Chapter

Larch: A Promising Deciduous Conifer as an Eco-Environmental Resource

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Abstract

Larch species are widely distributed in the northern hemisphere where permafrost and seasonal frozen soil exist. This species with heterophyllous shoots has been intensively planted in northeast Asia as well as in northeast China as the principal afforestation species for restoring agricultural lands to forests from 1999. Although approximately 15 species exist in the northern hemisphere and they are easy to hybridize. Among them, Japanese larch grows the fastest and was exported to Europe as a breeding species from early 20s. Although Japanese larch is tolerant to cold, it suffered from various biological stresses. After nearly 40 years of vigorous breeding effort, hybrid larch F_1 (Dahurian larch × Japanese one) was developed with simple propagation methods. With the use of free-air CO_2 enriched (FACE) systems, we revealed growth responses of the F_1 and its parent larches to environmental conditions. From experiments, F_1 showed high responses to elevated CO_2 and O_3 but not so much to N loading. As future perspectives for larch plantations as an important eco-environmental resource, we expect to afforest F_1 seedlings infected with ectomycorrhizae (e.g., *Suillus* sp.) for efficient afforestation at nutrient-poor sites and at the same time for the production of delicious mushrooms.

Keywords: larch, hybrid, heterophyllous shoot, growth, changing environment

1. Introduction

The larch species are a typical light-demanding deciduous conifer, ectomycorrhizal (ECM) tree species, and dominant in the northern hemisphere [1, 2]. Among genus *Larix*, Dahurian larch (*Larix gmelinii*; including *L. cajanderi*) is especially dominating permafrost ecosystems has an essential role in climate change in the Far East of Eurasia [3–5]. If we would follow the idea of the well-known Köppen [6] and Whittaker [7], "estimated" vegetation at Far East Russia and northeast (NE) China should be a type of steppe. However, actual vegetation there is light-Taiga (dominating Dahurian larch) due to the existence of permafrost [2, 3]. In this chapter, we discuss the environmental role of larch forests and global climate change.

Some larch species are typical afforestation species in NE China, Russian Far East, Korea, and Japan. Most larches can tolerate cold and late frost [8], thus

attaining significant biomass with a high growth rate in cold regions [2, 3]. Due to these good growth traits, larch (Japanese larch: *Larix kaempferi*: syn. *Larix leptolepis*) was exported to Europe as a pollen resource. Also, Japanese larch had intensively planted in the Korean peninsula and NE China; these forests are used for timber production. From 1999, the Chinese government decided to reforest farmland (<25° slope) and degraded area (i.e., Natural Forest Conservation Program [NFCP]) and employed Dahurian larch (*L. gmelinii*) in NE China to increase forests [9]. From physiology and genetics to ecological point of view where the larch species will contribute as a resource of the sustainable developmental goals (SDGs).

The physical environment surrounding the biosphere has been dramatically changing worldwide. Especially, atmospheric CO_2 concentration ($[CO_2]$), nitrogen (N) deposition, and ground-level atmospheric ozone concentration (O_3) have increased rapidly since the Industrial Revolution [10, 11]. Furthermore, these physical environmental changes will become serious in the near future because of increased energy demands due to rapid economic growth, industrialization, and urbanization in Asian countries. For sustainable use and adequate management of forest resources, we must therefore clarify the response of trees to these environmental changes.

Nowadays, larch trees are intensively planted and lumbered not only in northern Japan [12, 13] but more widely in the northern Eurasian continent. However, knowledge about the susceptibility of this species to environmental stresses is still limited, except for biological stresses, for example, shoot blight and root rot disease [14], and physical stresses, that is, low temperature [8]. Will larches maintain their high growth rate and extensive establishment under the changing environment? Recently, several researchers have studied effects of environmental changes on larch species [2, 4, 13, 15]. The information will be useful for sustainable use and adequate management of larch plantations. In this chapter, we integrate previous studies examining the growth and ecophysiological responses of larch species including their hybrid to environmental changes, and propose the future direction for utilization of larch species.

2. Botanical traits

2.1 Larch species feature

Genus *Larix* is broadly distributed in the northern hemisphere and consists of 17 species including variety [16]. Among them, four species are dominant (**Figure 1**): Siberian larch (*Larix sibirica*) distributes from the Ural mountain to Lake Baikal, Dahurian larch (*L. gmelinii* var. *gmelinii*: syn. *L. dahurica*, partly including *L. cajanderi*) covers eastern parts of the Eurasian continent; mainly on Sakha Republic (Yakutia; Russia) and northeastern part of China; Mandsburica larch (*L. olgensis*) and Hokshi larch (*L. principis-rupprechtii*) are distributed there [3].

Other variety of Dahurian larch (*Larix gmelinii* var. *japonica*) distributes in the Kuril Islands, and in Japan around more than 10,000 years ago; currently, Japanese larch is naturally distributed in the central part of Japan and the northern limit is located Mt. Mano-kami at Northern Honshu Island [17, 18].

In central Europe, European larch (*L. decidua*) is widely distributed even in forming tree-line at the central Alps along with way of an avalanche. American larch (*Larix laricina*) distributed in North America [19, 20]. From 1900's days, Japanese larch had exported to Europe to increase growth rate and stress tolerance because larch species are easily formed by means of a hybrid produced by interspecific crosses [21, 22]. Details of larch species in China are referred to Section 3.2 (Y. N. Wang).
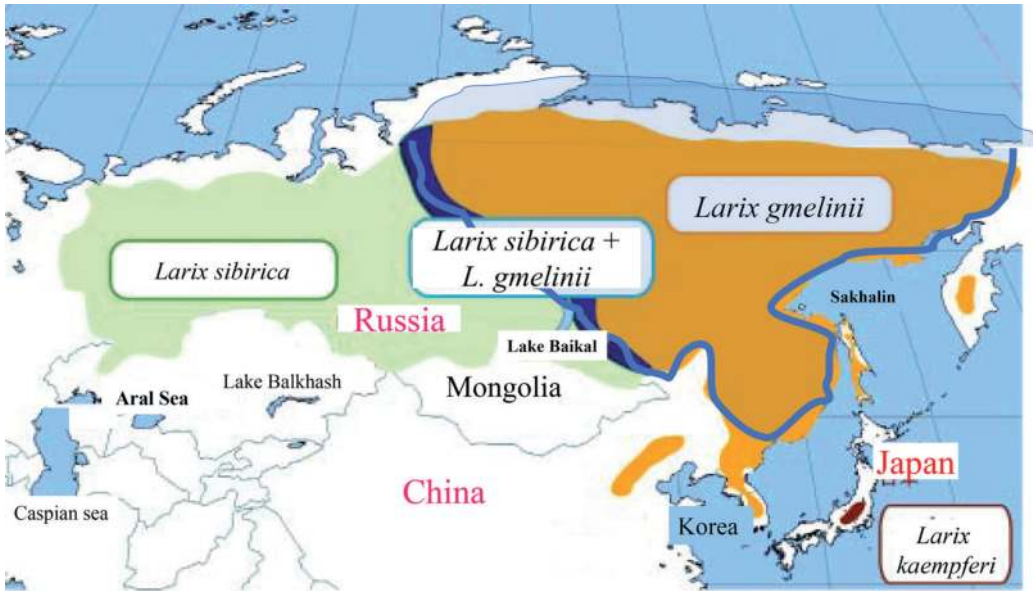
Figure 1.
Distribution of larch species in Eurasian continent and Far East Asia (illustrated from: Abaimov et al. [3], Larix gmelinii *including* L. cajanderi*).*

2.2 Water relations

Deciduous needle habit of larch species may contribute to the dominance of these species in permafrost regions as compared with an evergreen conifer (*Picea mariana*) in Alaska [23]. This deciduousness in leaf habit implies that larch can avoid severe water deficits (including winter desiccation damage) during early spring when soil is still frozen (**Figure 2**). Seedlings and lower branches of larches usually keep their over-wintering needles until the xylem pressure potential is above −1.5 MPa (Koike unpublished data). In fact, winter desiccation damage in Sakhalin fir (*Abies sachalinensis*)
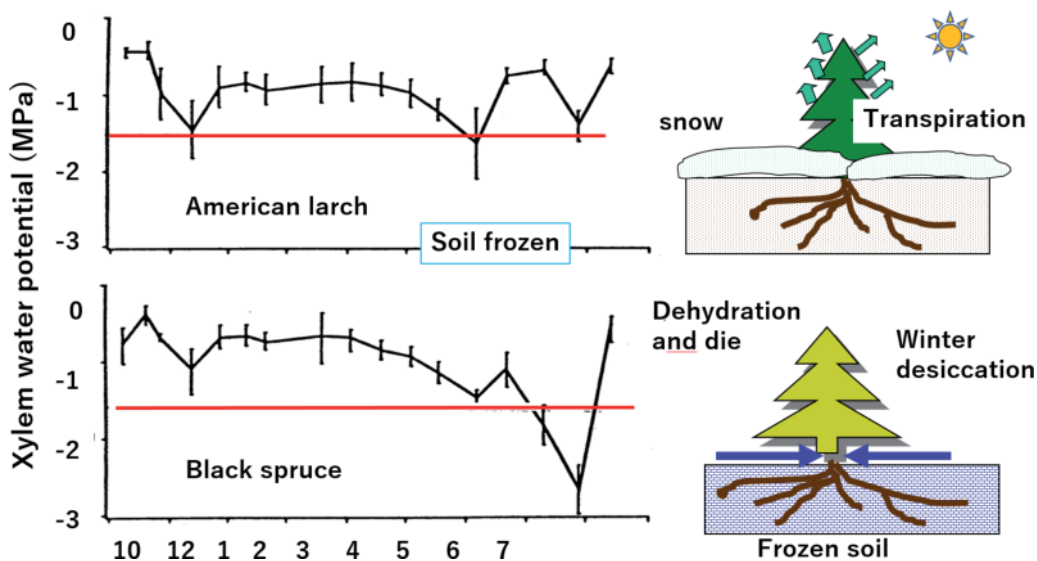

Figure 2.
Seasonal change in the water relation in American larch and Black spruce (left), schema of winter desiccation mechanism (right) [24]. American larch: deciduous, Black spruce: evergreen (Adaptation from: Berg and Chapin [23]).

frequently occurs in plantations facing the Pacific Ocean side in Japan where they have shallow snow depth Sakai [24].

2.3 Needle morphology and photosynthesis

The photosynthetic rate of larches is markedly higher than that of other conifers [25]. However, the initial slope of the light-photosynthetic curve for larch is gentler than that for several conifers, and has similar traits to the C_4 plant [26]. The possibility that the larch is a kind of C_4 plant was nevertheless disproven by a photosynthesis experiment using ^{14}C-labeled CO_2 [26]; larch is concluded as a C_3 type plant.

This high growth results from its high photosynthetic rate and unique arrangement of two different types of needles, that is, short-shoot and long-shoot needles [27]. To reveal the photosynthetic characteristics of short- and long-shoot needles of the sunny canopy of the larch trees *in situ* using a canopy tower, the seasonal change of gas exchange characteristics were measured accompanied by leaf mass per area (LMA), foliar nitrogen content (N) of the heterophyllous needles over 3 years. No marked difference in light-saturated photosynthetic rates (P_{sat}) was observed between short- and long-shoots after leaf maturation to yellowing, although the difference was found in a specific year (**Figure 3**), which only indicates that seasonal fluctuation in temperature and soil moisture determines the photosynthetic capacity of needles [27].

The large annual and seasonal variations in P_{sat} in both shoots were found to be mainly determined by climatic variations, while shoot types determined the strategy of their photosynthetic N utilization (N use efficiency, retranslocation, etc.) as well as the stomatal regulation as found in deciduous broadleaved tree saplings grown under larch forest [28].

Although there is no difference in the growth and development of seedlings of Japanese and hybrid larch F_1, the temperature dependence of photosynthesis in
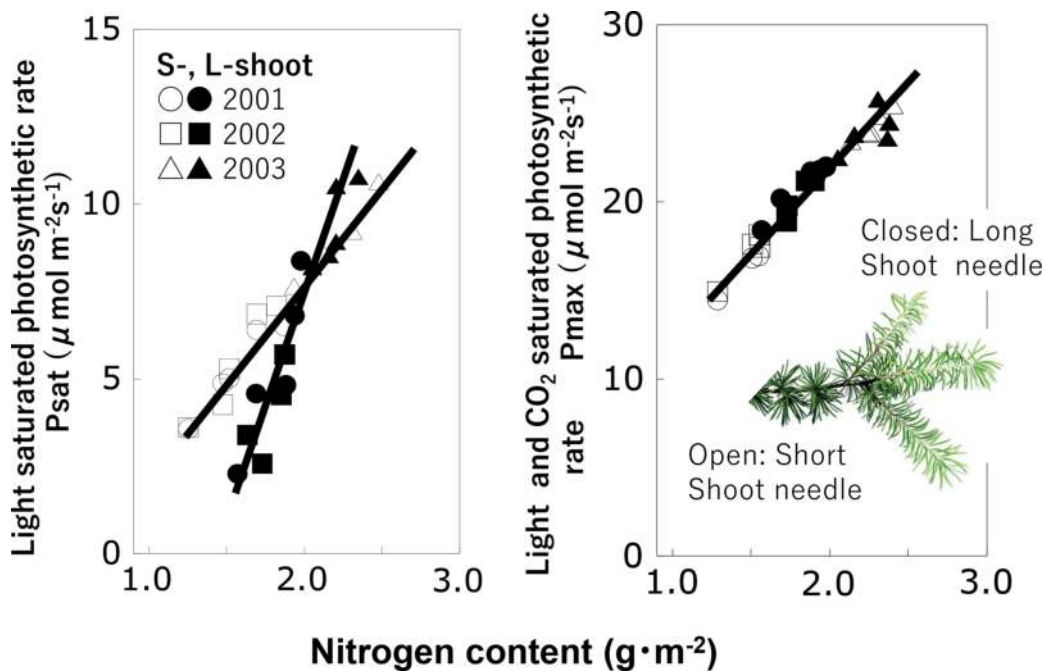
Figure 3.
Variation of light-saturated photosynthetic rate (P_{sat}) at ambient (left) in short- and long-shoot needles at larch canopy and no variation of P_{max} at CO_2 saturation (right) located at larch canopy in terms of N content, measured during 2001–2003 in situ (Adaptation from: Kitaoka et al. [27]).

hybrid larch shows greater photosynthetic starch accumulation capacity than in Japanese larch [29].

2.4 Photosynthates allocation: Individual scale

Carbon (C) allocation pattern of photosynthates may be essential for the growth and survival of plants [30]. Allocation of photosynthates to the root system in larch seedlings, for instance, can maintain growth at low soil pH [31]. Symbiotic microorganisms in larch root require 10–20% of photosynthates of host plants [32]. Larch seedings inoculated with commercial ectomycorrhiza: ECM (*Pisolithus arrhizus*: *Pa*) increased photosynthesis, which is more accelerated by a mixture of ECM collecting from the larch forest floor (**Figure 4**). From Farquhar et al. [33], A-Ci (intercellular CO_2 concentration: Ci and assimilation rate: A) indicates efficient use of photoassimilate in ECM infected hybrid larch F_1. With an increasing number of infected ECM, stomatal limitation (Ls) decreased.

In fact, the growth of larch species is closely connected with the ubiquitous ectomycorrhizal fungal association. Symbiotic ECM improves nutrients (phosphorus, P; nitrogen, N) and water uptake, and buffers against environmental stress [34–38].

2.5 Individual to forest scale

Photosynthate allocation is essential not only for plant growth and survival but is also directly related to the photosynthetic productivity of forested stands. Photosynthetic production is a compromise between the instantaneous photosynthetic capacity of leaves and leaf longevity (e.g., [22, 34]). Photosynthetic production (biomass) is therefore tightly linked to leaf area index (LAI; leaf area per unit area; $m^2 m^{-2}$). As a result, LAI has been studied in several terrestrial ecosystems. Larch forests have a relatively small LAI value of 4.1 [39] (**Table 1**). The aboveground production rate of larch in early autumn is estimated to be similar to that of evergreen conifers (e.g., *Picea abies*) in a cool-temperate environment.

2.6 Continental scale

As summarized by Osawa et al. [2], carbon (C)-allocation of permafrost ecosystem has unique characteristics and key of survival of larch on permafrost in Central and Far East Russia where a vast area of forest exists on continuous permafrost [45]. According to them, "Deciduous coniferous taiga, larch ecosystem is one of the unique biomes in northeastern Eurasian Continent, where a vast area of forest exists on continuous permafrost." We defined the active soil layer as the melted soil layer between the ground surface to the front of frozen soil. Based on the field survey, three representative sites were selected: (1) a forest near Yakutsk in Yakutian Basin, eastern Siberia (62 N–129E), (2) a forest near Tura in central Siberian Plateau (64 N–100E), and (3) a forest tundra transition near Chersky in Kolyma lowland (69 N–160E) [45]. C storage in these ecosystems was estimated in both aboveground and belowground biomass, in the forest floor, and in active layer as for soil organic C and as carbonate-carbon (**Figure 5**).

Matsuura et al. [45] well summarized that organic C in the soil in active layer was the largest component in the sites. Soils in Russia (Yakutsk and Tura) sites indicated carbonate-C accumulation in the active layer, which might result from an extreme continental climate with low annual precipitation of around 200–500 mm $year^{-1}$ and big temperature range C storage in above- and below-ground biomass varied among sites, however, ratios of above–/below-ground biomass C had a narrow range from 1.1 to 1.5. The high allocation rate of C to below-ground
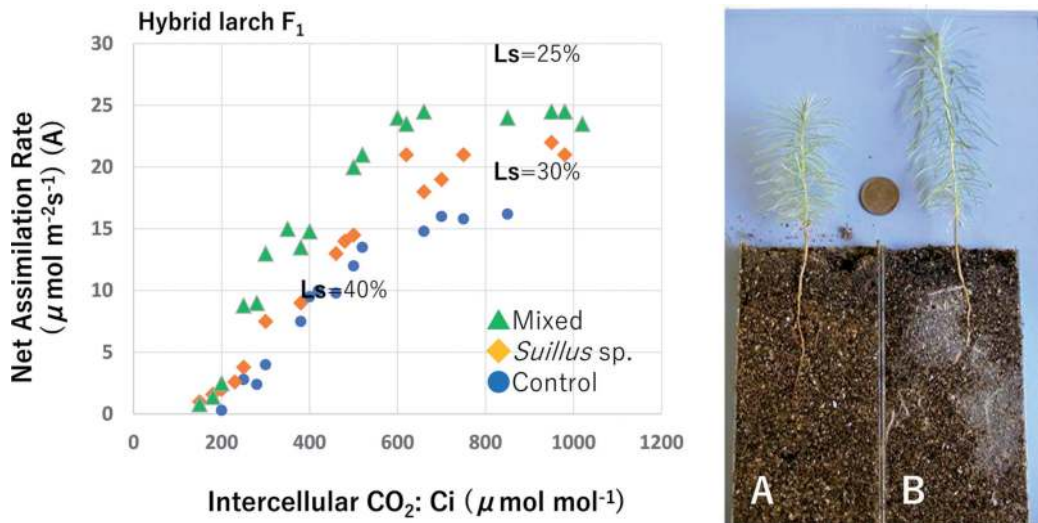
Figure 4.
Assimilation and intercellular CO₂ concentration (A-Ci) relation in hybrid larch F₁ inoculated with ECM (one species vs. multi-infection) and stomatal limitation (Ls %). Right: A: control; no infection of ECM, B: in infected with commercial ECM (Pisolithus arrhizus) (Adaptation from: Qu et al. [32]).

Forest type	Foliage mass (ton hm⁻²)	Leaf area index (LAI) (m m⁻²)	No. stands	References
Deciduous forests	2.9 ± 1.5	3.0–6.0	98	[40, 41]
Larch stand	2.9 ± 1.0	2.5–4.5	28	[41, 42]
Pine (red and black)	6.8 ± 1.8	3.5–6.0	60	[41, 42]
Evergreen forest	8.6 ± 2.6	5.5–9.0	46	[41, 43, 44]
Evergreen conifers	16.0 ± 4.5	5.0–10.0	49	[40, 42]
Cryptomeria (cedar)	19.4 ± 4.9	4.5–8.5	97	[42, 43]

Table 1.
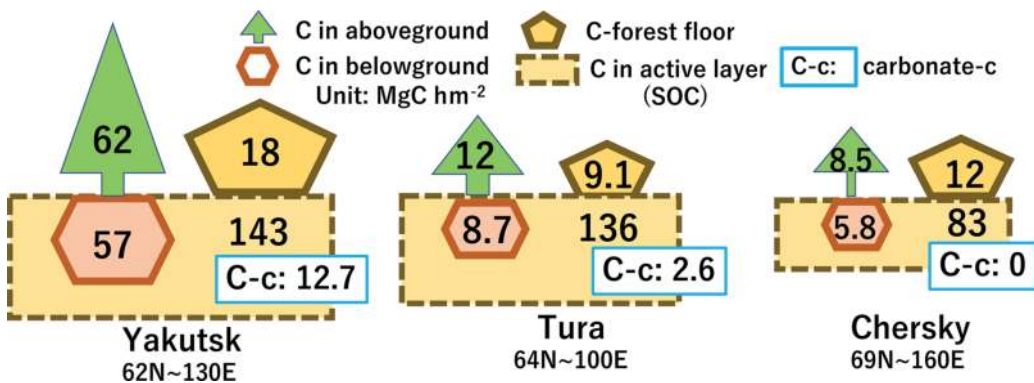*Forest types, foliage mass, and LAI.*

Figure 5.
Carbon storage and allocation in different larch ecosystems in eastern Eurasia (Adaptation from: Matsuura et al. [45]).

part resulted from a kind of adaptation to effective water and nutrient acquisition under nutrient-limited environment due to low soil temperature for litter decomposition [46].

3. Vegetation characteristics

3.1 Russian Far East and central Siberia

In this section, we should point out important evidence; "Permafrost layer nurtures light-Taiga and the canopy protects permafrost" [2], especially at Yakutia; northern Far East (FE) Russia. According to the classic idea of climatologists and community ecologists [6, 7], Yakutian vegetation should be steppe or grassland, however, light Taiga mainly composed of larch is well developed [47]. Even under the low precipitation of continental climate, the permafrost provides water from belowground to aboveground, which is accelerated by extra-harvesting, forest fires, global warming [2, 48], etc. However, the accumulation of salt (mainly of Natrium compounds) on the ground surface will inhibit forest regeneration [49]. Much worse, the emission of greenhouse gas (CO_2, CH_4, N_2O, etc.) and unknown microbes will increase from melted permafrost. As an old saying of Yakutian people, "we can make one grave per one." Alas (=pond appeared after harvest or fire in the Taiga)", which points to their method of sustainable forest management method (**Figure 6**).

Regeneration of larch is moderate and larch-dominated Taiga is recovered (canopy closure) 20 years after forest fires. This is attributed to an increase in depth of the active soil layer by heat from fires and/or charcoal accumulation. Another 80–100 years and more after the canopy closure, the closed canopy gradually becomes sparse because sunlight to the forest floor is intercepted and will recover the depth of the active soil layer. As a result, competition of aboveground may be caused by limited amount of water and nutrients, but not only by light resources [2, 48].

3.2 Distribution of larch in China (Y. N. Wang)

In China, there are two sections in genus *Larix*: Sect. *Larix* and Sect. *Multiseriales*, 11 species (with four endemic species, two introduced species) as shown in **Table 2** [53].

Figure 6.
The Alas developed after harvesting by local people of Yakutia (Adopted from: Koike [50], with permission).

Section	Species	Elevation (m)	District, location habitat	
Sect. *Larix*	*Larix gmelinii*	300–2800	Hebei, Heilongjiang, Northwestern Henan, Jilin, Nei Mongol, Shanxi (Daxing'anling, Xiaoxing'anling Mt.)	Rocky slopes, peatlands, swamps, lowland subarctic plains, river basins, valleys
	(*L. gmelinii* var. *principis-rupprechtii*)	600–2800	Hebei, Northwestern Henan, Shanxi	Usually on rocky slopes
	Larix olgensis	500–1800	Jilin, Eastern Liaoning	Mountains, moist slopes, swamps
	Larix sibirica	500–3500	Xinjiang, Altai M., Eastern Tianshan M., lowland taiga	Cold, relatively dry, long day-time during July to August
	Larix kaempferi		Hebei, Heilongjiang, Henan, Jiangxi, Jilin, Liaoning, Shandong	Introduced, cultivated
	Larix decidua		Jiangxi (Lu Shan), Liaoning	Introduced, cultivated
Sect. *Multiseriales*	*Larix griffithii*	3000–4100	Southern and Eastern Xizang	Mountains
	Larix speciose	2600–4000	Southeastern Xizang, Northwestern Yunnan	Mountains
	Larix kongboensis	3200–3500	Southeastern Xizang (Gongbo'gyamda)	Rocky slopes
	Larix mastersiana	2300–3500	Sichuan	Mountains
	Larix himalaica	3000–3500	Southern Xizang	River basins, valleys
	Larix potaninii	2500–4300 (−4600)	Southern Gansu, Southern Shaanxi, Sichuan, SE Xizang, Northern Yunnan	Mountains, river basins

Refs: Fang et al. [51], Li et al. [52], and Flora of China [53].

Table 2.
Larch distribution in China.

L. gmelinii are mainly distributed in the Daxing'anling, Xiaoxing'anling mountains in Northeast China, especially in the Daxing'anling mountains (**Figure 7**). It is the most representative species of cold temperate coniferous forest with stands occupying the large area with high biomass stocks.

It is the main wood production base in China and one of the main tree species for forest management, and artificial afforestation in Northeast China. With the thawing and shrinking of permafrost, the distribution of *Larix Xing'an* will gradually move northward, and the proportion of *L. Xing'an* in the ecosystem of *L. Xing'an* forest will also gradually decrease as suggested by Abaimov et al. [22]. According to the prediction of the distribution model of larch in Xing'an, the distribution of larch in the community of *L. Xing'an* forest will gradually move northward or even outward under the climate change in the future [52].

Larix principis-rupprechtii is a typical zonal-type tree in the middle and high mountains of North China. Its rapid growth, excellent resistance to cold and drought, and woody materials play an important role in an ecological component and strategic timber reserve in the mountainous areas of North China [51]. The natural distribution is mainly in Shanxi and Hebei provinces. With the promotion of cultivation technology, in recent years, its plantation area was
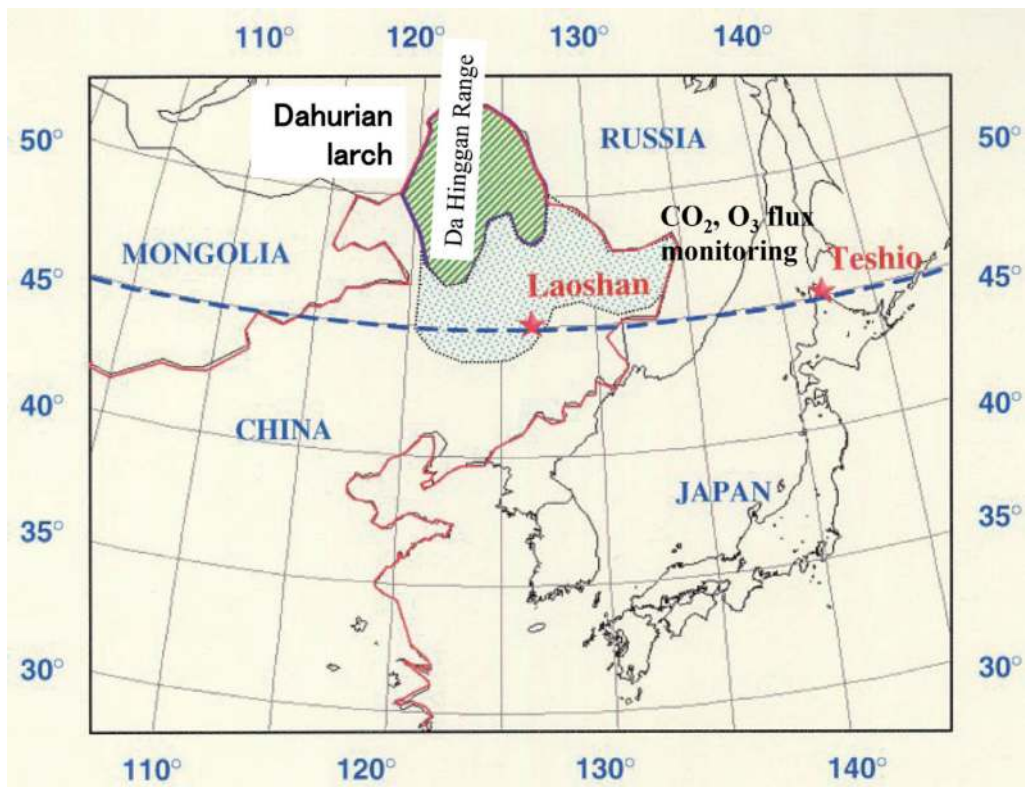
Figure 7.
*Distribution of Dahurian larch (*Larix gmelinii*) forest in NE China (adaptation from: Mao et al. [54], Wang et al. [55], and Shi et al. [46]).*

been widened to the low altitude areas of Shanxi and Hebei provinces, Inner Mongolia, Beijing, Shandong, Liaoning, Shaanxi, Gansu, Ningxia, Xinjiang, and other provinces and cities. Due to the great influence of geographical environment and natural conditions, as well as the influence of climate change, most of the introduction and cultivation in other areas except the original place are not good.

Japanese larch (*Larix kaempferi*) is native to Japan and was introduced to China in the late 19th century, which has a wide range of adaptation, rapid initial growth. It has become the main afforestation tree species in the mountains south of 45 N in the eastern northeast of China, mainly cultivated in NE China, North China, NE China, and SW China [53].

Larix sibirica is a coniferous species endemic to NW China, only distributed in a small amount in Xinjiang areas distributed in the northern part of NE China. It is generally distributed in cold mountainous areas or on the banks of low mountain valleys, is one of the most distributed building species in the Altai Mountains. It is mainly distributed on the slopes of wet airflow and the shady and semi-shady slopes of river valleys [53].

4. History of afforestation in Far East Asia and forest fires

Forests in Russian are mainly regulated by forest fires and are naturally regenerated [13, 16, 47]. The Chinese government has been intensively planting three species including larch from 1999 [9, 56]. In Japan, the establishment of plantations of Japanese larch was not successful due to several biological stresses, especially in Hokkaido island [13, 15].

4.1 Far East Russia and central Siberia

Larch forest conservation and silviculture in Far East Asia should be considered on the high pressure of forest fires [2, 3, 46, 57]. Forest fires have been regulating vegetation dynamics there, especially Russian Far East [47, 57]; the essential role of biochar is well evaluated (**Figure 8**) [58, 59].

4.2 China

Larch (*Larix* spp.) is one of the most representative forest component species in mountain and temperate zone under cold conditions, forming the northern coniferous forest with the largest area and the highest volume in the eastern part of the Eurasian continent. As native species are widely distributed in NE and north China, larch forests play a pivotal role in maintaining forest ecosystem functions and mitigation of carbon concentration in the atmosphere.

Larch is naturally distributed in mountain areas of NE China, Inner Mongolia, North China, and SW China. Due to its characteristics of cold resistance, fast growth, fine wood structure, and strong corrosion-resistance, it has become the main afforestation and fast-growing high-yield tree species in northern China [9]. Since the founding of the People's Republic of China, a large area of larch plantation has been built successively, which is an important reserve forest resource in China [60]. Larch usually forms a large area of the pure forest after forest fires [15, 46, 47, 57], or composition of larch-based mixed forest with birch, poplar, spruce, and other coniferous and broad-leaved trees [46].

According to the data of the 9th National Forest Inventory in China (2014–2018), the national forest coverage rate is 22.96%, with a forest area of 220 million hm^2, including 79.54 million hm^2 of the artificial forest, ranking first in the world [60].

Figure 8.
A view of burned larch forest after trunk fire at around Amur state, Russia (Photo courtesy by: Dr. Semyon Bryanin and Dr. Makoto Kobayashi).

According to the report of Global Forest Resources Assessment (FRA) in China, the growing stock in the forest of larch species reached about 1,200 million m^3 [56]. As dominant tree species components, the top three tree species are oak (*Quercus mongolica*) forest, Chinese fir (*Cunninghamia lanceolata*) forest, and larch forest. It can be seen that larch plays an important role in the forest composition of China [9].

As mentioned above, the Chinese government has been intensively planting three kinds of tree species (Dahurian larch for NE, Chinese fir for SW, and poplar for all parts) on farmlands and degraded areas. This project is called as NFCP, which emphasizes "expansion of natural forests and increasing the productivity of forest plantations" [9], and attained the largest new plantation area in the world [56, 60]. This area by 2019 is larger than the whole Japanese land area. On the occasion of the announcement of the leader Mr. Xi Jinping, one of the Chinese ecological policies orients us on how to conserve forest as an ecological unit. Based on this statement, the conservation of the forest ecosystem is one of the national key projects for "ecological culture city" [61]. However, NFCP proposed they would not harvest their own trees. In connection with this, Chinese trade in timber may strongly depend on forests in Amur state, Russia, and other states located in the opposite bank where no "border" between the two states due to the river frozen during winter.

4.3 Japan

In Japan, the establishment of larch plantations had been not successful due to several biological stresses, in Hokkaido island as well as a central part of Japan [39]. From silviculture records [53, 62], larch plantation started to use mountain stock in Nagano prefecture in central Japan during 1624–1645. At around 1890, the production method of larch seedlings has established in central Japan and had expanded to Hokkaido around 1910 [18, 53]. Intensive plantation of larch was intended to produce mine timber equipped with high compressive strength by short term rotation culture of around less than 30-year-old.

At the latter 1970's days, the outbreak of grazing damages on the needle by larch sawfly (*Pristiphora erichsonii*) spread around the southern part of Hokkaido and continued around mid-1980 [18]. The grazing by sawfly again started from 2000 and continues until now in whole Hokkaido Island (**Figure 9**). This may be due to recent dry and warm climatic conditions and big stresses caused by attacking by *Armillaria* sp. [18]. The responses of the Japanese larch (*Larix kaempferi*) to graze by the larch sawfly (*P. erichsonii*) were examined from the perspective of the carbon/nutrient balance (CNB) hypothesis [64]. The defoliation intensity was determined from canopy photos taken from 2009 to 2012 in seven Japanese larch plantations in central Hokkaido, Japan. A decrease in foliar nitrogen and increases in phenolics, tannins, and the CN ratio was found in the years following severe defoliation. The influence of defoliation was fluctuated over years. These results indicated that the past defoliation history additively affected the foliage properties in the 2 years following insect grazing. Phenolics and sugars did not increase linearly with the leaf CN ratio, indicating that limitations affected their synthesis. These results suggest that the induced changes in *L. kaempferi* properties are partially up-regulated under N limitation, but that secondary compound synthesis was affected by external site-dependent factors other than N limited condition.

Effects of insect defoliation were studied on the formation of secondary cell walls of tracheids in *L. kaempferi* with a focus on the defoliation timing [65]. The secondary cell walls of tracheids produced in a defoliation year in *L. kaempferi* trees on which needles were attacked in July (Gypsy Moth, GM samples) or August (Larch sawfly, LS samples). GM samples produced non-lignified tracheids in the transition zone between earlywood and latewood, as well as thin-walled latewood
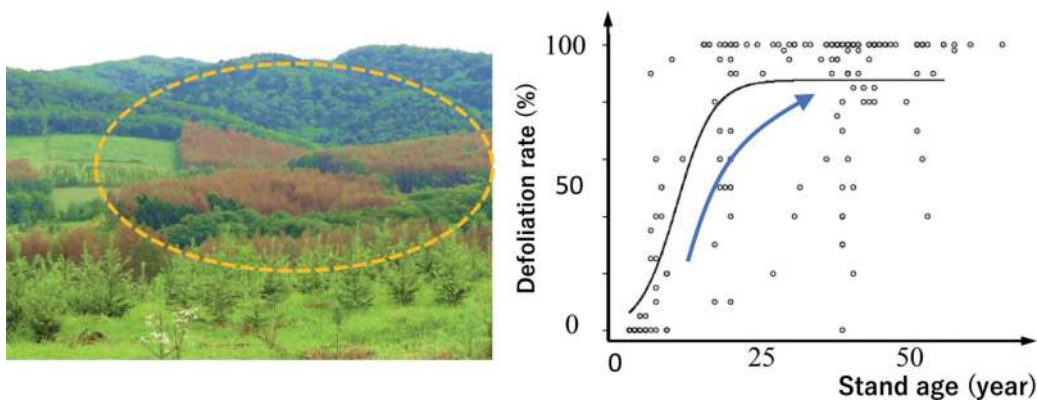
Figure 9.
*Yearly trend of larch sawfly in Hokkaido Island (after Fujita et al. [63]). Larch sawfly (Pristiphora erichsonii)
grazes mainly shoot-shoot needles, and then defoliation increases with increasing stand age due to high
proportion of short-shoot needles (Photo courtesy by: Kitami office of Hokkaido Pref.) defoliation rate was
detected by aerial photography, and recently by unmanned aerial vehicle (UAV). After the grazed area was
detected by these methods, defoliation rate (%) is expressed against plantation area by the records. The dashed
orange circle shows larch plantations that have been damaged by larch sawfly grazing (left; photo courtesy by:
Kitami office of Hokkaido Pref.). The right graphs indicate the relationship between the defoliation rate (5)
and stand age. As larch sawfly (P. erichsonii) mainly grazes on the short-shoot needles, and the defoliation rate
increases with increasing stand age as the proportion of short-shoot needles also increase with stand age. For
Larix kaempferi seedlings, current year shoot and root growth were decreased with defoliating intensity and
traumatic resin canals were also observed from stem cross-sections (after Fujita et al. [63]).*

tracheids, and non-lignified tracheids were observed near the cambial zone in LS
samples following defoliation for two consecutive years. Changes in wood structure
depend on the date of insect defoliation and that insect defoliation affects the for-
mation of secondary cell walls of tracheids, presumably in response to inadequate
photosynthates supply due to defoliation. We can recognize them as "white ring" as
reported in birch and poplar [66, 67].

5. Genetics and breeding effort

5.1 Russia and China

Collection of larch seed, representing larch over the whole range of genetic and geo-
graphic variation has been discussed between Russian and Swedish authorities since
the 1950s [14, 22]. The objective of the Russian-Scandinavian Larch Project is to study
the genetics of the four main larch species within Russia, *L. sukaczewii* Dyl., *L. sibirica*
Ledeb., *Larix gmelinii* Rupr., and *L. cajanderi* Mayr., and to make future research on
genotype-environment interaction in other parts of the northern hemisphere possible
[14, 22]. Up to the end of 2000 seed and wood cores were collected from 1005 larch
trees distributed over 16 regions and 45 stands. In addition to that larch seed has been
bulk collected from eight stands. Collected seed from 802 open-pollinated families
were tested for seed germination in the summer of 2000 [22]. The average germination
rate of the seeds was 25%, but with great variation among larch species [22, 39].

5.2 Japan

5.2.1 Brief history

Japanese forestry engineers successfully created hybrid larch F_1 with high
tolerance to various stress and also improved timber quality. Efforts are also made

to establish larch plantations with considerations to biodiversity management, however, the outbreak of diseases of Japanese larch are reported in even UK [68]. Elite tree of larch was selected 270 clones from 20 to 40 years old plantations during 1955–1961; these clones were originated from central Japan. Among them we preferred to use Dahurian larch originated from the Kuril Islands but not from Sakhalin Island because leaf senescence is delayed in the Kuril one [18, 69].

Seed orchards were made by randomly planted with elite trees of Dahurian arch and Japanese larch, and provided seeds of hybrid larch F_1 [14]. At 2000, we used hybrid larch F_1 for plantation of 300 hm^{-2} $year^{-1}$ (=800,000 planting stocks), however, these production activities were far from the demand of forestry industries [18]. This may be attributed to the low capacity of producing fertility of seeds of F_1. The crossing ratio fluctuated mainly depending on the pollen father of Japanese larch; it reaches 56.3% in the good harvesting year while it was 23.2% in the bad harvest year, based on DNA marker [70]. On the way of selection of ideal F_1, we isolated "Clean larch" (nick name of this new species) which showed a high growth rate and density in the stem ($\fallingdotseq$0.55); more than 20% larger than those of Japanese larch [17, 71].

5.2.2 Hybrid larch F_1

In northern Japan, hybrid larch F_1 (*Larix gmelinii* var. *japonica* × *L. kaempferi*; hereafter F_1) was produced to improve tolerance to grazing damage by voles and stem straightness, thus enhancing growth rate, timber quality [15, 70]. Nowadays propagation methods have improved, that is, cutting from only current seedlings, so the F_1 is becoming a principal afforestation tree species in northern Japan [14]. These new benefits bring a new plantation method from the traditional method: high planting density with several thinning to low planting density [18]. As shown in **Figure 10**, the relationship between the growth of the annual ring and bulk density (kg m^{-3}) in several trees [72]. From this, it is shown that the larch species keeps its high bulk density-independent of annual ring growth (over 320 kg m^{-3} should be needed) because of clear change from "spring wood" to thick "summer wood."

If we would plant larch with low density (standard planting density is 3000 ha^{-1}), we can keep commercial important wood strength. This means we can save our labor power in weeding in the initial stage of planting. Regional Forestry Institute proposes low-density plantation from 1,500 to 1,000 hm^{-2} [18]. With low density, we can expect the invasion of several kinds of species that regenerate at open gaps. As efforts are also being made to establish plantations with considerations made to biodiversity management, the invasions of these gap species may be beneficial. In addition, topics on diseases of Japanese larch in the UK should be considered [68].

5.2.3 Improve CO_2 fixation capacity of a forest ecosystem

Clear-cut harvesting is one of the mainly performed forest management methods but is it considered to be the cause of large CO_2 emissions. Understanding how this form of harvesting or logging affects site-specific CO_2 balance is important for determining a considerate management method, however, data on how timber harvesting affects the CO_2 balance of the ecosystem is still limited (**Figure 11**).

An experimental clear-cutting and plantation establishment study have been conducted in a cool-temperate mixed forest in northern Japan [73]. Before planting a the promising F_1 (*Larix gmelinii* var. *japonica* × *Larix kaempferi*), dwarf-bamboo: *Sasa* sp. was stripped to secure space. We obtained a complete series of pre- and post-harvest data on the net ecosystem CO_2 exchange (NEE) between the ecosystem
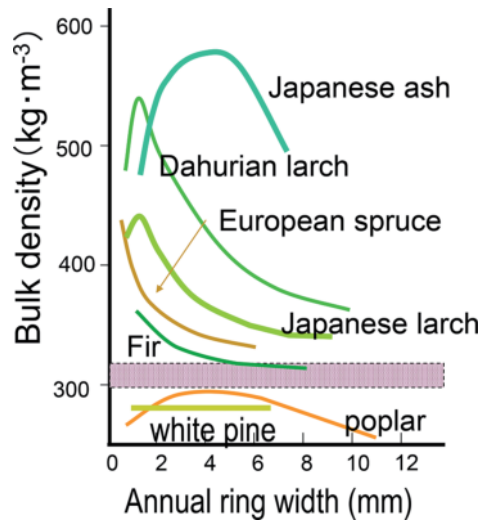
Figure 10.
Annual ring width and bulk density in several tree species planted in Hokkaido Island, Japan (Adopted from: Miyajima [72]).
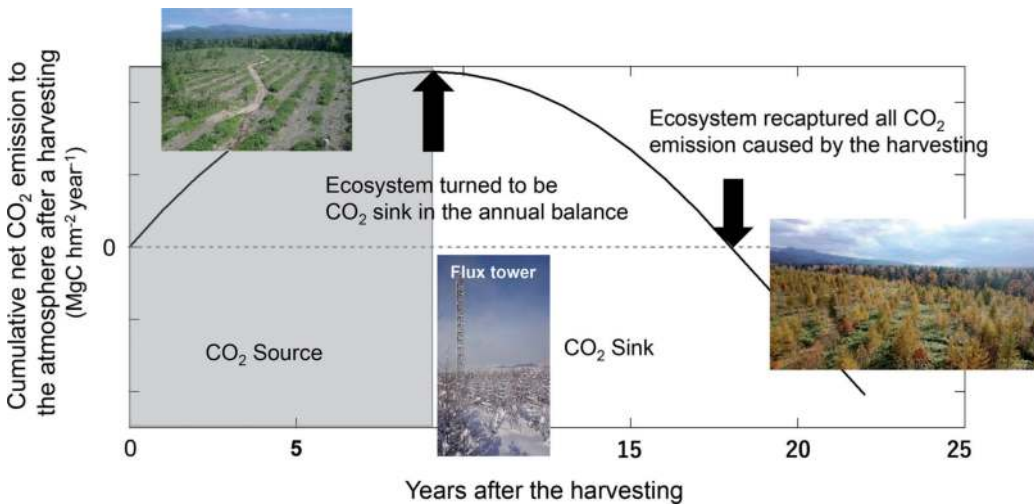

Figure 11.
Concept of the forest CO_2 balance after the harvesting from a spare mixed stand to make new plantation of hybrid larch F_1 (a view in mid-October in yellow color) at Teshio Experiment Forest located at northern most Japan (Takagi et al. [73]).

and the atmosphere until the disturbed ecosystem was once more a net CO_2 sink in the annual budget and recapture all the emitted CO_2 after the harvest and weeding. An over-harvested mixed forest, which had been a weak CO_2 sink with dense *Sasa* sp. (=dwarf bamboo) community was disturbed by the harvest of remaining trees and was replaced with a hybrid larch F_1 plantation. The ecosystem turned to be a large CO_2 emission source just after the harvesting in 2003, and the cumulative net CO_2 emission reached up to 15.4 MgC hm^{-2} at 7 years after the harvesting, then the "new" ecosystem turned to be a CO_2 retrieve mode (i.e., CO_2 sink in the annual budget). This ecosystem with F_1 recaptured all CO_2 emissions, 18 years after the harvesting in 2020, not considering off-site carbon storage in forest products. This means that a single harvest procedure works to change the CO_2 balance because the large invisible and long-lasting effect on the forest ecosystem CO_2 balance at the northern most experiment forest in Japan.

6. Ecophysiological responses of F_1 to environmental changes

We focus on the effects of environments (light, water) on larch species in Far East Russia to understand further responses of larch to the rapid change of environment including pollutants.

6.1 Russia and China

One of the topics will be described in this section to understand functional traits of larch in permafrost habitats (limited precipitation but rich in water via permafrost) in a continental climate, for example, Siberia (Russia): needle CO_2 assimilation, respiration, and intra-tree carbon transfer using ^{13}C labeling of mature larch trees. In China, the ecophysiological study is very limited but most studies were oriented CO_2 flux monitoring to contribute CO_2 balance in the atmosphere [74] but the acute estimation of non-photosynthetic organs [75] and soil respiration under different land-use [56]. Here we mainly focus on the ecophysiology of central Siberia studies.

6.1.1 Needle CO_2 exchange at Tura forest (Masyagina O. et al.)

The study area locates in the larch ecosystem (*Larix gmelinii* Rupr. Rupr.), which is a typical forest of the northern part of Central Siberia (Tura, Krasnoyarsk region, Russian Federation) with continuous permafrost presented (**Figure 12**). The climatic conditions of the study region and detailed characteristics of the chosen area are described by [77]. The study site (116 m^2) is a dwarf shrub-*Carex*-green feathermoss larch stand with an understory of *Salix* spp. The stand average age is 104 years as of 2013. The stand density is 9,052 hm^{-2}, the average tree height is 4.89 m, and DBH is 4.44 cm. Soil type is Typic Aquorthels.

6.1.2 Whole-tree ^{13}C-labeling experiments

At Tura site, nine mature larch trees were ^{13}C-labeled using whole-tree chambers (**Figure 12C** and **D**) in 2013–2014 (three trees in August 2013 and six trees in June and July 2014) [77]. A transparent plastic chamber (film thickness = 125 μm) was specifically designed to label the whole crown of the mature larch trees (about 104-year-old as of 2013). The chamber size (about 7 m^3) was related to the dimensions of the target trees. Mixing fans were used to enable uniform distribution of ^{13}C-labeled CO_2 inside the chamber and for regulation of the inner air temperature and humidity, to prevent the photosynthetic apparatus from damaging due to the high temperature, which is expected in the closed chamber under intensive insolation [78, 79]. The ^{13}C-labeling procedure is described by Masyagina et al. [77].

During the growing seasons (05 August 2013–19 September 2013 and 14 May 2014–15 September 2014), we sampled larch organs and tissues (brachiblasts: short-shoot needles; auxyblasts: long-shoot needle), twigs, phloem, xylem, and roots) for isotopic analysis of bulk $\delta^{13}C$ from ^{13}C-labeled trees on the selected dates (−1 = before labeling), 0 (−1 = before labeling, 0 = day of the labeling, 1, 4, 8, 15, 28, 40, 60, 75, and 90 days after labeling). In the following years after labeling, the sampling was undertaken monthly from June to September (2013–2018). Needles have been collected from the sun-exposed position of the larch crown between 11:00 and 18:00 hours (sampling was not conducted on rainy days). After collection, the needles were inactivated with a microwave oven at the middle regime (ca. 350 Watt) for 3 minutes to stop enzymatic and metabolic activities [80] (in details, please refer to * part in **Figure 12**).
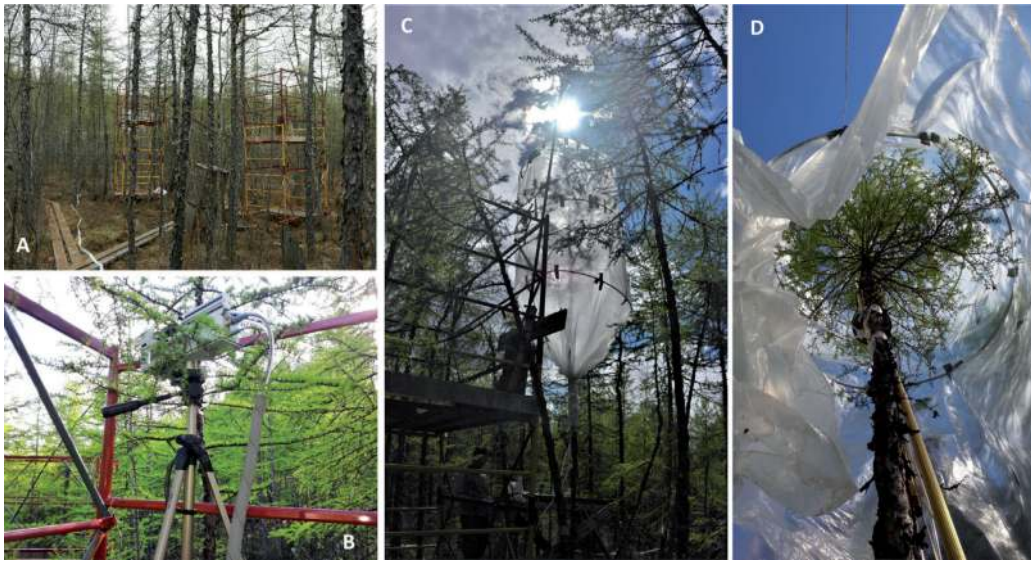
Figure 12.
Tura site layout (A), needle CO_2-exchange measurement (B), whole-tree ^{13}C-labeling experiment in June 2014 (C) and ^{13}C-labeled mature larch tree inside the chamber (D) [76]. *: The samples were then dried for 48 hours at 60°C and ground to a fine powder. $\delta^{13}C$ analyses of the samples were done using automated device HeliView (MediChems Engineers Co., Ltd., Chungcheongnam-do, Korea) comprised of mass-spectrometer and gas chromatograph (N = 1447) in NRC Kurchatov Institute, Moscow, Russia), Isotope Ratio Mass Spectrometer Isoprime 100 (Isoprime), Elemental Analyzer Vario Isotope Cube (Elementar) (N = 118) in Sukachev Institute of Forest SB RAS, Federal Research Center "Krasnoyarsk Science Center SB RAS," Krasnoyarsk, Russia), and an elemental Analyzer-isotope ratio mass spectrometer (N = 395) in the Stable Isotope Laboratory of the Natural Resources Institute Finland (Luke) in Helsinki (Finland). All devices were inter-calibrated by analyzing the same samples to ensure the same accuracy of the devices. **: CO_2 gas exchange rates were measured at the middle part of the larch crown as it demonstrated mean values of pigment contents and average needle CO_2 gas exchange rates compared to the bottom and upper part of the crown. To access all control trees, we constructed 4-m-height monitoring tree towers. CO_2 exchange rates were calculated per needle projection area ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$). Foliar projection area was measured with flatbed scanner CanoScan LiDE 700F and further calculated using software «AreaS» 2.1 (developer Permyakov A.N., www.ssaa.ru).

6.1.3 CO_2 exchange measurements in larch needles

Seasonal CO_2 exchange of larch needles of six non-^{13}C-labeled larch trees in the mid-June, mid-July, and mid-August of 2013–2014 was measured using an infrared gas analyzer Walz GFS-3000 equipped with the chamber for conifers (3010-V80) with the inner area of 8 cm^2 as described by Masyagina et al. [77] (**Figure 12B**). *In vivo* measured with the infra-red gas analyzer, the net CO_2 assimilation represents a net balance between the carbon flux entering the leaf (the gross photosynthesis) and departing the leaf simultaneously (the photorespiration and the mitochondrial respiration in the light) [81] (in details please read ** part in **Figure 12**).

6.1.4 CO_2 exchange of larch trees in permafrost habitats

Diurnal dynamics of needle CO_2 exchange of larch trees were studied over the growing season of 2013–2014. CO_2 exchange values varied seasonally from −3.6 to 8.9 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ in 2013 and −3.9 to 9.1 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ in 2014. Similar maximal values of photosynthetic rates for *Larix gmelinii* have been reported from Eastern Siberia (2.7–10.1 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ by Vygodskaya et al. [82] and ca. 11.3 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ by Korzukhin et al. [83]), Central Siberia (7.5–11 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ [50]), and China (8–11 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ [74]).

Midday depression of photosynthesis has been registered almost in all studied trees except for one individual in July of 2013. The most profound depression was found in June of both years when soil water accessibility remains little due to the

shallow active soil layer (<20 cm) and in July 2014. In the permafrost zone, the physiological activity of *L. gmelinii* is essentially dependent on soil water supply from the seasonally thawed active layer [84].

Diurnal dynamics of photosynthesis slightly varied among months of the growing season, for example, its length per 24 hours varied in the range of 11–16 hours due to environmental conditions. For example, in June, photosynthesis was registered from 6 a.m. to 9 p.m. in 2013 or 7 p.m. in 2014; in July, photosynthesis was active from 5 a.m. to 8–9 p.m.; in August, photosynthesis lasted from 6 a.m. to 5 p.m. in 2013 and from 8 a.m. to 7 p.m. in 2014. Interesting, the average values of photosynthesis were on a similar level of ca. 1–3 μmol CO_2 m^{-2} s^{-1} (**Figure 13**) in various months. In mid-July, we observed a slightly higher rate of CO_2 assimilation compared to the rest of the growing season.

6.1.5 Intra-tree $\delta^{13}C$ carbon transfer (^{13}C labeling of mature larch trees)

To understand how C is traveling and allocating within a larch tree, we conducted several ^{13}C labeling experiments at the beginning (June), in the middle (July), and at the end (August) of growing seasons of 2013 and 2014. Here, we will discuss only June-labeled trees, namely labeled on June 10–12, 2014. The main C-accepting tree organs were needles and long shoots; their enriched $\delta^{13}C$ values achieved about 1700‰ in several hours after the ^{13}C-labeling experiment completion (**Figure 14**). Our study showed similar CO_2 assimilation capacity that resulted in the insignificant variation in ^{13}C excess (about 136 ± 1% [mean value ± SE], CV = 4%, unpublished) in needles among the trees labeled in various periods of the growing season (mid-June, mid-July, and mid-August) in the day of the ^{13}C-labeling experiment. It is a very interesting phenomenon since we found high variation in the environmental variables [77]. The ^{13}C-enrichment of phloem, xylem, twigs, and roots did not exceed 500‰ just after the labeling experiment (**Figure 14**).

In the year of the ^{13}C-labeling experiment, the highest decay rate of $\delta^{13}C$ was observed in needles and long shoots (**Figure 14**, panel 0). Two months after the ^{13}C-labeling experiment there were peaked $\delta^{13}C$ values (about 150‰) found in phloem due to intensive transfer of C at that time. At the end of the growing period of 2014 (year of a ^{13}C-labeling experiment), the average $\delta^{13}C$ values in yellow needles and long shoots were ca. 300‰, in twigs and wood (phloem and xylem),
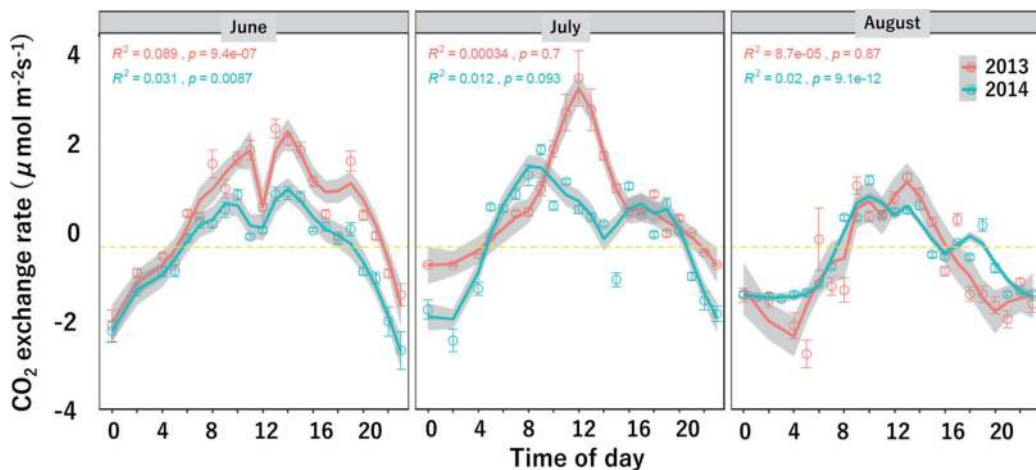

Figure 13.
Differences in diurnal curves of needle CO_2-exchange rate for different months of the growing season (June–August of 2013 and 2014) in permafrost habitats. Trends are loess regressions. Grey shadows represent confidence intervals (standard error) of the regression.
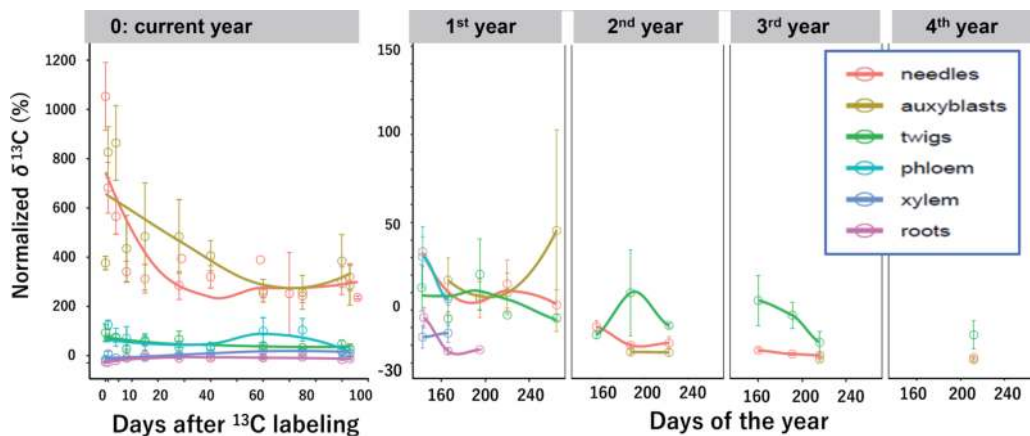
Figure 14.
Dynamics of normalized δ¹³C (mean ± SE) over 2014–2018 in various organs and tissues (short-shoot needles: brachiblasts, long-shoot needles: auxyblasts), twigs, phloem, xylem, and roots) of larch (Larix gmelinii Rupr. Rupr.) trees, which were ¹³C-labeled in June of 2014. Grey panel represents year after ¹³C-labeling: 0—a year when ¹³C pulse-labeling was conducted; 1–4—year are following the 0 year. Trends are loess regressions; 0 day at 0 year is a day when ¹³C labeling was conducted. DOY, day of the year.

were ca. 21‰, and in roots were about −14‰. Such a high build-in C amount in senesced larch needles plays an important role in the metabolism of soil microbiota, including mycorrhiza, since it is an easy-destructive substrate.

Enriched δ¹³C values have been observed in studied tissues of trees at least over 4 years after ¹³C-labeling experiments (**Figure 14**, panel 1–4). At the beginning of the following growing season on 23 May, 2015, we registered enriched δ¹³C values (from −22 to 49‰) in all larch organs and tissues. The most ¹³C-enriched organs were needles, long-shoot needles, phloem, and twigs. It pointed to the intensive usage of the last-year C reserves in the early spring (bud-break period) for growth processes that confirms our previous results [77]. In other words, carbon is being involved in the exchange processes within a tree for a long time. However, Kagawa et al. [85] showed that after 2–3 years, there was little ¹³C excess left in the needles of larch saplings. These differences from our results may be due to the age differences since Kagawa et al. [85] ¹³C-labeled saplings of larch of heights of 10–73 cm.

6.1.6 Response of larch species to environmental changes in China (Y. N. Wang)

At present, Dahurian larch (*L. gmelinii*) showed a continuous distribution in the northeast of Inner Mongolia and the northwest of Heilongjiang Province, and the distribution in the north and central part of Heilongjiang Province with forest fires [46, 47]. Since *L. gmelinii* distributed in China is located in the southern margin of the global northern forest, there is no climatic suitable area for *L. gmelinii*, and all the climatic indicators cannot reach the optimum level for growth and development.

Forest dynamics of larch in NE China is strongly regulated by forest fires [46, 57]. Stand density in the young and middle-stage (around 100 years) is relatively high (about 2,300 hm⁻²), but it sharply decreased over 100 years after the fire, and reached about 1,500 hm⁻². The aboveground was estimated to be around 115 Mg ha⁻¹. There was an altitudinal gradient of above biomass at Daxingan Mt. range (latitude 47 N to 52 N from 85 to 42 Mg hm⁻², respectively), and 32 Mg hm⁻² at Tura in Siberia (N62) [46]. Ecosystem productivity of China to Siberia decreases sharply with increasing latitude (**Figure 15b**) accompanied by an increase in shoot/root ratio [55].

Under the government of China's environmental program known as Returning Farmland To Forests (RFTF = NFCP), about 28 million hectares of farmland have been converted to tree plantations. This has led to a large accumulation of biomass carbon, but less is known about underground carbon-related processes [56]. One permanent plot (25 years of observation) and four chronosequence plot series comprising 159 plots of larch (*Larix gmelinii*) plantations in northeastern China were studied. Both methods found significant soil organic carbon (SOC) accumulation (96.4 gC m^{-2} year^{-1}) and bulk density decrease (5.7 mg cm^{-3} year^{-1}) in the surface soil layer (0–20 cm), but no consistent changes in deeper layers, indicating that larch planting under the RFTF program can increase SOC storage and improve the physical properties of surface soil. Nitrogen depletion (4.1–4.3 gm^{-2} year^{-1}), soil acidification (0.007–0.022 pH units year^{-1}), and carbon/nitrogen (C/N) ratio increase (0.16–0.46 per year) were observed in lessive soil, whereas no significant changes were found in typical dark-brown forest soil.

This SOC accumulation rate (96.4 gm^{-2} year^{-1}) can take 39% of the total carbon sink capacity [net ecosystem exchange (NEE)] of larch forests in this region and the total soil carbon sequestration could be 87 Tg carbon within 20 years of plantation by approximating all larch plantations in northeastern China (4.5 M hm^{-2}), showing the importance of soil carbon accumulation in the ecosystem carbon balance. By comparison with the rates of these processes in agricultural use, the RFTF program of reversing land use for agriculture will rehabilitate SOC, soil fertility, and bulk density slowly (69% of the depletion rate in agricultural use), so that a much longer duration is needed to rehabilitate the underground function of soil via the RFTF program. Global forest plantations on abandoned farmland or function to protecting farmland are of steady growth and our findings may be important for understanding their underground carbon processes.

However, climate change has significantly affected the geographical distribution, population pattern and community productivity of *L. gmelinii* in recent years. Prediction of potential distributions under future climates shows its geographical distribution range gradually reduced, and may even move out of the north altogether, future climate warming will have a negative impact on the distribution of *L. gmelinii* in China.

6.1.7 Japan

In northern Japan, Japanese larch (*Larix kaempferi* Carr.) has been planted widely in reforestation schemes. This larch was introduced to northern Japan from the central subalpine region of Japan in the 1870s [15, 18]. Larch species were believed to be the most promising tree species for afforestation, similar to the Sakhalin fir (*Abies sachalinensis* Masters) native to Hokkaido, because they grow
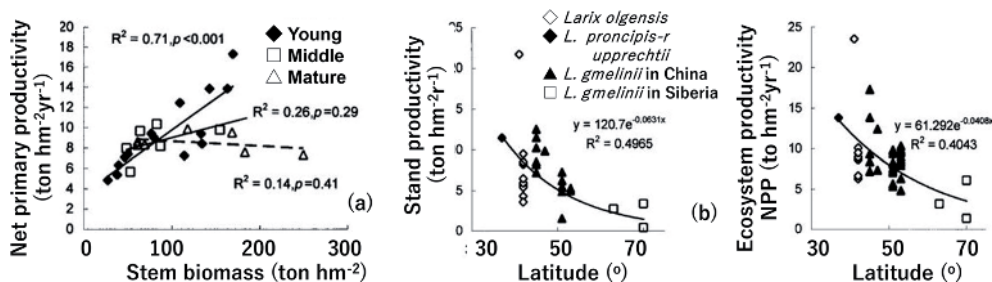

Figure 15.
Biomass of stem and net primary production (NPP) (a), latitudinal gradation and strand productivity or ecosystem productivity (b) (Modified from: Wang et al. [55], with the authors' permission).

more rapidly and are more tolerant against cold than other traditional silvicultural species in Japan [8, 13]. Consequently, larch covers widely Hokkaido Island, matching the shape of the island [13], however, there were some problems with Japanese larch on Hokkaido because Japanese larch is introduced species. It was susceptible to diseases such as root rot and shoot blight, and to grazing by redback voles [14]. Growth traits are mainly analyzed by plant biomass productivities, and improvements have been made on survival and timber quality [13, 39].

7. Environmental factors affecting larch species

Izuta [86] well summarized the current condition of the impact of environmental pollution on forest and farmland ecosystem. Since the 1960s, with the rapid economic development, air pollutants have impacted forest health and vigor in NE Asia [87]. SOx pollutants were reduced by desulfurization equipment during the 1970s; however, NOx including precures of O_3 has hardly decreased because it is mainly produced by traffics [86]. Lockdowns applied amid the Covid-19 pandemic may decrease the rate to about 7 ppm year^{-1} between 2019 and 2020 as found in O_3 emission in Europe [88]. Finally, we also discuss ECM under environmental change.

7.1 CO_2

Effects of environmental changes on larch growth under elevated atmospheric CO_2 concentration [CO_2]. Globally, [CO_2] has been increasing steadily since the Industrial Revolution. As CO_2 is a resource for photosynthesis in green plants, an increase in [CO_2] appears to be favorable for photosynthesis and the growth of trees. Although net assimilation rate and growth of trees were enhanced by elevated [CO_2], the positive effects on light-saturated photosynthetic rate (P_{sat}) do not persist over the long term [87]. Trees usually acclimatize to elevated [CO_2] conditions. The P_{sat} of plant species grown at elevated [CO_2] decreases with time to the same level as that at ambient [CO_2], which was found by Tissue and Oechel [89]. This trend was especially observed under severe conditions, for example, infertile soil, root restriction, and/or dilution of nutrients in the plant body [87]. This phenomenon is called "down-regulation" or photosynthetic adjustment [87, 89].

We should also consider the combined effects of high [CO_2] and N deposition as a promoter of tree growth [90]. Physiological effects of nitrogen deposition on CO_2 fixation are summarized as follows: Eguchi et al. [91] studied the photosynthesis of 2-year-old Japanese larch seedlings raised under ambient [CO_2] (360 µmol mol^{-1}) and high [CO_2] (720 µmol mol^{-1}), using environmental control growth cabinets (Phytotron). They found that high [CO_2] increased the light and CO_2-saturated photosynthetic rate (P_{max}) of seedlings and changed the inner structure of needles of the seedlings grown in high-nutrient soil. The internal mesophyll surface area per unit needle surface area (A^{mes}/A or S^{mes}) increased with high [CO_2], leading to a reduction in diffusion resistance of CO_2 [91]. They concluded that the increase in the photosynthetic rate at high [CO_2] was mainly due to easier transport of the CO_2 to chloroplasts in needles.

Growth response and nutrient status of 2-year-old Japanese larch seedlings raised under different [CO_2] during two growing seasons were determined by using an open-top chamber (OTC) [92]. At the end of the second growing season, high [CO_2] increased the total biomass of Japanese larch seedlings, while only root biomass increased by elevated [CO_2] was detected at the end of the first growing season. The different [CO_2] levels did not give rise to any difference in nutrient concentration in the plant body, or in mycorrhizal formation in roots of seedlings.

The greater total biomass under high $[CO_2]$ was due mainly to the increased root biomass during the first growing season, allowing better absorption of nutrients and stimulation of growth during the second growing season [92].

The xylem structure of Japanese larch seedlings under a combination of two $[CO_2]$ and nutrient regimes in phytotron for one growing season [91, 93]. Stimulation of secondary growth by high $[CO_2]$ was observed only with the high nutrient treatment. High $[CO_2]$ also increased the stem base diameter and changed some anatomical features of the tracheids, especially cell diameter. Development of more branches was observed for *L. sibirica* seedlings grown under high $[CO_2]$. However, elevated $[CO_2]$ had no effects on dry-matter production or tree height of the seedlings.

7.2 Ozone

Ozone (O_3) in the troposphere is recognized as a widespread phytotoxic air pollutant. Since even ambient levels of O_3 adversely affect growth and physiological functions, such as photosynthesis, of forest tree species, this gas is considered to be one of the most important factors involved in forest decline and reducing photosynthetic production in the USA, Europe, and Japan [10, 94]. The effects of oxidants on plants have been studied since the 1940s and have been reported that ozone generates reactive oxygen species such as O_2- and H_2O_2 in leaves, having adverse effects on fatty acids in protoplasm and proteins in leaf. Based on experimental studies, Japanese larch is relatively sensitive to O_3 exposure compared with other tree species in Japan [95]. In general, sensitivity to O_3 of plants is greatly affected by growth conditions, such as temperature, light intensity, and soil moisture and nutrient status.

Watanabe et al. [96] reported that the sensitivity to O_3 of Japanese larch seedlings grown in soil supplied with N at 50 kg N hm^{-2} $year^{-1}$ was less than at 0 and 20 kg N hm^{-2} $year^{-1}$. Nitrogen-induced changes in sensitivity to O_3 must therefore be considered in risk assessment of O_3 toward Japanese larch. Since $[O_3]$ in Hokkaido is currently low, the negative effect of O_3 on larch species in this area may not be serious at present. However, relatively high $[O_3]$, sufficient to induce a reduction in the growth of larch species, is estimated in other parts of Japan [95]. Furthermore, $[O_3]$ has been increasing in Japan over the last two decades [10]. This trend will continue with an increase in precursors of O_3, such as nitrogen oxides and volatile organic compounds, especially in the East Asian region [10].

It is predicted that photosynthetic production in terrestrial plants of the northern hemisphere will be reduced by more than 20–30% due to O_3 in the near future [94]. The effect of high $[O_3]$ on larch species should therefore be considered because larch is dominant species in northern hemisphere.

According to the recent NO_2 trend in Asia [97], we should pay attention to the rapid increase in NO_2 emission and also the Biological volatile organic compound (BVOC) of larch as a precursor of O_3 [98].

Based on the statistics of EU (LRTAP: Long-range Transboundary Air Pollution) and US (EPA: Environmental Protection Agency), the NO_2 emission from Asia reached about 43 Tg NO_2 $year^{-1}$ which is four times larger than that from EU or UAS (**Figure 16**). Therefore, we should know this evidence and try to give O_3 tolerance to larch plantation as suggested by Watanabe et al. [96].

The biomass of Japanese larch decreased at 80 ppb, but it was lower at low O_3 (<5 ppb) compared to 25 ppb [100]. This phenomenon is regarded as hormesis [101]. As almost all practical production of larch seedlings is done in the suburbs, we tried to use ethylenediurea (EDU) to moderate the adverse effects of elevated O_3 on larch seedlings [102]. An effective concentration of EDU is 400 mg EDU
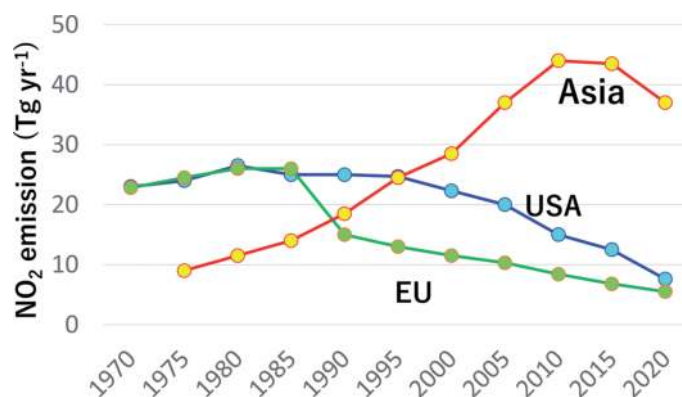
Figure 16.
Yearly trend of NO₂ emission of three regions. Data are cited from Akimoto [99] and Kurokawa and Ohara [97]. 1990~: EU-LRTAP convention; USA-EPA Air Pollutant Emission and NIES (adopted from Qu et al. [5]).

L^{-1} applied as soil drench it protects both Japanese and F_1 plants against toxicities induced by exposure to elevated O_3 for up to 3–4 years. Methods using container grown seedlings in forestry practices are including mushroom production.

7.3 N deposition

Nitrogen is often a limiting resource for plant growth in the forest ecosystem [82], and N fertilization frequently results in increased photosynthesis and enhanced growth of trees. Excessive amounts of N can nevertheless have a negative effect on the physiology and growth of the forest ecosystem. Forest declining due to high N load is suggested to have occurred in some coniferous forests, as recognized by the N saturation story [103]. N deposition has been increasing dramatically, especially in East Asia [11]. The main sources of atmospheric N deposition are anthropogenic emissions due mainly to fossil-fuel burning, and food production, relating mainly to agricultural waste and overuse of N-fertilizer. In Hokkaido, the annual deposition of N ($NH_4 + NO_3$) has increased to about 1.2 kg N hm^{-2} $year^{-1}$ (as of 2012 [104]). Unfortunately, this increment will continue in the near future.

However, negative effects of N loading have not been observed yet. For example, N loading N load did not significantly affect the growth and net photosynthetic rate of Japanese larch seedlings grown in the soil of Andisol [96]. Furthermore, no growth and photosynthetic stimulation of Japanese larch and hybrid larch F_1, grown in a mixture of clay loam, peat moss, and vermiculite with balanced fertilizer containing N and other nutrients such as P and K [4]. In contrast, growth and photosynthesis of Japanese larch seedlings grown in a mixture of clay loam and well-weathered pumice (nick name Kanuma), were stimulated by balanced fertilizer [92, 93]. Although the experimental periods differed among these studies, the soil type used in the experiment may be one of the important factors that induce the difference in the response of larch to N load (or fertilization).

Enzymes in N metabolism are affected by irradiance conditions [105], so that growth and photosynthetic responses of larch to N load are also regulated by light levels. Qu [4] examined the effects of different light intensities (8, 16, 32, and 100% of open condition) and two fertilization regimes (high/low) on seedlings of Japanese larch and F_1 raised in a mixture of clay loam, peat moss, and vermiculite (the fertilizer was composed of balanced nutrients, like Hyponex: N:P:K = 6:10:5 and micro-elements). When light intensity exceeded 16%, dry-matter growth of Japanese larch was greater than that of F_1, independent of fertilization regimes.

However, the growth of Japanese larch in high-nutrient conditions was dramatically suppressed at 8% light intensity. This result indicates that high N load will make Japanese larch susceptible to shading, which was also found in nursery condition [106]. Ryu et al. [15] examined the effects of high N load on growth and ectomycorrhiza infection of Japanese larch, Dahurian larch, and their hybrid F_1 seedlings growing in serpentine soil at low light intensity (8% against open) assuming forest floor conditions. It is well known that ECM symbiosis is important for the growth of host plants by assisting in the uptake of water and essential nutrients and by excluding heavy metals [34, 107]. No significant effects of N load on growth and infection by ECM were found. Inadequate light intensity and shortage of essential materials are suggested as possible factors for this phenomenon.

Several researchers indicated a fertilization effect of N load on other tree species such as Sugi-cedar (*Cryptomeria japonica*), Siebold's beech (*Fagus crenata*), and deciduous oak (*Quercus serrata*), however, N load did not necessarily stimulate the growth of larch species [4, 15, 108]. On the other hand, N load to the level of 50 kg N hm^{-2} year^{-1} will not negatively affect the growth of larch species. We may have to avoid shading seedlings when we introduce multistoried forest and/or natural regeneration to Japanese larch forest under high N load [4, 106], because of N-load induced reduction in shade tolerance. Although N is an essential nutrient for plant growth, information on its combined effects with other environmental factors on larch species in northern Japan is very limited [15] and further investigation is needed.

7.4 Soil acidification

In northeast Asia, pine and larch forests have declined in the vicinity of industrial or urban regions. Important factors causing this decline are the decrease in available nutrition and the increased metallic toxicity induced by soil acidification [86, 109]. Likely factors limiting the growth of plants in acid soil are the high acidity itself, phytotoxic metals such as aluminum (Al) or manganese (Mn), and reduced availability of important elements for plant growth [86]. However, infection with ECM fungi improves tolerance to environmental stresses by reducing the toxicity of metals [110]. The ECM role in growth responses of larch species under acid soil is therefore important in clarifying the effect of soil acidification on larches. The growth response of Japanese larch seedlings infected with several ectomycorrhizal fungi and raised under different soil acidification levels (proton concentrations of 10, 30, 60, and 90 mmol H$^+$ kg^{-1}) [109]. They quantified the ECM symbiosis that leads to improvement of the rhizosphere of larch seedlings. The results suggested that water-soluble phytotoxic elements (such as Al^{3+} and Mn^{2+}) and essential elements (such as Ca^{2+}, Mg^{2+}, and K$^+$) in soil increased with increasing soil acidification.

Concentrations of Al in the root and Mn in needles also increased. It is well known that Al^{3+} reduces the growth of roots, and Mn^{2+} replaces Mg^{2+} bound to the carboxylation enzyme (Rubisco; ribulose-1,5-bisphosphate carboxylase/oxygenase) and reduces photosynthetic activity [27]. Photosynthesis and the total dry mass of larch seedlings infected with ECM fungi were higher than in controls in all soil treatments. Also, the total dry mass of ECM seedlings was less at an acid level of 90 mmol H$^+$ kg^{-1} than in unacidified ECM control seedlings; the ratio was about the same as without ECM infection.

As shown in Choi [109], severe soil acidification reduces the growth and photosynthesis of Japanese larch. At a lower level of acidification, ectomycorrhiza will help the larch to maintain growth, but will not help at severe acidification level. Based on the growth response to the concentration ratio of base cation (Ca^{2+}, Mg^{2+},

K$^+$) to Al^{3+} (i.e., BC/Al ratio; BC/(Al + Mn) ratio) in the soil solution or water extract of soil, the sensitivity of Japanese larch to soil acidification is similar to that of Sugi-cedar, Red-pine and Sieblod's beech [86, 109]. Soil acidification is important in the long term as, if the deposition rate of acid exceeds the rate of recovery of buffering capacity by weathering, the acid neutralization capacity of soil will be reduced in the future and soil pH will decrease. Considering that the lifespan of the tree is long, a serious reduction of growth of larch species due to soil acidification could occur in the future.

7.5 Role of ECM

Since the 1950s, with the rapid economic development, air pollutants (NOx, SOx, Ozone: O_3) and increasing CO_2 have impacted forest health and vigor. The photosynthetic rate is usually reduced by elevated CO_2 under root restricting conditions. SOx pollutants were reduced by desulfurization equipment during the 1970s; however, NOx has hardly changed because it is mainly produced by diesel cars [86]. NO_2 is converted by O_3 and NO via UV radiation [111]. In addition, atmospheric CO_2 concentration [CO_2] has increased since the Industrial Revolution and has reached around 418 ppm at the current rate of 2.2 ppm year^{-1}. However, lockdowns applied amid the Covid-19 pandemic decreased the rate to about 7 ppm year^{-1} between 2019 and 2020.

Except for O_3 (troposphere or ground-level O_3), sufficient CO_2 and adequate N are regarded as the productive atmospheric environment for forest trees. We summarize the effects of changing environment (CO_2, N deposition, and O_3) on the growth of larch and larch-ECM interactions.

7.5.1 Responses to elevated CO_2

In many cases, we found down-regulation of photosynthesis under elevated CO_2, even in a FACE (Free Air CO_2 Environment [87]) system. We expected ECM to act as a carbon sink and moderate down-regulation in photosynthesis, although for red pine seedlings inoculated with a kind of ECM (*Pisolithus arhizus*) down-regulation was not observed [109].

The same trend was expected in larch. Hybrid larch F$_1$ was planted in the FACE for 3 years and tended to fall down because of increased above-ground biomass [110]. After 5 years of CO_2 fumigation in FACE, Japanese larch decreased biomass allocation to branches and increased it by about 20% in the stem compared with ambient CO_2. In contrast, birch (*Betula platyphylla* var. *japonica*) and kalopanax (*Kalopanax septemlobus*) allocate about 10% less biomass to their stems. Almost no anatomical structure changed with elevated CO_2 [112].

7.5.2 Responses to elevated O_3

Ozone levels have been increasing around the northern hemisphere in the past several decades [94]. With the GIS method, Watanabe et al. [113] predicted that the growth of Japanese larch (*Larix kaempferi*) would be reduced by elevated O_3 around the Kanto plain, and in contrast, the decline will not be as significant in northern Japan. Ozone concentration is generally high in the suburbs due to the oxidation of NO_2 (exhaust gas: NO from diesel cars plus UV) [111]. This cycling of NOx under UV can lead to the generation of O_3 (NO + $O_3 \rightleftharpoons NO_2$ + UV-radiation) in suburban green areas around big cities. Based on screening using OTCs (open top chambers), Yamaguchi et al. [95] summarized the O_3 sensitivity of potted 18 tree seedlings in Japan, and among them, the Japanese larch showed a moderate sensitivity. What about the hybrid larch F$_1$ under elevated O_3?

The specific difference in O_3 sensitivity was examined between Japanese and hybrid larch F_1 seedlings planted on the ground of OTCs (<5, 25, 45, and 80 ppb). The growth of both larches was significantly suppressed by 80 ppb (**Figure 17**; [14, 114]). The biomass of F_1 seedlings decreased under 25 ppb, compared to <5 ppb, but this was due to its heterosis and maintained a similar biomass with Japanese larch seedlings in elevated O_3 treatments.

7.5.3 Elevated CO_2 and O_3

Plants usually close their stomata under elevated CO_2 to reduce the absorption of O_3. We examined the effects of elevated O_3 (80 ppb) on the growth and ECM infection and diversity of hybrid larch F_1 seedings under elevated CO_2 in OTCs [37]. Under elevated O_3, ECM infection rate and species diversity were reduced; however, these trends were moderated by elevated CO_2 (600 ppm). Only early successional types of ECMs were found at ambient and elevated CO_2. However, larch specialist *Suillus* sp. was dominant under elevated O_3 (**Figure 18**).

This evidence suggests that a kind of ECM, *Suillus* sp. may support the growth of the host plant, larch hybrid F_1. As Qu et al. [32] suggested the photosynthetic rate in larch species infected with multiple ECM species was higher compared to when infected with a single ECM species. This phenomenon is recognized as follows: most ECM activity depends on soil pH; some ECMs prefer low pH but some require neutral or high pH (6 ~ 8), such as *Rhizopogon rubescens* [115]. Aluminum (Al) is released below pH < 4.5 and inhibits root growth. These are species-specific traits, and this may be the reason why multiple ECM infections may benefit the host plants more significantly.

7.5.4 Nitrogen deposition and elevated O_3

The combined effects of N and elevated O_3 were studied in seedlings of two broadly distributed species: Siebold's beech and larch, with the use of OTCs. The beech is classified as highly sensitive to O_3 [95]. With increasing N (NH_4NO_3), O_3 sensitivity of the beech increased in terms of Accumulated Exposure Over Threshold (AOT) of 40 ppb O_3 (AOT40). In contrast, O_3 sensitivity of Japanese larch decreased with increasing N up to 50 kg N hm^{-2} $year^{-1}$. However, hybrid larch F_1 had slightly increased O_3 sensitivity with 50 kg N hm^{-2} $year^{-1}$ under free-air O_3 exposure [116], which may be due to decreased leaf life-span with N application [100].

In general, phosphorous (P) is the second most important nutrient after N; for the growth of hybrid larch F_1, an adequate supply of P and N is required. Mg was
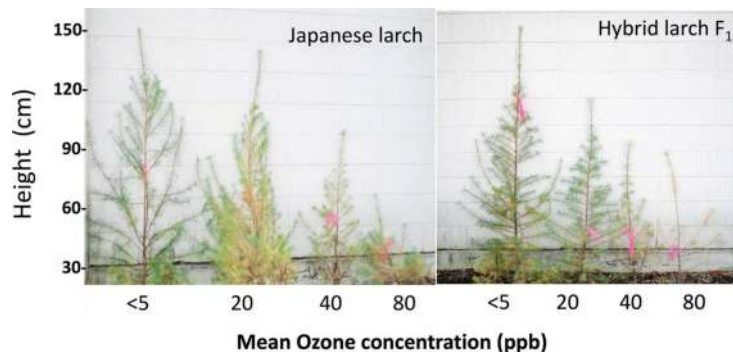

Figure 17.
Ozone concentrations and height in Japanese larch and its hybrid larch F_1 (Adopted from: Kita et al. [14], with authors' permission).
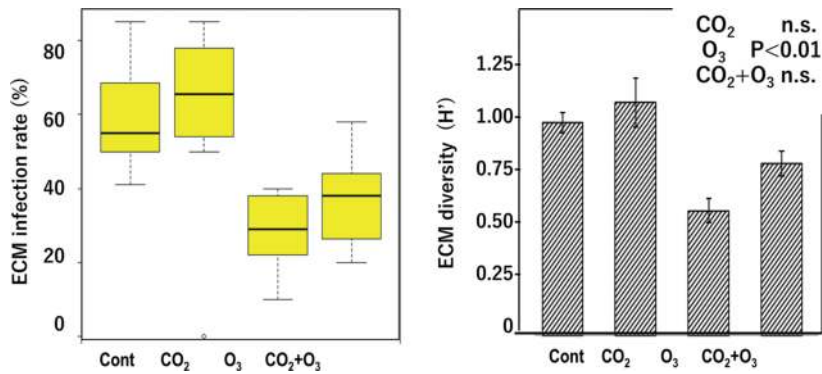
Figure 18.
Infection rate and diversity of ECM of hybrid larch treated with combination of elevated CO_2 (600 ppm) and O_3 (80ppb) (Adopted from: Wang et al. [37]).

the limiting element in the nursery of Hokkaido University [117]. In this edaphic condition, we examined the effects of N deposition (NH_4NO_3) on the growth of hybrid larch F_1 for 8 years. Surprisingly, as a result, except for N application to F_1 by the second year, almost no difference in the growth of F_1 was found between the N treatment and the control (=no N application). Based on DNA analysis of the ITS region in symbiotic ECM, most of them infecting Japanese, Dahurian, and hybrid larch F_1 were nitrogenous species [38], and were not altered by N application.

7.5.5 ECM-larch: Conclusion

We expect a new CO_2 sink when planting a new plantation in northern Japan. In Far East Russia and central Siberia [4, 5], they recognize the real essential role of the larch ecosystem on permafrost area, and they try to increase their timber quality to use genetically ideal larch and conserve permafrost ecosystem. Japanese larch is intensively used after considerable improvements in timber utilization. After harvest, we should make plantations with container-grown seedlings to save labor and attain high plantation efficiency. If we make new plantations with hybrid larch F_1, we should ensure larch plantations do not increase N deposition under elevated O_3. To make planting stock of F_1, we should inoculate larch seedlings with ECMs (*Suillus* sp.) for increased tolerance against environmental stress.

8. Conclusion

In conclusion of this chapter, it can be said that urgent considerations should be made to moderate elevated ground-level O_3 including dynamics of NO_2 as precures of O_3 against green infrastructure around big cities [5, 102], as larch forests is a vital component of global as well as local resources.

In this chapter, emphasis was made on the essential role of the larch ecosystem for environment conservation via highly forest management techniques. For this objective, we should point out detailed aspects of the larch forest ecosystem, specially developed on permafrost in Far East Russia and NE China. Recently, TV programs suggest the fear of melting of permafrost under changing environment in Alaska even though biological importance has been revealed back in the 1990s [23]. With the melting permafrost layer, many kinds of greenhouse gasses (CO_2, CH_4, N_2O, NO_2 as precures of O_3, etc.) may be released and destroy our environment. Further knowledge on the ecophysiology of larch is still needed [50, 118–120],

phylogeny [121], as the wise use of larch ecosystems will contribute to nature conservation and the sustainable use of the world's natural resources.

Acknowledgements

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