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

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Abstract: Variation in size structure and annual height growth of a *Larix gmelinii* (RUPR.) RUPR. population was documented along a timberline ecotone from the closed forest margin (910 m altitude) up to the last trees of *L. gmelinii* (960 m altitude) on the western slope of Mt. Dal'nyaya Ploskaya, central Kamchatka. The maximum height and total basal area of *L. gmelinii* trees decreased gradually along the timberline ecotone. The stretch of this timberline ecotone reached to *ca*. 300 m in distance, being shorter than that of Mt. Paektu, North Korea. No apparent wind-shaped trees occur along the timberline ecotone even at the uppermost part of it. It might be concluded, from the previous two points, that the most important factor promoting this timberline ecotone is a shortage of summer heat. Tree height distribution of a stand of *L. gmelinii* generally shows higher a number of taller trees with a smaller number of shorter trees, suggesting discontinuous regeneration of *L. gmelinii*. The wide variety of annual height growth of *L. gmelinii* within a stand supports discontinuous regeneration. The population of the upper part of the timberline ecotone maintains its regeneration mainly by layering of branches.

1. Introduction

Larix species are common trees in boreal and subalpine coniferous forests in the Northern Hemisphere. They form particularly extensive forests in the eastern Siberia and of mountains of northeastern Asia. In these regions some *Larix* species are typically dominant in the northern and mountain timberline ecotone, a transition from closed forest to open tundra with gradual reduction of tree size. In Kamchatka peninsula, Far East Russia, *Larix gmelinii* (RUPR.) RUPR. (Nomenclature follows VOROSHILOV (1982)) occurs exclusively in the central part of the peninsula, forming a conifer island surrounded by regions dominated by *Betula ermanii* forests. It forms a timberline ecotone on mountain slopes there.

A number of studies describe the physiognomy and the major species composition of the vegetation along the timberline ecotone of the mountains of central Kamchatka (*e.g.* GRISHIN, 1988a, b, 1993; MAN'KO and SIDEL'NIKOV, 1989). However, there is insufficient information on the dynamic aspect of the timberline ecotone. This paper documents the changes in the size structure, height growth and regeneration of *L. gmelinii* along the timberline ecotone of Mt. Dal'nyaya Ploskaya, central Kamchatka.

2. Study Site and Method

Mt. Dal'nyaya Ploskaya is a late-Pleistcene volcano (4050 m altitude), situated in the Klyuchevskaya volcano group, central Kamchatka at 56°04'N, 160°27'E (Figs. 1, 2). 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 *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 and total basal area upward, forming a timberline ecotone.

The vegetation around the timberline ecotone consists mainly of open woodland of *L. gmelinii* with undergrowth of *Pinus pumila* scrub, forest islands of *Betula ermanii, Alnus maximowiczii* shrubs, and subalpine meadows dominated mainly by *Geranium erianthum, Calamaglostis langsdorfii, Epilobium angstifolium, Aruncus dioicus,* etc. The alpine tundra gradually replaces the timberline ecotone. The major components of the tundra are *Betula exilis, Carex koraginensis, Hedysarum hedysaroides, Oxytropis erecta, Salix arctica, Vaccinium uliginosum,* etc. (OKITSU, 1996).

A 300 m long transect was established along the timberline ecotone, from the margin of the closed forest (910 m altitude) to the last trees of *L. gmelinii* (960 m altitude), on the west slope of the mountain (Fig. 1). Thirty successive stands (10 by 10 m) were situated along the transect. In each stand the diameter at the breast height (dbh) and the tree height of all the trees of *L. gmelinii* taller than 200 cm were measured. The number of trees shorter than 200 cm was counted. The existence of

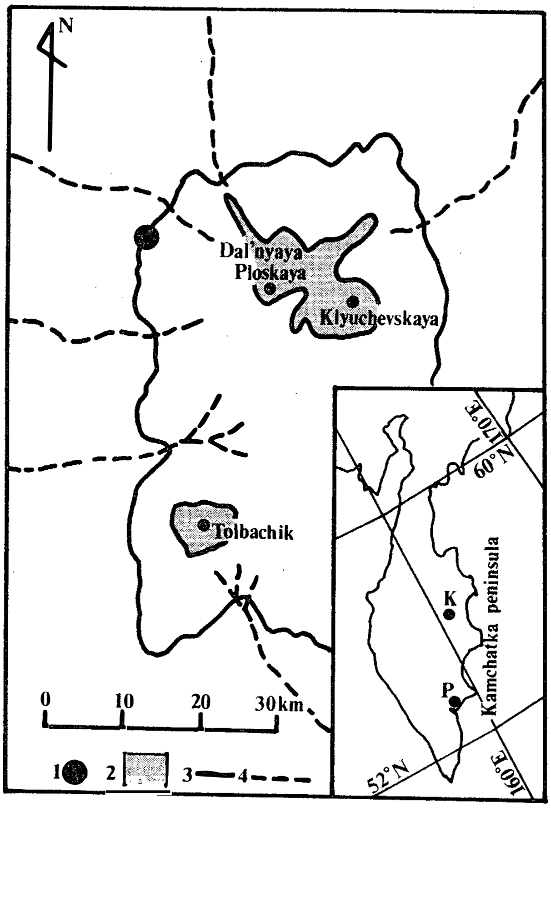

Fig. 1. Location of Mt. Dal'nyaya Ploskaya in Klyuchevskaya volcano group, central Kamchatka and approximate position of study transect (modified after GRISHIN, 1988a). Klyuchevskaya volcano group includes Mt. Tolbachik (3624 m), Mt. Klyuchevskaya (4750 m) and Mt. Dal'nyaya Ploskaya (4050 m). Mt. Klyuchevskaya is the highest peak in Kamchatka peninsula. The region between 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.

Fig. 2. A view of the alpine tundra and nival zone on the west slope of Mt. Dal'nyaya Ploskaya.

multitrunk clusters of *L. gmelinii* was recorded.

Annual height growth was estimated for the selected one to five trees including the largest individual in dbh in a stand 90 m upward from the closed forest margin, on the basis of tree height and tree age counted by cutting.

3. Results

3.1. Size structure

The last trees of *L. gmelinii* occurred at 280 m from the closed forest margin (Fig. 3). The timberline ecotone extended *ca.* 300 m in distance and *ca.* 50 m in altitude (from 910 m to 960 m).

Maximum tree height of *L. gmelinii* in a stand decreased gradually from the closed forest margin (12 m height) toward the last trees (0.3 m height) (Fig. 3A). Total basal area of *L. gmelinii* of the stand at the closed forest margin was *ca.* 40 m^2/ha. It decreased gradually to *ca.* 30 m^2/ha to 90 m, and was reduced rather abruptly to *ca.* 10 m^2/ha between 90 m and 180 m (Fig. 3B). It maintained its total basal area of less than 2 m^2/ha from 200 m.

The total number of trees in a stand showed no gradual decrease along the transect. The number of trees at the stand with the last trees of *L. gmelinii* was, however, reduced to only two. The number of tall trees (>2 m high) was greater than or equal to that of short tree (<2 m high) up to 160 m (Fig. 4). Tall trees were absent from 230 m upward (Fig. 4, *cf.* Fig. 3).

3.2. Existence of multitrunk clusters

Multitrunk clusters of *L. gmelinii*, which means clumps of trees or tree islands,

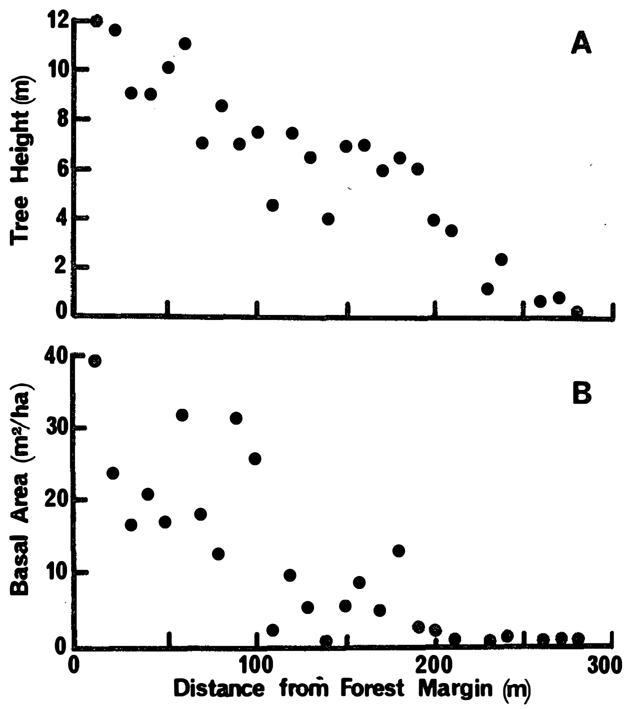

Fig. 3. *Changes in maximum tree height (A) and total basal area (B) of* L. gmelinii *trees at the stands along the transect. The altitude at the closed forest margin (0 m in the transect) is 910 m, and that of the last stand (300 m in the transect) is 960 m.*

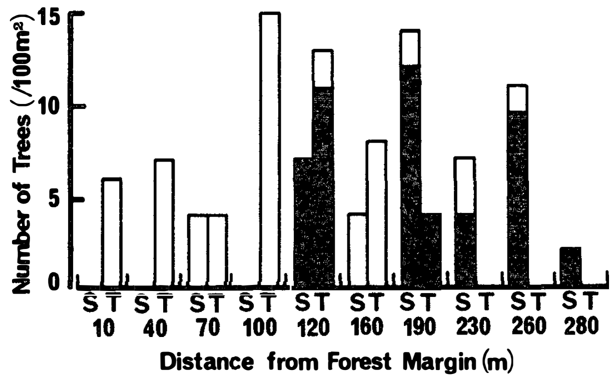

Fig. 4. *Number of short trees (<2 m in height) (S) and tall trees (≧2 m in height) (T) in 10 stands along the transect. The figures under the bars show the distance of the stand from the closed forest margin. Open bars indicate the solitary trees. Solid bars indicate the trees by layering.*

appeared from 120 m upward (Fig. 5) mixed with solitary stems. The clusters became smaller in size and lower in height, and finally they appeared as low prostrate shrubs with a few erect trees at the upperend of the transect (Fig. 6). The trees within a cluster arose mainly by layering of lower branches (Fig. 7). The ratio of trees by layering to total trees in a stand increased from 120 m upward (Fig. 4). Trees within clusters and solitary trees both showed symmetrical crown form (Fig. 5).

Fig. 5. Multitrunk clusters of L. gmelinii *on the transect. The height of proximate trees is ca. 180 cm. Trees show no apparent wind-shaped form. Trees within a cluster regenerate by layering of lower branches.*

Fig. 6. Short erect trees within a mat form of L. gmelinii *at the upper most part of the transect. The height of erect trees is ca. 60 cm. The surrounding vegetation is dominated by* Betula exilis, Vaccinium uliginosum *and* Hedysarum hedysaroides.

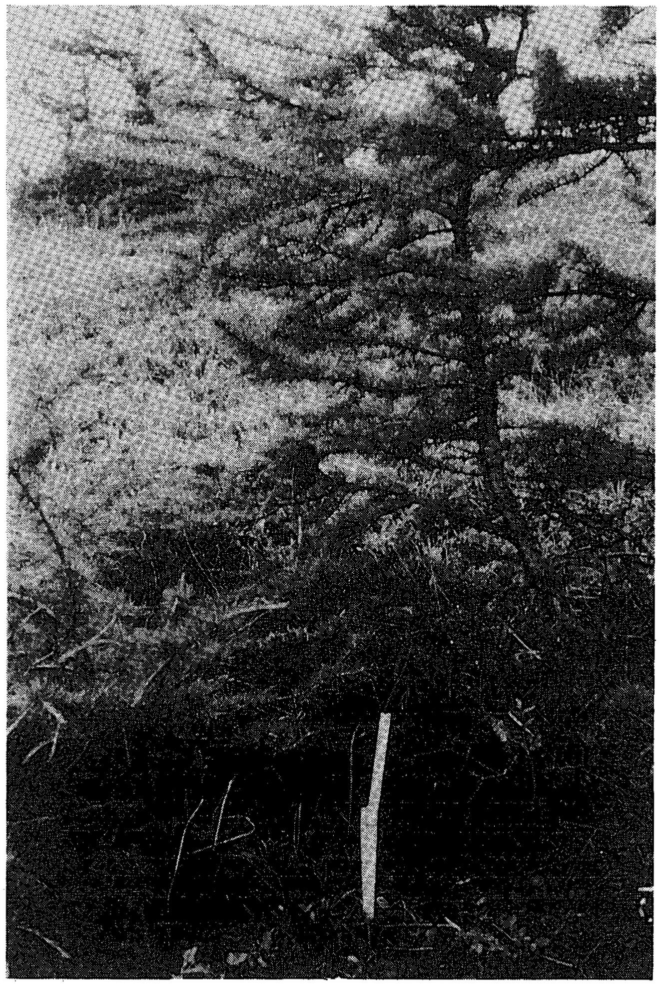

Fig. 7. A layering of a lower branch of a L. gmelinii *tree with an erect short tree from the branch. The length of the measure is ca. 30 cm.*

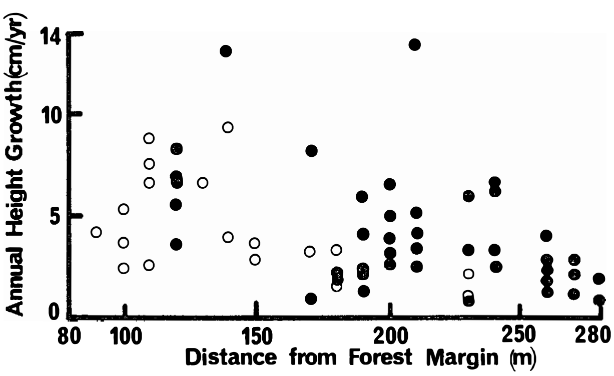

Fig. 8. Changes in annual height growth of sample trees along the transect. Open circles indicate solitary trees. Solid circles indicate trees by layering.

3.3. *Height growth*

The maximum annual height growth of *L. gmelinii* in a stand maintained *ca.* 14 cm/yr up to 210 m (Fig. 8). It decreased to *ca.* 3 cm/yr at the last trees of *L. gmelinii.* The annual height growth varied widely within a stand; the lowest value was *ca.* 2 cm/yr up to 150 m, and 1 cm/yr deom there upward (Fig. 8). The annual height growth of trees by layering was larger than that of solitary trees (Fig. 8).

4. Discussion

4.1. Changes in stand structure

The transition from the *L. gmelinii* closed forest to the alpine tundra on the west slope of Mt. Dal'nyaya Ploskaya covers a horizontal distance of *ca.* 300 m. Tree height, total basal area and maximum annual height growth of *L. gmelinii* gradually decrease along this transition. Such gradual change of tree dimensions is typical of alpine timberline ecotones (TRANQUILLINI, 1979)

A similar gradual transition from *Larix olgensis* closed forest to alpine tundra arises on the southeast slope of Mt. Paektu, northern Korea (SRUTEK and KOLBEK, 1994; SRUTEK and LEPS, 1994). This transition extends *ca.* 1700 m in distance and 130 m in altitude. Trees are shorter at the same dbh, and solitary trees in particular are wind-shaped. SRUTEK and LEPS (1994) postulate that the shaping of tree crowns is caused mainly by such environmental factors as wind shaping and abrasion, desiccation, frost damage, and snow pressure (*cf.* MARR, 1977; TRANQUILLINI, 1979; DALY, 1984)

In the timberline ecotone of Mt. Dal'nyaya Ploskaya, however, wind shaping and abrasion, and snow pressure do not seriously affect the shaping of trees. The tree form of *L. gmelinii* is generally symmetrical, never of wind-shaped form.

One might speculate, from the relatively small width of the timberline ecotone of Mt. Dal'nyaya Ploskaya in comparison with that of Mt. Paektu, that *L. gmelinii* trees ascend the slope to nearly the thermal upper limit without strong effects of wind and snow on Mt. Dal'nyaya Ploskaya. The maximum annual height growth of a stand decreases rather abruptly at the uppermost part of the timberline ecotone. This supports previous speculation. In contrast, a timberline 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.

4.2. *Regeneration of* L. gmelinii *along the timberline ecotone*

It is inferred, from the height distribution of the stands, that *L. gmelinii* regenerates rather discontinuously. Only trees with rapid height growth can grow tall, while trees with slow height growth remain short. The successful establishment of trees is frequently related to better growing conditions within a small area in climatically extreme conditions (WARDLE, 1971; TRANQUILLINI, 1979), although it still remains uncertain what difference of environmental conditions causes the wide variation of height growth of *L. gmelinii* on Mt. Dal'nyaya Ploskaya. SZEIZ and MACDONALD (1995) report that recruitment/survival patterns of *Picea glauca* at the subarctic alpine treeline of north-western Canada are episodic.

The dominance in number of trees by layering from 120 m upward indicates the dominance of vegetative reproduction there. Trees by layering generally show higher height growth than the solitary trees. One possible reason might be that in more climatically extreme stands, the existence of close neighbors has some advantage, providing some microclimate protection (*cf.* VACEK and LEPS, 1989). Under severe conditions vegetative reproduction by layering is much more favorable than sexual reproduction. Many coniferous species around the timberline ecotone reproduce by layering (Griggs, 1938; Oosting and Reed, 1952; Wardle, 1968; Marr, 1977; Legere and Payette, 1981; Shea and Grant, 1986). Some *Larix* species around the timberline ecotone also show layering. Some of them include *L. gmelinii, L. olgensis* (Srutek and Leps, 1994), *L. leptolepis* (personal observation), and *L. laricina* (Elliott, 1979). Arno and Habeck (1972) report, however, that *L. lyallii* in the Pacific Northwest of the U.S.A. does not spread by layering to any appreciable extent. Nonetheless, some *Larix* species in northeastern Eurasia are characterized by vegetative reproduction by layering.

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