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RESEARCH PAPER

Aspen groves in Northeast Russia: young or suppressed mature stands

Daniel I. Berman[1], Arkady V. Alfimov[1], Ulyana I. Bocharova[1]* & Renat R. Bichurin[2]

Daniel I. Berman [1]
e-mail: dber@yandex.ru

Arkady V. Alfimov [1]
e-mail: arcalfimov@gmail.com

Ulyana I. Bocharova [1]*
e-mail: ulyana.bocarova@gmail.com

Renat R. Bichurin [2]
e-mail: terpomo@bk.ru

[1] Institute of Biological Problems of the North FEB RAS, Magadan, Russia

[2] Institute of Geography RAS, Moscow, Russia

* corresponding author

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ABSTRACT

This study investigates the size-age structure and mean lifetime radial growth of aspen (*Populus tremula* L.) in ten groves across Northeast Russia, along a transect from Magadan to the Sette-Daban Range. These groves are confined almost exclusively to dry southern slopes. Trees in all groves exhibit prevailing diameters of 3–9 cm and heights of 3–6 m, resembling young stands in more favorable parts of the species' range. Age determination revealed an uneven-aged structure: some groves included long-lived individuals (> 100 years), whereas only one grove consisted entirely of trees younger than 30 years. At diameters of 4–8 cm, tree age varied unpredictably (24–80 years). Mean radial growth was negligible (1.2–2.9 mm/year). The stunted growth habit of mature aspens throughout the region, and their strict confinement to specific topographic positions, indicate common growth-limiting factors. The consistency of aspen habit across northeastern Asia thus allows it to be regarded as a regionally distinctive ecobiomorph.

Keywords: *Populus tremula*, extreme climate conditions, permafrost, wildfires, stunted growth habit, size-age structure, radial growth, geographic transect, Sea of Okhotsk, Aldan River basin

РЕЗЮМЕ

Берман Д.И., Алфимов А.В., Бочарова У.И.*, Бичурин Р.Р. Рощи осины на северо-востоке России: молодые или угнетенные зрелые древостои. Исследованы размерно-возрастная структура и радиальный прирост осины (*Populus tremula* L.) в 10 рощах северо-востока России, связанных почти исключительно с южными сухими склонами, на трансекте от Магадана до хребта Сетте-Дабан. Деревья во всех рощах с преобладающими диаметрами 3–9 см и высотами 3–6 м, похожие на молодые поколения в благоприятных частях ареала. По данным дендрохронологического анализа, рощи разновозрастные, некоторые – с деревьями-долгожителями (более 100 лет); лишь в одной все деревья моложе 30 лет. При диаметрах 4–8 см деревья могут быть непредсказуемо любого возраста (24–80 лет). Средний радиальный прирост ничтожен (1.2–2.9 мм/год). Единый габитус зрелых осин и топическая приуроченность – свидетельство близкого комплекса лимитирующих факторов. Своеобразие и постоянство формы роста осины на северо-востоке Азии позволяет рассматривать ее как специфическую, свойственную региону экобиоморфу.

Ключевые слова: *Populus tremula*, экстремальность климата, влияние мерзлоты, пожары, малорослость, размерно-возрастная структура, радиальные приросты, географический трансект, Охотское море, бассейн р. Алдан

The forest zone of Northeast Asia is characterized by monotonous woody vegetation, consisting primarily of larch open forests and thickets of dwarf Siberian pine. The distribution of the few other tree species is largely confined to river valleys and the sea coast. This pattern appears to be primarily attributed to the severity of the region's environmental conditions: the lowest winter temperatures in Eurasia (down to -68°C in northeastern Yakutia), a short frost-free period often lasting less than a month in continental areas (Izumenko 1989, Orlantseva 1990) and nearly ubiquitous permafrost.

The extremity of these conditions exerts a pronounced influence on woody vegetation, resulting not only in reduced tree species diversity but also in sporadic distribution patterns and slow growth rates. European aspen (*Populus tremula* L.) is a clear example of how such an extreme environment affects a species, occurring in small, discrete groves. Although aspen typically forms stands on mountain slopes, on the fluvial terraces above floodplain of rivers in the Sea of Okhotsk basin, as well as along the Kolyma and Omolon rivers, it grows as solitary trees or occasionally in small groups of three to five individuals. The trunks are contorted, frequently affected by various types of rot, and do not exceed 16 m in height (Starikov 1958).

Aspen groves are distributed throughout forested areas of Northeast Asia, ranging from Chukotka to the Kava River valley and from the Sea of Okhotsk coast to the Sette-Daban Range (Starikov 1958, Chereshnev 2008, Nikolin 2013, GBIF Secretariat 2023). Although they occupy small areas, their occurrence is consistent across the region. On slopes, these groves consist of slender, low-growing trees that resemble young, even-aged post-fire stands (Dokucha-

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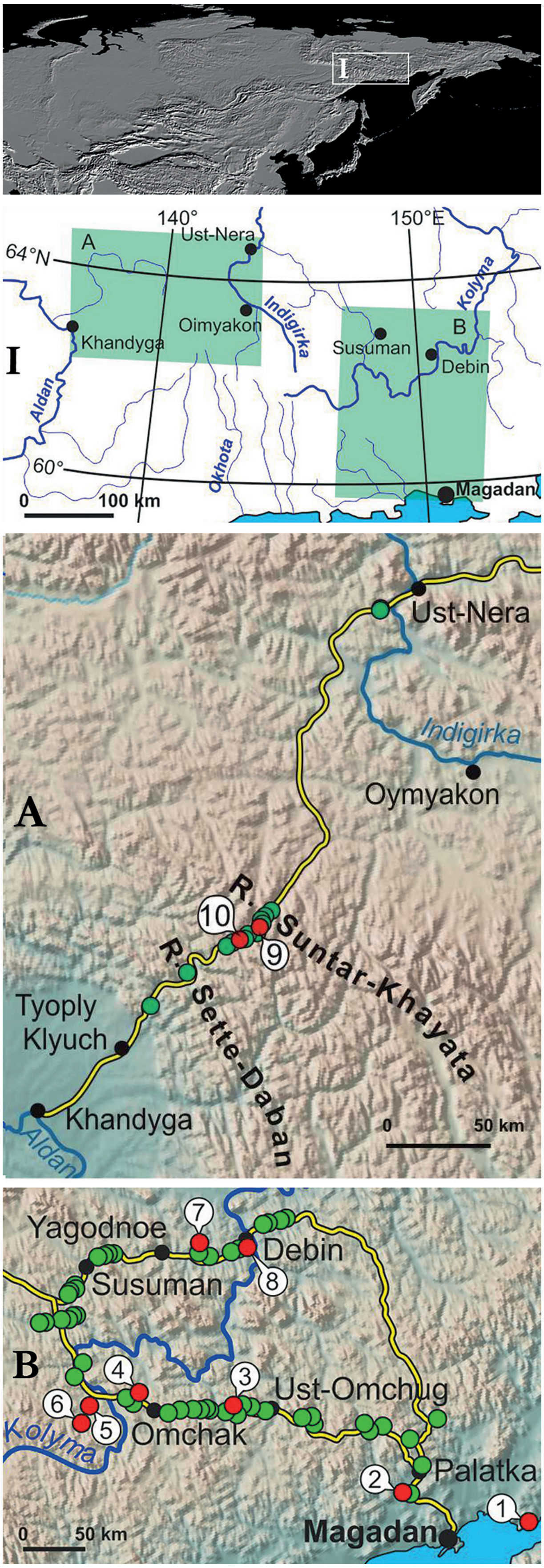

Figure 1 Location of aspen groves in the study area. Green circles indicate aspen groves recorded along road survey routes, red icons mark studied groves. Numbers from 1 to 10 show the names of locations as indicated in Table 1

eva 2001); this impression is often corroborated by evidence of fire. To determine whether the widespread occurrence of low-growing aspens in Northeast Asia results from continuous stand rejuvenation due to frequent fires or from the influence of severe conditions at the climatic edge of the species' range, we examined the size–age structure and mean lifetime radial growth of aspen stands. Comparing these parameters with data from climatically optimal regions resolves this alternative and defines the objective of the present study.

To achieve this objective, two tasks were addressed:

1. Along a geographical transect extending from the temperate maritime climate of the Sea of Okhotsk coast to the extreme continental subarctic climate of the Aldan River valley (Alisov 1969), conduct a geobotanical description of aspen groves, identifying key trends in their topographic distribution and associated vegetation cover composition.

2. Determine the size–age structure and mean lifetime radial growth of selected model aspen stands, comparing these parameters both regionally (along a continentality gradient) and with stands from climatically optimal regions for the species.

MATERIAL AND METHODS

During 2023–2025, eight aspen groves were surveyed in continental and coastal areas of the Magadan Region, together with two groves in the Suntar-Khayata Range (Yakutia). In addition, aspen groves were recorded along two road survey routes: the Magadan–Gavryushka Pass section (431 km of the Tenkinskaya road) and the Magadan–Khandyga route (1,455 km from Magadan) (Figs 1, 2, Table 1).

Eleven sample plots of 10 × 10 m were established and described following standard geobotanical methods (Tikhodeeva & Lebedeva 2015). All trees within the plots were censused; height was measured using an RGK DQL-15.0 clinometer, and diameter at breast height (DBH) was recorded.

To determine tree age, cores were collected from two to three trees in each diameter class (0.1–3.0, 3.1–6.0, 6.1–9.0, and ≥ 10 cm) using a Pressler's borer (Cook & Kairiukstis 1989). When a sample plot contained fewer trees in a given diameter class, supplemental sampling was extended to areas outside the plot boundaries. Trees exhibiting signs of heart rot were noted. In total, cores and cross-sections were collected from 162 trees. At the "Khasyn" sample plot, which

Table 1. Location of sample plots in aspen groves.

N	Name	Coordinates, degrees	Altitude, m a.s.l.	Aspect / Slope
1	Naydennaya	59.30546N 151.88170E	58	SE / 27–30°
2	Khasyn	60.09406N 150.82751E	320	S / 30°
3	223 km	61.28271N 149.01558E	695	S / 30°
4	338 km, part 1	61.85303N 147.51976E	762	SW / 35°
	338 km, part 2	61.85148N 147.52564E	754	SW / 28–32°
5	Neryuchi 1	61.89676N 147.14151E	710	SSE / 37°
6	Neryuchi 2	61.89382N 147.11241E	702	SSE / 30°
7	Yagodnoye	62.52199N 149.61951E	518	– / 0°
8	Debin	62.33995N 150.76233E	321	– / 0°
9	Kyurbelyakh	63.11586N 139.05927E	947	SE / 30°
10	Sukhaya Rechka	63.11995N 138.97536E	926	S / 35°

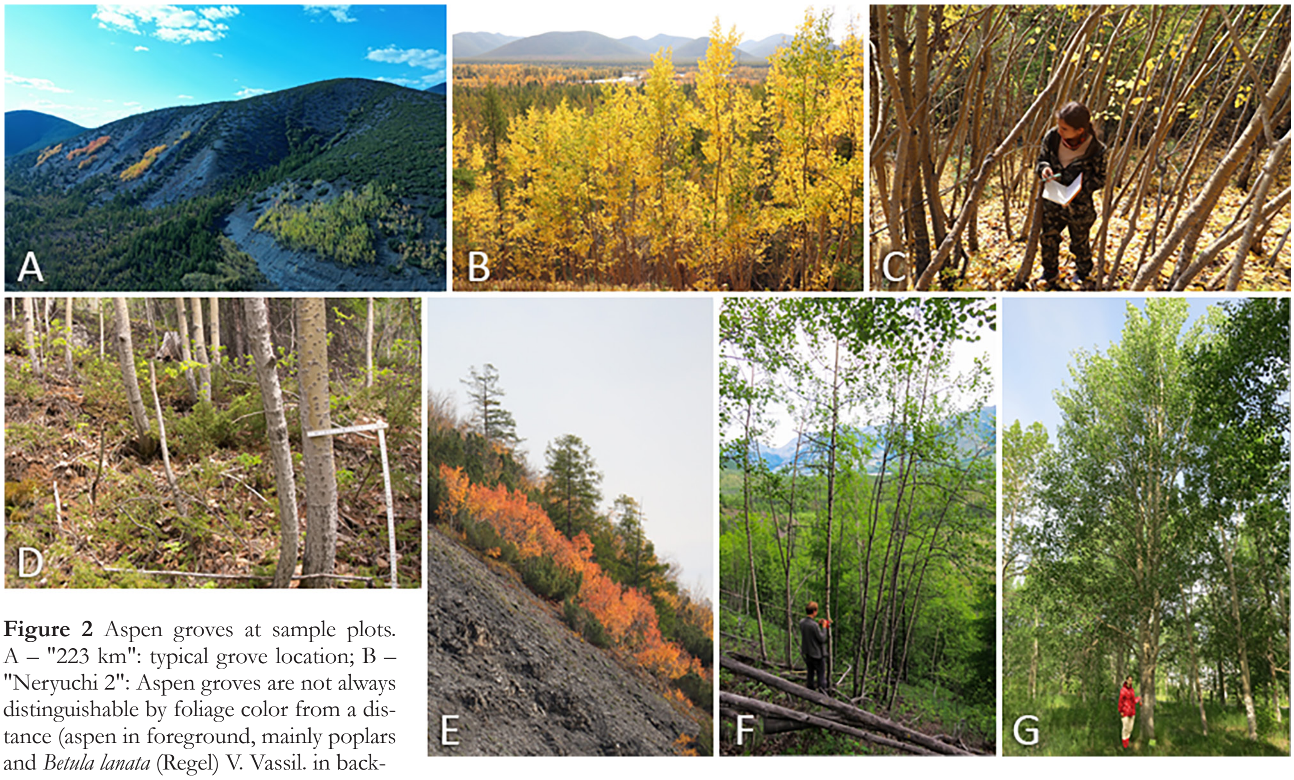

Figure 2 Aspen groves at sample plots. A – "223 km": typical grove location; B – "Neryuchi 2": Aspen groves are not always distinguishable by foliage color from a distance (aspen in foreground, mainly poplars and *Betula lanata* (Regel) V. Vassil. in background, 31 August 2023); C – "Neryuchi 2": Characteristic Northeast Asian aspen grove with stem diameters of 3–6 cm and tree ages of 7–79 years; D – "Khasyn": Trees with diameters of 4-8 cm can be aged from 24 to over 100 years; E – "Neryuchi 1": Grove with the lowest mean aspen height (3.5 m) and age range of 24–104 years; F – "Sukhaya Rechka": Grove with typical stem diameters (3–6 cm) but relatively tall trees (up to 8 m); G – "Debin": The largest recorded aspen in Northeast Asia, found in plantings on the Kolyma River terrace in Debin settlement (height 19.5 m, diameter 33.5 cm; human height 160 cm shown for scale)

contains mixed aspen–larch stands, additional sampling targeted five Cajander larches (*Larix cajanderi* Mayr).

Dried samples were mounted on wooden supports with PVA adhesive and progressively sanded with abrasive paper. Prepared samples were scanned at a resolution of 3,200–4,000 dpi. Tree-ring counts were obtained using Cybis CooRecorder. Cross-dating was performed with Cybis CDendro, first between radii within individual trees and subsequently among different trees. Following cross-dating, each ring was assigned a calendar year, and dating accuracy was verified using COFECHA. The mean lifetime radial growth rate was calculated by dividing trunk diameter by tree age. From August 2023 to August 2024, DS1922L loggers (E-lin, Russia; calibrated accuracy of +0.2°C at 0°C) recorded soil temperatures at 2 cm and 20 cm depths every 6 and 12 hours, respectively, at four continental sample plots and adjacent open areas.

RESULTS

Along the Magadan–Gavryushka Pass road survey route, 23 aspen groves were recorded, whereas at least 44 groves were documented along the Magadan–Khandyga route. In the Suntar-Khayata Range, 12 aspen groves were identified, 10 of which were clustered within a 27 km segment between the mouths of the Setorym (63.137823°N 139.259187°E) and Atmole (63.123687°N 138.865903°E) rivers – tributaries of the Vostochnaya Khandyga River. In contrast, only two groves were recorded in the Sette-Daban Range section.

Notable characteristics of the studied aspen stands

The "Naydennaya" grove is the only documented coastal aspen stand known within the region. The "338 km" site represents the largest stand recorded; two sample plots were established therein and are referred to collectively in subsequent sections, except where tree age assessments are considered separately. The "Khasyn" and "Sukhaya Rechka" stands are distinguished by their mixed forest composition: the former includes Cajander larch and fragrant poplar (*Populus suaveolens* Fisch.), and the latter frequently contains poplar. The "Yagodnoye" and "Debin" plots are artificial plantations located within their eponymous settlements.

Shrub and herb–dwarf shrub layers

The shrub layer exhibited consistent species composition across all aspen groves. *Rosa acicularis* Lindl. was present at all sites; *Pinus pumila* (Pall.) Regel occurred at all sites except the "338 km, part 1, 2" and "Debin" plots; and *Juniperus sibirica* Burgsd. was recorded at only 4 of the 10 sites. The ground vegetation layer demonstrated high species similarity: *Vaccinium vitis-idaea* L., *Saxifraga omolonensis* Khokhr., and *Chamaenerion angustifolium* (L.) Scop. co occurred at 6 of the 10 sites. Settlement-based sample plots differed in species composition by including adventitious species (see Table A1).

Aspen groves frequently occur adjacent to mesoxerophytic and xerophytic communities, including meadow–fo-

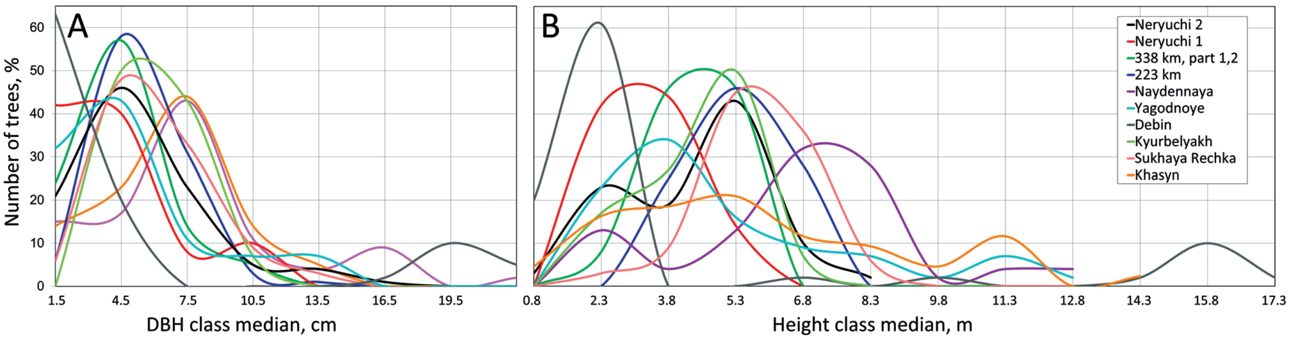

Figure 3 Distribution of trees (%) by diameter classes (cm) (A) and height classes (m) in the selected groves

rest complexes, upland xerophytes, and steppe formations. Representative examples, such as the "223 km," "338 km, part 1, 2," "Neryuchi 1," "Neryuchi 2," "Sukhaya Rechka," and "Kyurbelyakh" groves—correspond to the xerophytic shrub–herb aspen forest association. In contrast, the "Khasyn" and "Naydennaya" stands support a cowberry–forb ground layer with absent or negligible occurrence of xeromorphic species.

Dimensions of trees in the groves

All groves contain aspens of youthful appearance, characterized by slender trunks and consistently low tree heights. The predominant diameter range is 3–9 cm (Fig. 3A), and the predominant height range across nine plots is 3–7.5 m (Fig. 3B).

Large-diameter aspens were exceptionally rare across all sample plots, and their dimensions remained modest (Fig. 3A, Table A2). The "Debin" settlement, situated on a sandy fluvial terrace above floodplain of the Kolyma River, exhibited the highest recorded proportion of such trees (Table 1). Here, approximately 10 % of sampled trees exceeded 18 cm in diameter at a minimum age of 70 years, having been planted in 1957 (Dorozhevets 2021; personal communication). Tree height on the sample plots was uniformly low, reinforcing the impression of young stands; maximum heights seldom reached 12 m (Fig. 3B).

Age structure of aspen stands

Despite the uniformity of tree height and diameter within the sample plots, the age structure proved complex. Core samples indicate that trees attain a diameter of 4 cm only after 20–25 years, whereas at diameters up to 8 cm, age varies unpredictably, ranging from 24 to over 100 years. All groves are uneven-aged, albeit to varying degrees.

Maximum tree age differed considerably among the surveyed stands, ranging from 27 to 119 years, and no correlation was found between age and trunk diameter. For instance, six trees aged 92–119 years exhibited diameters ranging from 6.5 to 20 cm.

Even within a single aspen grove ("338 km"), the age–size structure varied sharply between sections: one section contained trees no older than 30 years, whereas the other included individuals exceeding 70 years of age (Fig. 4B, C).

All aspen stands exhibit periods lacking successful regeneration. These periods are asynchronous across sites, vary in duration, and occur after different intervals since grove establishment (Fig. 4). Such recruitment gaps may result from fire or tree mortality due to other causes (e.g., stem rot). The total duration of extended periods without new tree establishment (exceeding 10 years) accounted for 40–55 % of the entire lifespan of the aspen groves at several study sites (Fig. 5, Table 2). Similar, though rare, recruitment gaps have been documented in the considerably larger *Populus tremuloides* Michx. groves of western North America (Kurzel et al. 2007).

Lifetime average radial growth of aspen in the groves

Mean radial growth rates over the lifespan varied among the surveyed groves, ranging from 1.23 mm/year ("Neryuchi 1") to 2.9 mm/year ("Naydennaya"). At the latter site, the fastest-growing specimens reached 4.8 mm/year (Table 2).

At most sample plots, growth rates declined over time; however, this trend was obscured by substantial within stand variation, even among trees of the same cohort. For example, at the "Naydennaya" site, the mean growth rates of aspen groups aged 35–42 and 17–25 years differed by a factor of 1.7 (Table 2). Furthermore, among 17 trees aged

Table 2. Characteristics of the age structure of aspen groves.

Sample plot	Age interval (years)		Older cohort			Younger cohort		
	Full age interval	Recruitment gaps >10 years (from...to...)	*n*	Age range	Growth rate, mm/year	*n*	Age range	Growth rate, mm/year
338 km, part 2	6–27	No gaps	**17**	22–27	**2.13± 0.11**	**7**	6–19	**1.56± 0.18**
Naydennaya	17–42	24–35	**3**	35–42	**4.49±0.18**	**21**	17–25	**2.65± 0.27**
338 km, part 1	7–71	15–24; 40–64	**11**	27–39	**2.35 ± 0.20**	**13**	17–26	**1.38± 0.16**
Neryuchi 2	7–79	22–52	15	51–79	1.67± 0.14	7	7–21	1.48± 0.39
Neryuchi 1	24–104	33–48; 81–105	**12**	49–80	**1.49± 0.18**	**7**	24–32	**0.87± 0.06**
223 km	13–118	65–91; 93–107	6	56–64	1.56± 0.32	12	13–55	1.05± 0.07
Khasyn	4–119	50–103; 105–118	**9**	37–119	**2.3± 0.2**	**13**	4–36	**1.28± 0.15**

Note: Growth rates in bold indicate statistically significant differences (Mann-Whitney test, $p < 0.05$); n = number of aspen trees in the group.

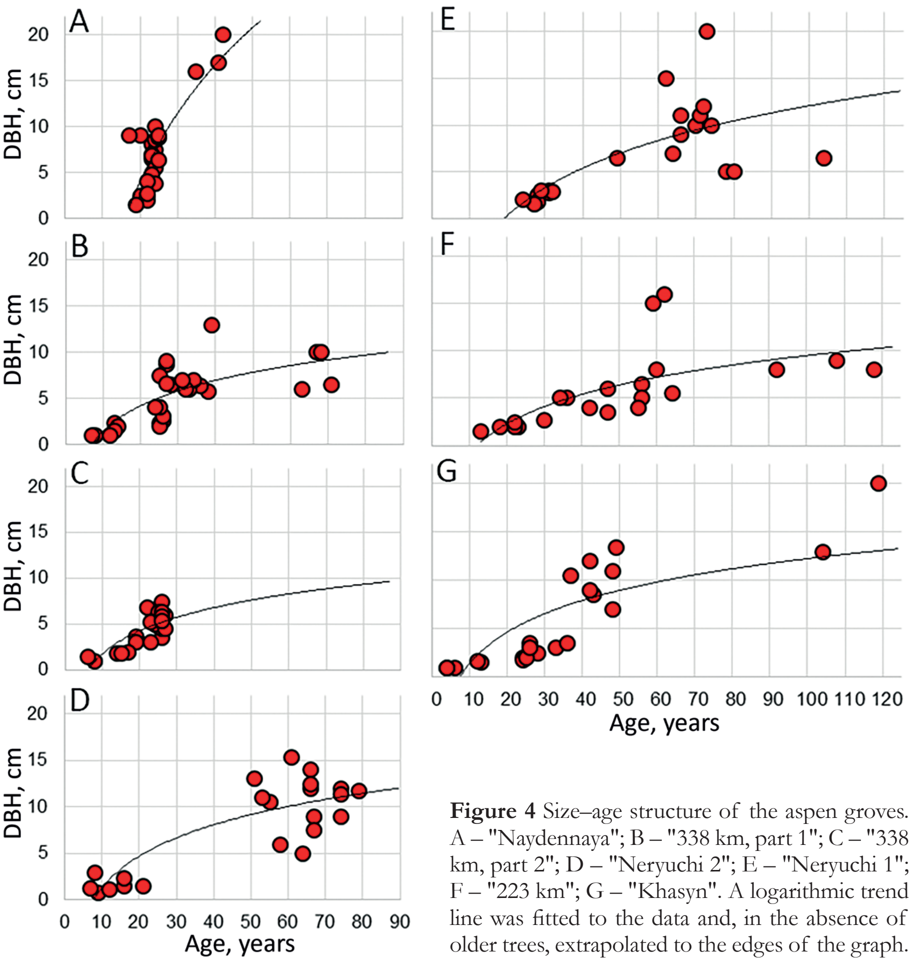

Figure 4 Size–age structure of the aspen groves. A – "Naydennaya"; B – "338 km, part 1"; C – "338 km, part 2"; D – "Neryuchi 2"; E – "Neryuchi 1"; F – "223 km"; G – "Khasyn". A logarithmic trend line was fitted to the data and, in the absence of older trees, extrapolated to the edges of the graph.

22–25 years, growth rates varied 4.6 fold, ranging from 0.91 to 4.17 mm/year.

Typically among the fastest-growing tree species, aspen here grows more slowly than larch. In the “Khasyn” grove, larch growth rates (1.2–5.0 mm/year) exceeded those of aspen (0.8–2.9 mm/year), surpassing aspen even at minimum growth rates and exhibiting an approximately twofold difference at maximum values.

Heart rot occurrence

Of the 162 trees examined, 72.8 % exhibited signs of initial to moderate-stage heart rot. Heart rot was already detectable in half of the aspens by age 25, with the proportion increasing to 81 % by age 50. No unaffected trees older than 50 years remained in the sample (Table 3, Fig. 6). Although infection commenced at similarly juvenile ages across sites, its final incidence varied widely. At two sites (“Neryuchi 1” and “223 km”), incidence reached 90 %. However, early onset (at 4–6 years) did not invariably result in high overall incidence; at “Khasyn,” for instance, incidence reached only 49 %.

Table 3. Occurrence of heart rot in aspen trees in the Northeast.

Tree category	Age, years			Total
	<25	25–50	>50	
Trees in class, *n*	67	52	43	162
Infected trees, *n*	33	42	43	118
Infection rate, %	49.2	80.7	100	72.8

The false aspen polypore (*Phellinus tremulae* (Bondartsev) Bondartsev & P.N. Borisov) is widely recognized as a primary agent of heart rot in aspen (Yablokov 1949). Despite the high infection rates observed, no fruiting bodies of *Phellinus* or other polypore fungi were found on the trunks of the examined trees.

DISCUSSION

Dimensions of aspen in Northeast Asian groves and forests elsewhere in its range

Aspen groves composed of slender, stunted trees exhibit remarkable uniformity across their extensive distribution – from the Sea of Okhotsk coast to the western macroslope of the Sette-Daban Range. This consistency persists across both maritime–continental climate gradients and elevational ranges (60–950 m a.s.l.), with no discernible effect on stand structure. Only two distinct types could be distinguished among the groves studied, and they differ solely in the xerophytic character and cover of the herb–dwarf shrub layer. These differences do not influence the tree layer and show no association with climate or elevation. Geographically, the groves are unevenly distributed: they are frequent in areas such as the upper Kolyma basin and the Suntar-Khayata Range, yet remain scarce in others, including the Sea of Okhotsk coast and the Sette-Daban Range.

Comparison with aspen from its climatically optimal regions (Table 4) indicates that tree height is the key differentiating factor. Even in open, crooked-stemmed subalpine stands of the North Caucasus (Yablokov 1949), aspens attain nearly twice the height of northeastern specimens: 12 m versus 5–6 m. In most other regions, 30 to 50 year old aspens are typically three to four times taller than those in the Northeast.

In the study region, mean diameters range from 5 to 8 cm, and only occasional trees barely exceed 20 cm. The thickest aspens here are not the oldest individuals but rather those growing in particularly favorable microsites, as corroborated by their growth rates. Aspen diameters of 23–26 cm are exceptionally rare. In optimal parts of the species’ range, such diameters are characteristic either of trees no older than 20 years or of mature aspens under extreme stress. In contrast, aspens growing under normal conditions

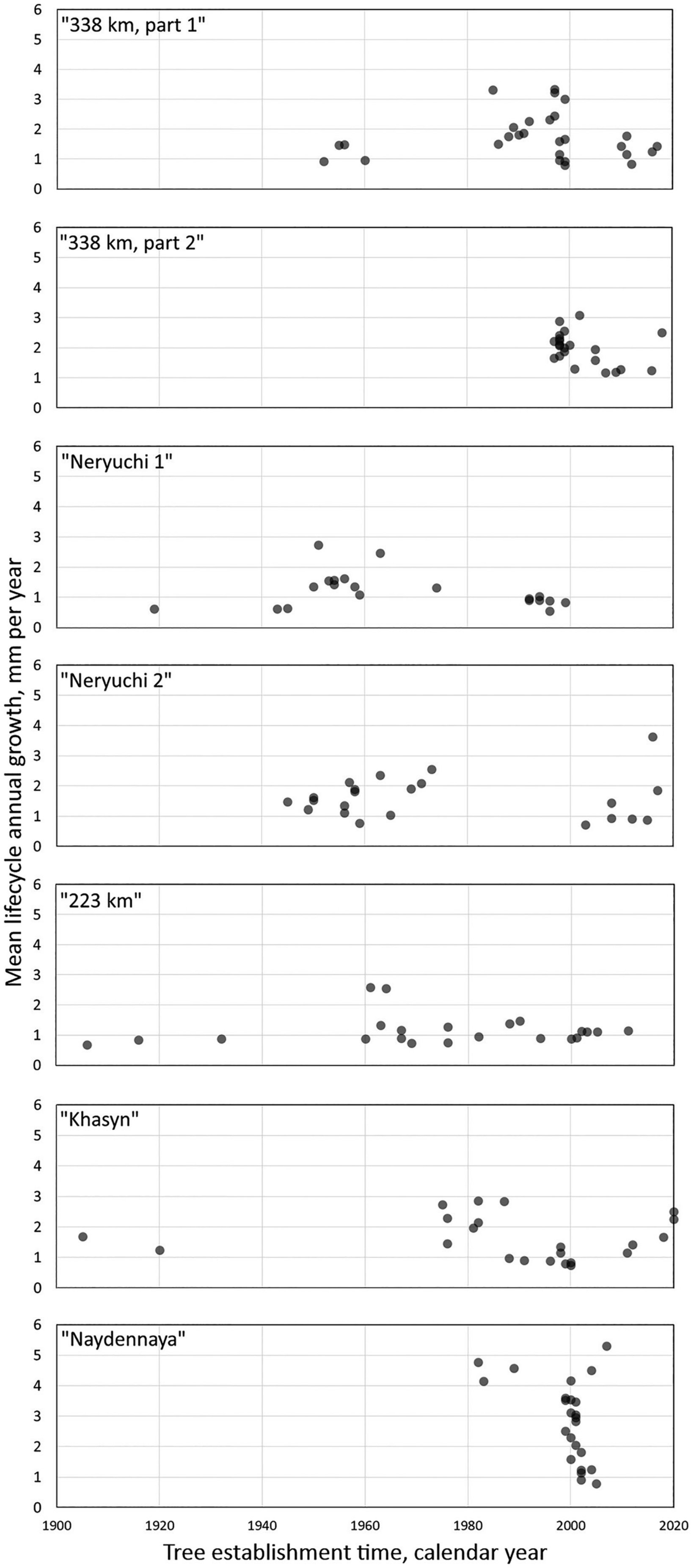

Figure 5 Age structure and mean lifetime growth rates of aspen trees

can attain diameters of 50 cm or more by 50–60 years of age.

Mean lifetime radial growth rates comparable to those in Northeast Asia can occur under markedly different conditions. Similar growth rates have been recorded in the northern taiga subzone (Arkhangelsk Region) for 70 year old aspens in mixed forests, although these trees were three to four times taller (Soldatova & Ilintsev 2020). Growth rates remain low in mature aspen stands affected by industrial pollution (Novgorod Region) and in waterlogged Latvian forests, where tree height is comparable to that of Northeast Asian groves (Smilga 1986, Ignateva 2019). In other peripheral areas of the species' range – from insular forest steppe in the Upper Yenisey basin to the northern slopes of the Caucasus – mean aspen growth rates exceed those in the Northeast by a factor of 2.0–2.5 (Table 4).

Across most of its range, including Northeast Asia, aspen attains its maximum annual growth rate at 30–40 years (Fig. 7), corresponding to the species' technical maturity age of 40–50 years (Leontev 2017). Aspens of this age are present in all surveyed groves of Northeast Asia except the youngest stands ("Naydennaya" and "338 km, part 2"). After reaching this threshold, growth rates decline more sharply here than in European Russia. The proportion of such trees in the population gradually decreases after 60–80 years, with only isolated individuals surviving to 100 years or more. By comparison, under favorable conditions, the natural maturity age of aspen is 60–90 years, although some individuals may reach 140–150 years (Mikhailov 1985). Thus, aspen groves in Northeast Asia are consistently younger than those in climatically optimal parts of the species' range.

Factors limiting aspen growth

The stunted growth of aspen in the Northeast undoubtedly results from extreme environmental conditions. A detailed discussion of all potential limiting factors is beyond the scope of this article owing to their multiplicity and space constraints. Therefore, at this stage we can only offer some general considerations.

Climatic factors

Northeast Asia is renowned for its severe climate: extremely cold winters, a short frost free period with limited growing degree days (> 10°C), insufficient or excessive moisture in various biotopes, and

Table 4. Height, diameter, and growth increments of aspen in selected parts of Its range

Region	Source	Location	Age, years	Height, m	Diameter, cm	Increment, mm/year
North Caucasus	Yablokov 1949	2000 m a.s.l., subalpine belt	40–50	12	30	6.0–7.5
		1200 m a.s.l., aspen forests with maple and fir	35–50	20	20	4.0–5.7
Central Siberia	Shevelev et al. 2021	Forest-steppe zone	47–61	18.3–19.1	18.7–20.1	3.2–4.3
Latvia[3]	Smilga 1986	Aspen groves I growth class	20–100	11–32	8–36	3–4.2
Nizhny Novgorod Region	Yablokov 1949	Aspen groves I growth class	105–110	29	35	3.2–3.5
Arkhangelsk Region	Tretyakov et al. 2013	Spruce-pine forest	89–91	24,5	26–32	2.9–3.6
Novgorod Region	Ignateva 2019	Pollution zone	–	–	–	2.0–2.5
Belarus	Asyutin 1994	Degraded lands	6	6.3–6.6	5.9–6.4	1.0–1.1
Latvia	Smilga 1986	Aspen groves V growth class	20–100	5–15	3–16	1.5–1.9
Upper Kolyma & Okhotsk Coast	This study	Naydennaya	17–42	6.5 (12)	7.4 (2–20)	2.9 (0.8–4.8)
		338 km, part 2	6–27	4,5	5.4 (1–8)	2.0 (1.2–3.1)
		338 km, part 1	7–70	4,5	5.3 (1–13)	1.7 (0.8–3.3)
		Neryuchi 2	7–79	6 (9)	7.8 (1–15)	1.6 (0.7–2.6)
		Khasyn	4–50	5.5 (7)	6.0 (1–20)	1.6 (0.8–2.9)
		223 km	13–118	5.5 (7.5)	8.5 (2–16)	1.2 (0.7–2.6)
		Neryuchi 1	24–104	3.5 (5)	7.3 (2–20)	1.2 (0.6–2.7)

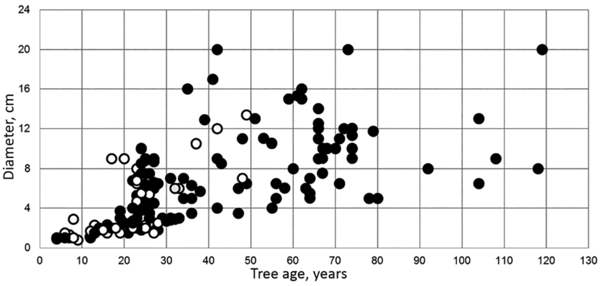

Figure 6 Age structure and eart rot in the studied aspen trees. White circles represent trees without rot; black circles with rot

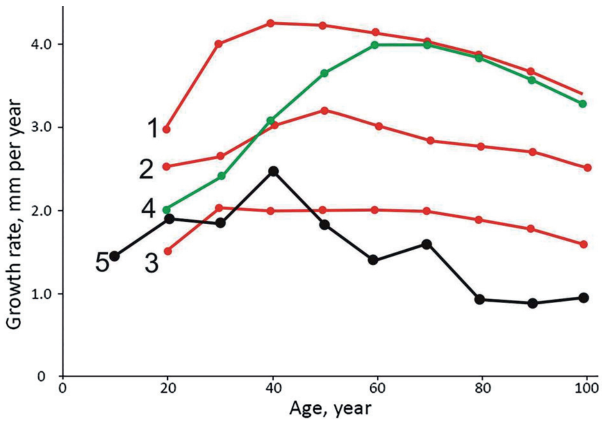

Figure 7 Age-related changes in aspen growth rate. 1–3 – Latvia, I, III, and V growth class, respectively (Smilga, 1986); 4 – Arkhangelsk Region, mixed forest (Tretyakov et al., 2013); 5 – mean (10-year moving average) growth rate for all sample plots on southern slopes discussed in the article

continuous permafrost except in coastal regions (Izumenko 1989, Orlantseva 1990, National Atlas 2007). It is reasonable to assume that the factors suppressing aspen growth are embedded within this set of constraints. As a preliminary approach, we can only outline certain considerations based on the spatial distribution of key climatic parameters.

The influence of winter temperature parameters remains unclear: conditions along the Sea of Okhotsk coast are no more severe than in most parts of the aspen range west of the Lena River. Yet aspen dimensions at the "Naydennaya" sample plot are as modest as those in the continental regions of Northeast Asia – the coldest winter part of Eurasia.

Analysis of standard summer climate parameters (Izumenko 1989, Orlantseva 1990, National Atlas 2007) also fails to demonstrate a clear relationship with aspen growth habit. The frost free period along the Sea of Okhotsk coast lasts approximately 90 days – similar to that in the Arkhangelsk Region, where aspen develops normally. Meanwhile, the sum of temperatures above 10 °C along the Sea of Okhotsk coast corresponds to European forest tundra conditions (≤ 800 °C), where aspen is absent. In continental interiors (the upper Kolyma, Indigirka, Central Yakutia), the thermal sum is nearly twice as high (up to 1600°C), but the frost free period may last less than 30 days – a growing season shorter than that in the tundra zone.

Moisture availability also varies dramatically across the region – from excessive (hydrothermal coefficient > 1.5) in coastal areas to arid (< 1.0) in Central Yakutia. This range encompasses the full spectrum of moisture conditions found across the aspen distribution west of the Lena River.

As the data indicate, identifying the limiting factors requires assessing the relationship between annual tree growth and climatic (including microclimatic) conditions, which lies beyond the scope of this study.

Aspen's strict confinement to dry southern slopes remains the sole evidence linking its distribution in Northeast Asia to climatic (including microclimatic) factors. Based on this pattern, Khokhryakov (1989) included aspen in the xerophytic steppe species complex, emphasizing its scarcity in mesophytic river terrace forests. All aspen groves we discovered were located on southern slopes of similar aspect and steepness, which may represent a thermally determined limit. Extremely low soil moisture likely prevents the spread of aspen, as well as larch, onto steppe patches. One may cautiously suggest that, in this context, the forest–steppe boundary represents a hydrothermal compromise between warmth and moisture favorable to aspen.

Permafrost

The integrated result of climatic severity, permafrost, varies across Northeast Asia from sporadic on the Sea of Okhotsk coast to continuous in continental regions (Ershov 1989, Pavlov & Zamoshch 2006). Permafrost prolongs winter cold in soils and ground layers during the warm season; however, its influence differs between maritime and continental areas and across topographic positions (Alfimov 1985). On sea facing slopes (e.g., at Naydennaya Bay), permafrost is absent, yet the aspen stands remain stunted, a key argument against attributing their growth form to permafrost influence. In continental regions, owing to favorable slope aspect, thin snow cover, and low ground ice content in the permafrost, the active layer develops rapidly on such slopes. Here, permafrost thaws to depths greater than 0.6–0.8 m by May and thus largely ceases to impede warming of the root inhabited horizon, which is 15–20 cm thick (Alfimov 2017).

Comparative analysis of temperature sums (>0°C and >10°C at 20 cm depth) between our studied aspen stands in Northeast Asia and reliably permafrost free sites in the species' core range (Mezen River basin) demonstrates the absence of a significant permafrost influence on the root inhabited horizon. This finding is illustrated by aspens in the lower reaches of the Mezen River (30 km from the White Sea) near the town of Mezen, where they attain only 4–6 m in height (Yablokov 1949), comparable to their stature in the Kolyma region. Moreover, the sums of positive soil temperatures recorded at the Mezen weather station (Research Institute of Hydrometeorological Information – World Data Center) closely match those in our studied aspen stands: while higher than those at the coldest Kolyma sites and lower than at the warmest, they fall within one standard deviation of the Kolyma values (Table A3).

In the middle reaches of the Mezen River (Koynas weather station, 200 km of the town of Mezen), aspens grow sufficiently large for dugout boat construction (Yablokov 1949), while temperature sums (> 10°C) here exceed those of the warmest Kolyma groves by one standard deviation.

It should be noted that weather stations measure soil temperatures in open areas, whereas our data from aspen groves were collected under forest canopy. Our measurements indicate that shading in aspen groves reduces the sum of positive soil temperatures by 5–30 % and the sum of temperatures above 10°C by 5–40 %, relative to adjacent, similarly xeromorphic biotopes. Therefore, even with a minimal estimate of shading's role, the difference in soil heat availability between stunted Kolyma aspen stands and fully developed stands in the species' core range becomes even smaller and, in some cases, may reverse.

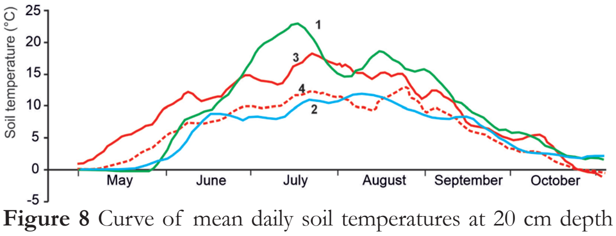

Figure 8 Curve of mean daily soil temperatures at 20 cm depth for individual years, smoothed with a 10-day moving average. 1 – Koynas meteorological station, 1970; 2 – Mezen meteorological station, 1986; 3 – aspen grove "338 km", 2023–2024; 4 – aspen grove "223 km", 2023–2024

A more compelling illustration of closely matched soil temperatures emerges from comparing the seasonal temperature curves in the Kolyma basin and the Mezen River area (Fig. 8). Notably, soils in the Kolyma groves are warmer than those in groves of the lower Mezen River, which lack permafrost. At the same time, notable temperature differences exist among the Kolyma groves themselves, yet without affecting the growth habit of the aspen trees or the associated vegetation (see below).

Thus, permafrost or, more precisely, its manifestations cannot be considered among the key factors unequivocally affecting the thermal regime of the root inhabited layer in aspen stands.

Fire regime

Fires constitute a noticeable factor affecting aspen groves. Evidence of burning (charcoal in soil, charred wood fragments) was found in all groves, although in most cases not all trees were burned, as clearly reflected in the size age structure of the stands (see Figs 4, 5). Observations by Dokuchaeva (2016) and our own data confirm that aspen groves survive repeated fires, though their ecological role requires further investigation. Most of the oldest trees (≥ 90 years) across all sample plots were located on grove peripheries, often in bare ground patches on slopes – a position that likely facilitated their survival through repeated fires. The aspen stands at "Naydennaya" and "338 km, part 2" represent exceptions, with no trees older than 42 and 27 years, respectively (Fig. 4), which may indicate severe fires.

Heart rot

Owing to its near ubiquitous occurrence in aspen, heart rot could be a potential factor contributing to early tree mortality, although the proportion of infected trees under 50 years old in the studied sample plots (Table 3) does not appear to differ from that in aspen stands elsewhere. In the Arkhangelsk Region, the average infection rate of stands is 27–33 % (up to 96 % maximum); aspen becomes infected at 10–20 years of age, with the first fruiting bodies appearing by 20–30 years (Ershov 2008). In the Southern Urals, infection rates range from 15.4–92.3 % (average 30–60 %) in trees aged 50–90 years (Safonov & Ostapenko 2017). The Ulyanovsk Region similarly shows high infection rates (86.4–90.6 %) in aspen stands aged 30–60 years (Churakov et al. 2013). In Northeast Asia, the severe climate combined with 100 % heart rot incidence in trees over 50 years likely accelerates their early mortality.

Unique dimensions of aspen in planted stands

The results of the survey of planted stands in the settlement of Debin (and, to a lesser extent, Yagodnoye) appear to contradict the previously presented assumptions about the causes of stunted growth. In Debin, aspens growing on a river terrace rather than a slope attained record dimensions for Northeast Asia: the largest tree measured 33.5 cm in diameter and 19.5 m in height, with several others reaching

20–26 cm and 15–17 m, respectively. By contrast, the largest slope grown trees reached only 23 cm in diameter and 13 m in height (Table A2). According to long term residents of Debin, the plantings never received watering, soil fertilization, or mowing, nor did they experience fires. The likely reason for the record sized aspens lies in the location of the planted stands on sandy deposits of the first fluvial terrace above floodplain. A nearby small quarry reveals the thickness and stratification of these sands. Such areas thaw early and deeply (up to two metres) and are potentially more fertile. Thus, the success of these aspens is probably attributable to edaphic factors.

The occurrence of small aspen groups on river terraces (Starikov 1958), despite adverse factors, may also relate to the higher fertility of alluvial soils, whereas most groves we observed grow on rocky (primarily schist) raw soils where humus rich layers have formed only in minor depressions. Only at the "Khasyn" sample plot was soddy soil observed, featuring well developed forest type herb leaf litter and a distinct humus horizon (N.S. Sobolev, personal communication), indicating the long term presence of the plant community at this location. It should be noted that aspen groves constitute the unique forest ecosystem in the region where the soil fauna features *Eisenia nordenskioldi* as a mass occurring species –the region's sole earthworm species. This remarkably cold resistant species (tolerates -35°C) appears only sporadically and in small numbers in floodplain willow stands along major rivers (Berman et al. 2019).

The forested areas of Northeast Asia as a marginal zone of aspen distribution

Stunted growth in aspen at ages slightly younger than typical for the species represents a response to adverse conditions, characteristic of naturally poor sites (Smilga 1986), polluted environments (Ignatieva 2019), and degraded landscapes (Asyutin 1994). The uniform growth habit and age structure of aspen groves across the vast territory, from the Pacific coast to the Sette-Daban Range, represent a pattern that likely intensifies north of the surveyed transects, up to the species' northern distribution limit. Furthermore, there is reason to extend the known range of stunted aspen growth southward, at least to the Dzhugdzhur (Topko Mountain) and Primorsky Ranges (S.D. Shlotgauer, personal communication).

Moreover, given the uniformity of summer climatic conditions within the hyperzone of Northeast Asia defined on this basis (Alfimov & Berman 2021), the distribution area of stunted aspen groves would occupy a territory stretching over 1000 km north–south (from the Maly Anyuy River headwaters to the Dzhugdzhur Range) and approximately 2000 km east–west (from the Maly Anyuy headwaters to the eastern slopes of the Verkhoyansk Range). However, it should be noted that aspen groves are not uniformly distributed across this territory. Specifically, they have not been found in the Okhotsk Forestry Unit, which extends from the Ulbeya River basin to the Inya River basin (O.S. Zavyalova, chief forester of the Okhotsk Forestry Unit, personal communication).

The range of this stunted aspen form likely extends across most of Yakutia (excluding southern and western areas). This conclusion is supported by photographs of stunted, deceptively young looking aspens on bedrock slopes in the Lena River valley near Yakutsk (E.G. Nikolin, personal communication) and the Muna River valley (68°N A.V. Kondratiev, personal communication). These trees may represent mature but stunted individuals, analogous to the groves we studied.

The same likely applies to an aspen stand in the middle Aldan River basin, where a model tree reached 8.3 cm in diameter (Shcherbakov 1975). It should be noted, however, that the same source describes an exceptionally productive aspen forest in the Aldan basin, unique for Yakutia, where 58 year old trees attained heights of 16.7 m with a mean diameter of 14.5 cm.

Classifying aspen in Northeast Asia as a distinct ecobiomorph

The identified characteristics of aspen in Northeast Asia – a persistent stunted growth habit, slow radial growth lagging behind that of larch in mixed stands, and strict confinement to a single habitat type (warm, dry slopes) – persist across a vast territory, indicating that the species is operating at its ecological limits.

The lack of growth form diversity in aspen contrasts sharply with the plasticity of Cajander larch, the dominant forest forming species in Northeast Asia. Larch exhibits multiple environmentally driven forms in response to various limiting factors, including wind, shallow active layer depth, hydrological regimes, and soil fertility (Mezhennyi 1976).

The stability of aspen traits across this vast area justifies recognizing the stunted form of Northeast Asian aspen as a distinct ecobiomorph, likely occurring also in Yakutia and the northern part of Khabarovsk Region. However, this form is unlikely to possess a distinct genetic basis, as evidenced by the substantially larger size of aspens transplanted young from slopes to settlement river terraces.

CONCLUSION

Aspen groves across Northeast Asia exhibit a striking uniformity in tree habit, their consistent occupancy of identical topographic positions, and a limited species composition across all layers. However, their complex size–age structure reveals them to be neither young nor even-aged stands, but rather long-suppressed communities persisting under extreme environmental conditions, with permafrost apparently not a primary limiting factor. Identifying these limiting factors, along with studying the ecological and biological traits of aspen, represents the next research phase for this remarkable species – a model for understanding adaptation mechanisms to harsh abiotic constraints. The stability of aspen habit across such a vast area suggests that its stunted form in northeastern Asia can be considered a distinct ecobiomorph, likely also occurring in Yakutia and the northern Khabarovsk Region.

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APPENDIX

Table A1. Brief geobotanical descriptions of sample plot.

Sample Plot Name	Tree layer		Shrub layer		Herb and dwarf-shrub layer	
	Density, %	Species composition	Cover, %	Species composition	Cover, %	Species composition
Naydennaya	90	100% *Populus tremula*	30–40	*Pinus pumila, Rosa acicularis*	75–80	*Vaccinium vitis-idaea, Maianthemum bifolium, Lathyrus japonicus, Galium boreale, Tanacetum boreale, Rubus arcticus, Trientalis europaea, Geranium erianthum, Chamaenerion latifolium, Calamagrostis langsdorffii*
Khasyn	70	70% *Populus tremula*, 30% *Larix cajanderi* (+ *P. suaveolens*)	40–55	*Betula middendorffii, Pinus pumila, Rosa acicularis, Juniperus sibirica*	30–45	*Vaccinium vitis-idaea, Chamaenerion angustifolium, Ledum decumbens, Galium verum, Atragene ochotensis*
223 km	70–80	100% *Populus tremula*	35–40	*Pinus pumila, Rosa acicularis, Juniperus sibirica*	50–60	*Artemisia glomerata, Saxifraga omolojensis, Vicia macrantha, Vaccinium vitis-idaea, Chamaenerion angustifolium, Allium strictum*
338 km, part 1, 2	60–70	100% *Populus tremula*	15–20	*Rosa acicularis*	40–45	*Dracocephalum palmatum, Saxifraga omolojensis, Vicia macrantha, Vaccinium vitis-idaea, Chamaenerion angustifolium, Calamagrostis langsdorffii*
Neryuchi 1	40–50	100% *Populus tremula*	30–35	*Pinus pumila, Rosa acicularis*	15–20	*Chamaenerion angustifolium, Saxifraga omolojensis, Vaccinium vitis-idaea*
Neryuchi 2	70–80	100% *Populus tremula*	30–35	*Pinus pumila, Rosa acicularis, Juniperus sibirica*	20–25	*Dracocephalum palmatum, Saxifraga omolojensis, Chamaenerion angustifolium, Galium verum, Allium strictum*
Kyurbelyakh	40–50	100% *Populus tremula*	10–15	*Pinus pumila, Rosa acicularis, Rubus sachalinensis*	10–15	*Vaccinium vitis-idaea, Saxifraga omolojensis, Chamaenerion angustifolium, Pulsatilla multifida, Atragene ochotensis, Artemisia* sp.
Sukhaya Rechka	40–50	90% *Populus tremula*, 10% *Populus suaveolens*	5	*Pinus pumila, Rosa acicularis, Juniperus sibirica, Betula middendorffii*	5–10	*Vaccinium vitis-idaea, Saxifraga omolojensis, Chamaenerion angustifolium, Orostachys spinosa*
Yagodnoye	55–60	80% *Populus tremula*, 10% *Populus suaveolens* (*Betula lanata*)	30–35	*Pinus pumila, Rosa acicularis, Rubus sachalinensis, Salix bebbiana, Ribes dikuscha*	20–25	*Vaccinium vitis-idaea, Saxifraga omolojensis, Chamaenerion angustifolium, Galium verum, Rubus arcticus, Tanacetum boreale, Artemisia* sp., *Poa* sp., *Calamagrostis langsdorffii, Trifolium pratense, Geum aleppicum, Ranunculus repens*
Debin	60–70	90% *Populus tremula*, 10% *Populus suaveolens*	5	*Rosa acicularis*	35–40	*Silene* sp., *Poa* sp., *Calamagrostis langsdorffii, Trifolium pratense, Ranunculus repens, Erigeron politus*

Table A2. Diameters (DBH, cm) and heights (H, m) of the top five largest trees at the sample plots.

Tree No	Kyurbelyakh		338 km, parts 1, 2		Sukhaya Rechka		Yagodnoye		Neryuchi 2		223 km		Khasyn		Neryuchi 1		Naydennaya		Debin*		Debin**	
	DBH	H	DBH	H	DBH	H	DBH	H	DBH	H	DBH	H	DBH	H	DBH	H	DBH	H	DBH	H	DBH	H
1	10.6	6.0	12.9	6.0	13.7	8.5	14.6	8.0	15.3	9.0	16.0	7.0	20.0	7.0	20.0	5.0	23.0	8.0	25.8	16.0	33.5	19.5
2	10.5	6.0	10.0	5.5	12.4	8.0	14.0	8.0	13.0	8.5	15.0	7.0	13.4	7.0	15.0	4.0	20.0	11.0	23.8	17.0	26.2	16.5
3	10.5	6.0	10.0	5.0	9.5	7.5	12.9	11.0	12.5	7.5	10.0	5.5	13.0	6.5	12.0	3.5	18.0	12.5	20.3	15.5	26.0	15.0
4	9.2	5.5	9.0	5.0	9.5	7.0	10.8	13.0	12.0	7.0	9.0	7.0	12.7	5.0	11.0	3.0	18.0	12.0	19.1	10.0	19.1	15.4
5	8.9	6.5	8.7	4.5	9.2	7.0	10.5	7.0	12.0	7.5	8.0	6.5	12.0	6.0	11.0	3.0	17.0	9.5	18.5	15.0	15.3	14.0

Note: * – within the sample plot; ** – outside the sample plot.

Table A3. Soil temperature regime (°C) at 20 cm depth in aspen groves on southern slopes of the Kolyma River basin and in the Arkhangelsk Region.

Location		223 km	Mezen[1]	338 km	Koynas[2]
Measurement years		2023–2024	Long-term average	2023–2024	Long-term average
Temperature sum	>0°C (air)[3]	1318	1397	1318	1561
	>0°C (soil)	1200	1226±148	1762	1760±169
	>10°C (soil)	524	739±209	1284	1436±191

[1] Mezen weather station (65.8500, 44.2333, 20 m a.s.l.); [2] Koynas weather station (64.7500, -47.6333, 63 m a.s.l); [3] Air temperature data from weather stations according to (Egorova 1965).