gmelinii* and *P. pumila*. The crown projection area was then calculated as an ellipse from the two axes. The cover and the maximum height of *P. pumila* scrub was also recorded when it occurs in a stand.

Annual stem elongation (height growth) of *L. gmelinii* trees was estimated for one to five selected trees including the largest individual in diameter at breast height. The height growth was calculated as tree height (cm)/tree age (years). Tree age was measured by counting the tree rings in cut stems. Height growth was estimated in stands located 90 m distance from the closed forest margin. Annual stem elongation of *P. pumila* was also estimated for one to five stems in stands where *P. pumila* scrub occurs, on the basis of stem length and stem age counted by cutting.

Results

Changes in the crown area of *L. gmelinii*, and the cover and the height of *P. pumila* scrub
Larix gmelinii kept the crown area of 0.8 ha/ha at the closed forest margin (Fig. 2A). It reduced the crown area to 0.4 ha/ha up to 190 m distance from the forest margin. It decreased sharply from there upward to the last trees (280 m).

Pinus pumila occurred from the closed forest margin to 190 m (Fig. 2B) on the transect. It never appeared in a closed forest. It stops at the 190 m point on the transect. The range of *L. gmelinii* completely overlapped that of *P. pumila* on the transect. The cover of *P. pumila* scrub constantly maintained ca. 20–40% up to 170 m, showing a peak of 60% at 90 m. It sharply decreased to less than 10% at the upper limit of *P. pumila*. The sharp reduction of the scrub cover of *P. pumila* coincided well with the sharp reduction of the crown area of *L. gmelinii*.

The scrub height of *P. pumila* maintained 150–200 cm up to 170 m, but it sharply decreased to ca. 30 cm, similar to the height of scrub cover, at the upper end of the *P. pumila* range (Fig. 2C).

Growth of *L. gmelinii* and *P. pumila*

The maximum annual stem elongation (height growth) of *L. gmelinii* in a stand maintained ca. 14 cm/yr up to 210 m (Fig. 3A). It decreased to ca. 3 cm/yr at the last trees of *L. gmelinii*. The annual height growth varied widely within a stand.

The annual stem elongation of *P. pumila* remained at ca. 5 cm/yr from the closed forest margin to its upper distribution limit (Fig. 3B). It slightly decreased toward the upper distribution limit of *P. pumila*, but this trend is not obvious. It did not vary widely within a stand, keeping a rather constant value throughout its distribution range.

Discussion

Distribution of *P. pumila* along the timberline ecotone

The most prominent feature of the distribution of *P. pumila* in this ecotone is that

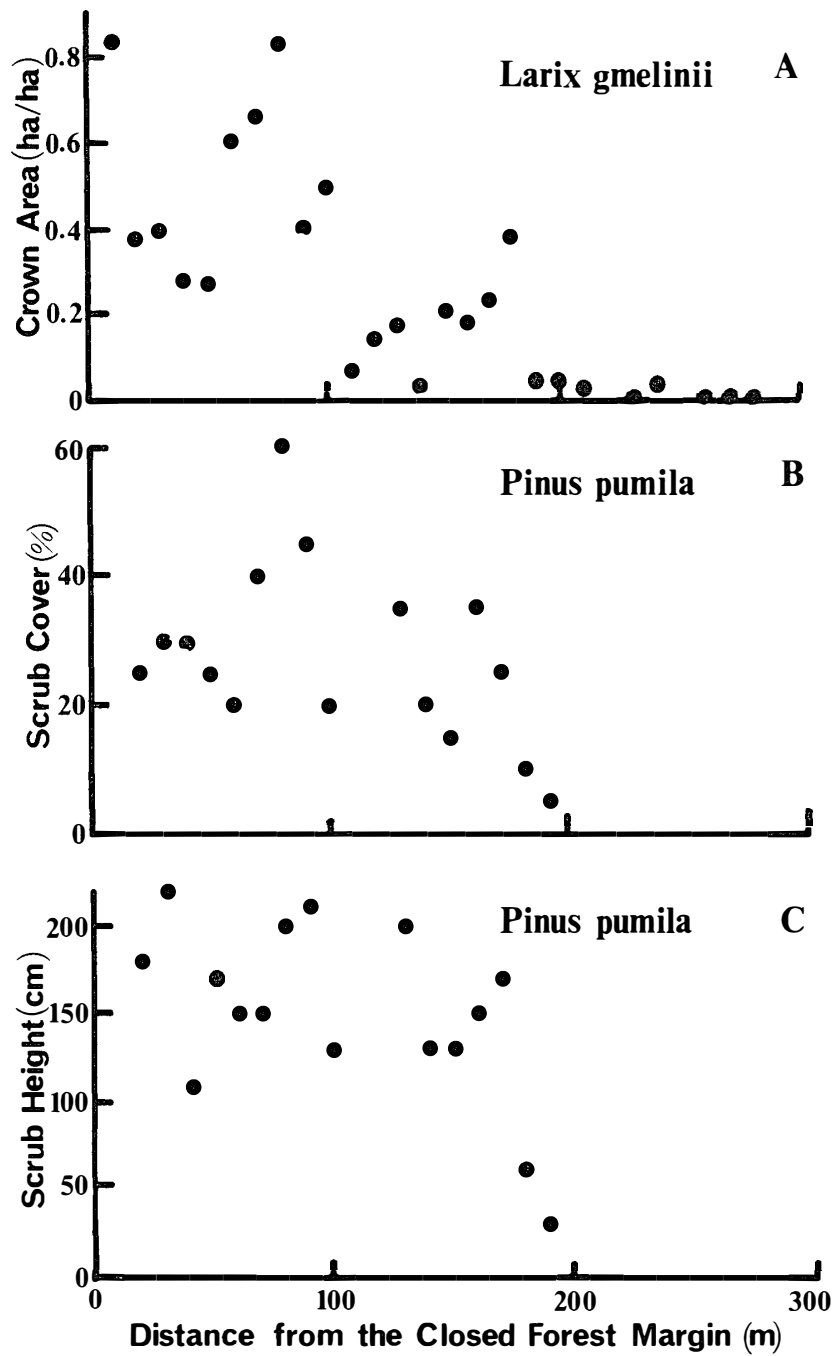


Fig. 2. Changes in crown area of *L. gmelinii* trees (A), Scrub cover of *P. pumila* (B), and scrub height of *P. pumila* (C) at the stands along the transect. The altitude at the closed forest margin (0 m in the transect) is 910 m, and that of the last stand (300 m in the transect) is 960 m.

P. pumila remains within the range of *L. gmelinii* (Fig. 4). The tree height of *L. gmelinii* decreased gradually from 12 m at the closed forest margin to 4 m at the limit of the *P. pumila* range (OKITSU, 1997). *Larix gmelinii* is always higher than *P. pumila* in this ecotone. This pattern seems to be in conflict with its highly shade-intolerant character (e.g. ТИХОМИРОВ, 1946). A relatively small portion of the crown cover of *L. gmelinii*

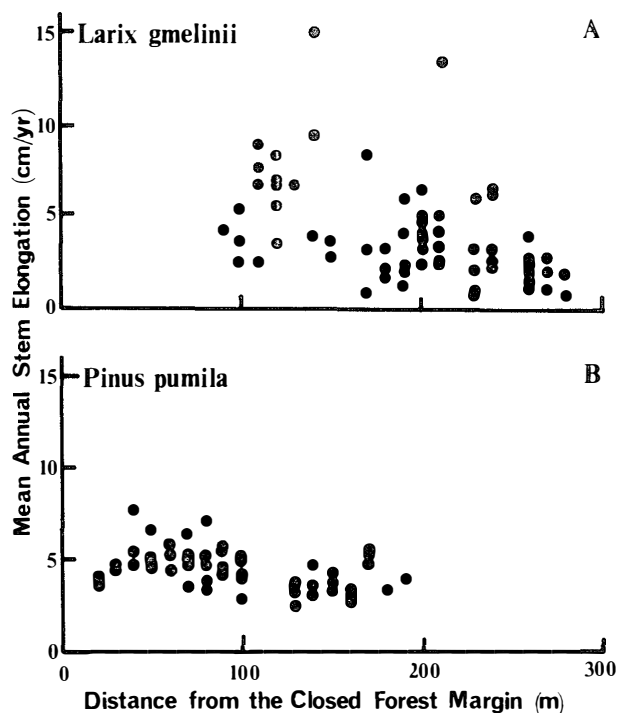


Fig. 3 Changes in mean annual stem elongation of *L. gmelinii* (A) and *P. pumila* (B) at the stands along the transect. Dots in the figures A and B show the individual stems sampled. Data for *L. gmelinii* (A) are redrawn from OKIISU (1997).

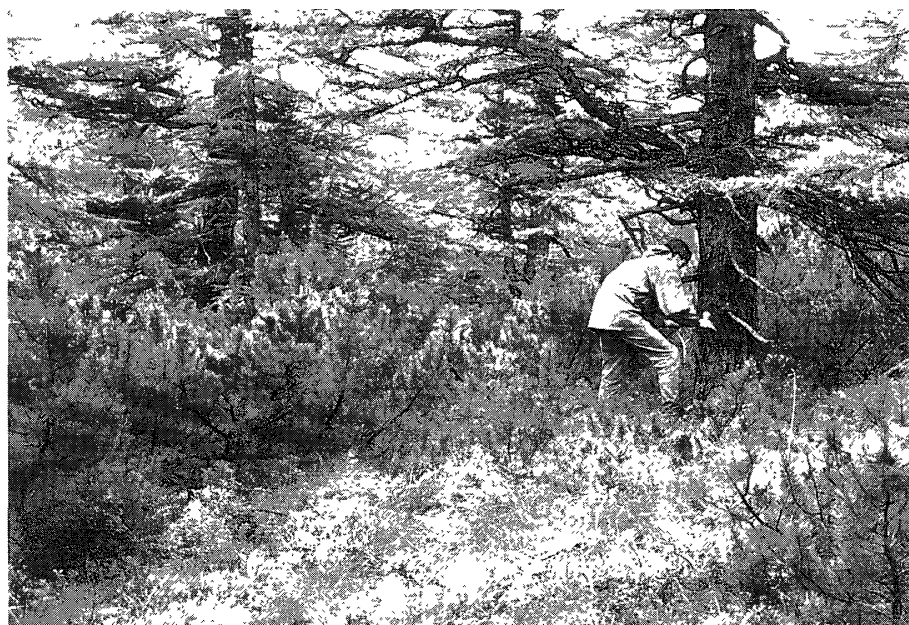


Fig. 4 A view of *P. pumila* scrub growing under high *L. gmelinii* trees (10m in height) 50 m distance from the closed forest margin in the transect.

in the ecotone (at most 0.8 ha/ha) may supply enough light to the forest floor, which probably assures establishment of shade-intolerant *P. pumila*. Additionally, *P. pumila* can receive full sunlight in spring before the emergence of the leaves of deciduous *L.*

gmelinii. Evergreen *P. pumila* can start photosynthesis in this season, although the rate may be low. Nonetheless, *P. pumila* never appears in a completely closed forest below the ecotone. However, the light condition alone cannot explain the absence of *P. pumila* in the upper part of the ecotone where the crown area of *L. gmelinii* decreases to nearly zero.

The thermal condition of this ecotone may explain the absence of *P. pumila* on its upper part. OKITSU (1997) observed that the tree form of *L. gmelinii* in this ecotone is generally symmetrical, never of wind-shaped form. He concluded, from these observations and the relatively small width of this ecotone and abrupt decrease of height growth of *L. gmelinii* at the uppermost part of the ecotone, that *L. gmelinii* trees ascend the slope to nearly the thermal upper limit suffering from no strong growth inhibition by wind and snow on Mt. Dal'nyaya Ploskaya. In contrast, the timberline zone controlled mainly by wind and snow tends to be broader; sufficient summer heat alone can maintain the existence of trees, although wind and snow gradually reduce tree size (OKITSU, 1997). The estimated mean temperature of the warmest month (July) at the ecotone of Mt. Dal'nyaya Ploskaya is ca. 10°C (Okitsu, 1996: estimated from the climatic data on Kozyrevsk, west foot of Mt. Dal'nyaya Ploskaya (MAN'KO and VOROSHIROV, 1978)). This temperature coincides well with the general value of the alpine timberline throughout the northern Hemisphere (DAUBENMIRE, 1954; TRANQUILLINI, 1979). OKITSU and ITO (1989) found that *P. pumila* can occur only within the thermal regime of the forest zone to support its high biomass and productivity, which are similar to those of a boreal forest (cf. OKITSU, 1981). The high elevations of this ecotone provide insufficient summer heat to support the high biomass and productivity of *P. pumila*.

Pinus pumila maintains the scrub height of ca. 180 cm from the forest margin (0 m) to just below its upper distribution limit along the ecotone. Its scrub cover is, however, at most only 40% at the lower part of the transect with one exception (60% at 90 m). On Japanese high mountains coverage of *P. pumila* scrub of height more than 100 cm usually attains almost 100% cover (OKITSU, 1991; OKITSU and ITO, 1984). The *P. pumila* scrub in this ecotone shows lower cover than that on the Japanese high mountains. This may partly result from the lack of strong effects of wind and snow on Mt. Dal'nyaya Ploskaya inferred from the symmetrical tree form of *L. gmelinii* (OKITSU, 1997). Under such conditions *P. pumila* can achieve higher scrub height than that in Japanese high mountains where strong effects of wind and snow on the growth of *P. pumila* are conspicuous (OKITSU and ITO, 1984, 1989). However, insufficient summer heat prevents *P. pumila* from growing vigorously. On the Japanese high mountains, sufficient summer heat promotes vigorous growth of *P. pumila*.

Growth of *L. gmelinii* and *P. pumila*, and their ecological relationship

The annual height growth of *L. gmelinii* along this timberline ecotone varies widely. Better height growth is frequently related to locally favorable growing conditions in climatically extreme conditions such as the low-thermal distribution limit (WARDLE, 1971; TRANQUILLINI, 1979). Only trees enjoying locally favorable growing conditions can attain better height growth.

In contrast, *P. pumila* keeps rather constant annual stem elongation along this ecotone. This may be due to the protection of *L. gmelinii* trees. The existence of trees

has some advantage, providing some microclimate protection (*cf.* VACEK and LEPS, 1989). Tree clumps provide wind-shelter, ameliorated temperature extremes, and higher humidity (ARNO, 1984). The climate within a more or less closed tree stand remains fairly uniform (TRANQUILINI, 1979). Climatic maxima and minima are less extreme. Within the protection of a stand individual trees can exist without damage at an altitude where they would not survive in isolation (TRANQUILLINI, 1979). Without the protection of *L. gmelinii*, *P. pumila* cannot accomplish sufficient frost resistance due to a lack of sufficient summer heat at its low-temperature distribution limit (TRANQUILLINI, 1979). At a clump of *L. gmelinii*, physiological processes are not as frequently limited by climate, and therefore stem elongations are less variable (SRUTECK and LEPS, 1994). The coincidence of the reduction of the scrub cover of *P. pumila* with the reduction of the crown area of *L. gmelinii* in this ecotone enhances the protection given by *L. gmelinii* trees to *P. pumila*.

Thus, *P. pumila* is principally ecologically an understory element of *L. gmelinii* open forests near its low-temperature distribution limit. Small *L. gmelinii* trees (*e.g.* tree height shorter than 200 cm) never outcompete *P. pumila* in this ecotone as their number is small (one to five individuals per 100 m²: OKITSU, 1997). The thermal regime of *L. gmelinii* open forests in Far East Asia is close to that near the forest limit. The distribution of trees is controlled by the thermal factor rather than by strong effects of wind and snow. North-eastern Siberia is a the typical region with such a climatic environment as well as this ecotone.

Pinus pumila succeeds in establishing its own vegetational zone, the *P. pumila* zone, only in restricted regions with peculiar environments where the thermal regime alone potentially permits arborescent trees to establish a forest, but actually strong wind, snow and the exposure of a rocky substrate prohibit them from forming a forest zone (OKITSU and ITO, 1989). During winter *P. pumila* lies under a snow crust which binds the branches of *P. pumila* firmly to the snow, protecting them from extremes of low temperature and desiccation (OKITSU and ITO, 1984). *P. pumila* can also be found on rocky substrates (OKITSU, 1984). In such peculiar environments *P. pumila* is ecologically not an understory element of *L. gmelinii* forests, but is the dominant element forming a distinct vegetational zone due to a lack of tall trees. The most representative regions of developing *P. pumila* zones are the high mountains of Hokkaido, northern Japan (OKITSU and ITO, 1989) as well as some mountains of Far Eastern Russia (GORCHAKOVSKY and SHIYATOV, 1978; HULTÉN, 1972; NESHTAYEV and NESHTAYEVA, 1975).

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