Ecophysiological study of the growth responses of larch species to changing environments

-Effects of elevated CO_2, O_3 and high nitrogen loading-

Summary

Larches are considered to be promising species for afforestation and woody resources because of the high specific gravity of their stem. They are common components of forest in the northern hemisphere, ranging from China to Japan, Siberian, and North America, and are recognized to be a major carbon sink. The Japanese larch (*Larix kaempferi*, Japanese) is a key afforestation species, but it is highly susceptible to biotic and abiotic stresses in Hokkaido. To overcome these problems, the hybrid larch F_1 (i.e. *L. gmelinii* var. *japonica* × *L. kaempferi*, in short F_1) was recently developed by crossing female Dahurian larch (*L. gmelinii* var. *japonica*, Dahurian) with pollen of the Japanese larch.

Our environment has been changing drastically since the last century due to human activity, in particular with increasing atmospheric carbon dioxide (CO_2), ozone (O_3) and nitrogen (N) deposition. CO_2 is an essential substrate for plant photosynthesis, and is also a significant greenhouse gas. Re-vegetation is needed to increase the carbon sink and moderate atmospheric CO_2, as well as for the production of sustainable resources. In our changing environment, what eco-physiological responses will be induced?

Below, the growth of F_1 is examined in response to various environmental changes: elevated CO_2, and then high N and P loading, which are also environmentally relevant. The effect of O_3 on larch growth was also examined with elevated CO_2. Three species of larch were planted, Dahurian, Japanese and F_1 (a hybrid), in brown forest soil in the Sapporo Experimental Forest of Hokkaido University. A Free-Air CO_2 Enrichment (FACE) system and Open Top Chambers (OTC) were used in the O_3 and high CO_2 studies, and N fertilizer was deposited in both brown forest soil and immature volcanic ash soil. The aim was to obtain better information for maintaining sustainable forests containing larch species, especially F_1.

Many reports find that elevated CO_2 stimulates photosynthesis and delays foliar senescence in the autumn, resulting in above-ground and below-ground growth. Photosynthetic down-regulation has also been reported in plants under elevated CO_2 (500 ppm), based on the *A* (assimilation) /*Ci* (intercellular CO_2 concentration) curve. In the present experiment, growth enhancement of larches in a FACE was found in the first year, but was not clearly observed in further years. What is the reason for this down-regulation in terms of nutrient status in the plant body and soil nutrient conditions? A possible explanation is root restriction under poor nutrient conditions, since clear down-regulation was observed in the hybrid larch after 2-year-CO_2 fumigation in our FACE, with a reduction in A_{max} (CO_2 and light saturation) and in V_{cmax} (i.e.

maximum capacity at light saturation in Rubisco: ribulose-1,5-bisphosphate carboxylase/ oxygenase) and J_{max} (maximum rate of electron transport).

Tropospheric ozone (O_3) is a phytotoxic air pollutant of major concern in causing forest decline, and its concentration has been increasing continuously. O_3 induces stomatal sluggish and progress in leaf senescence. Stomatal conductance is reduced at elevated CO_2, an effect which may hopefully reduce the uptake of O_3 and mitigate its harmful effects on larches. To test this hypothesis, seedlings of 3 larch species were cultivated under charcoal filtered ambient CO_2 (385 ppm), 60 ppb O_3, high CO_2 (600 ppm) and their combination. There was a significant reduction in growth as measured by diameter and needle mass of F_1 under O_3. A small reduction in these parameters was found in the hybrid larch F_1 under O_3 with high CO_2. The parent larches showed no consistent tendencies against O_3 and CO_2. Except for the Dahurian larch, a positive correlation was found between mass-based needle N (N_{mass}) and A_{max}.

Although N is an essential element for plant growth and is usually a limiting macro-element for tree growth, increased N deposition in forest ecosystems usually leads to enhanced primary growth. However, excessive N deposition induces nutrient imbalance and decline of trees and forests. N saturation has recently occurred in parts of Asia, Europe and North America, with deposition exceeding 50 kgN $ha^{-1}yr^{-1}$ and even reaching 100 kg N $ha^{-1}yr^{-1}$. We continued N application to simulate acid rain (NH_4NO_3) on the young F_1 plantation for 5 years. Except in the first year of N application, no marked increase was found in A_{sat} (light saturated assimilation rate at ambient CO_2), which may be due to denitrification and nutrient imbalance. A_{sat} increased with N for the first year, and the diameter increased slightly with increasing needle mass. After 3 years of N loading, the sun and shade crown was differentiated. N allocation differential in needles was induced, not by N application, but by crown positioning, i.e. light conditions. N is allocated mainly to Rubisco in the sun crown, whereas in the shade crown N is allocated more to electron transport, but not to the light harvesting chlorophyll protein; this may be related to light demanding traits in larch. What of the nutrient imbalance of brown forest soil with high N loading, besides P deficiency?

Most soils in Hokkaido include volcanic ash, which usually give rise to phosphorus (P) deficiency. P is an essential macro-nutrient for all plant functions, including photosynthesis. Specimens of F_1 were planted in 7 L pots filled with brown forest soil and were supplied with 0, 20, 50 , 100 kg N $ha^{-1}year^{-1}$ with/without P application (50 kg $ha^{-1}year^{-1}$). To ensure application of these nutrients, a matched tray was placed beneath each pot. The value of A_{sat} was positively correlated with concentrations of N, potassium and especially magnesium, but showed no correlation with P. This may be due to adequate P in the plant body; it is also possible that there was below-ground enhancement only. The pattern of biomass allocation was not influenced by N and P treatment. Plants usually have high plasticity in allocating biomass to obtain resources for survival and growth that are in short supply.

To determine the pattern of root growth of F_1, 3-year-old planting stocks of F_1 were planted in 15 L pots filled with Kanuma pumice and Akadama soil, to simulate immature volcanic ash soil. Nitrogen was supplied at 0, 50 and 100 kgN $ha^{-1}yr^{-1}$ together with 0 and 50 kg P $ha^{-1}yr^{-1}$ for two growing seasons. A novel method of detecting vertical root growth was used, and an in-growth method for detecting horizontal root growth. Vertical root growth was promoted in nutrient-poor conditions and was followed by horizontal growth. The root surface area was markedly increased by N only with P. Ectomycorrhiza infection was also found in roots of F_1 in nutrient-poor conditions.

The growth of these three larch species was found to be regulated by the most scarce resource, according to the soil conditions. If we plant F_1 on adequate site, it is a promising species in our changing environment.