Chapter 23
Effects of Elevated CO_2 on Ecophysiological Responses of Larch Species Native to Northeast Eurasia

T. Koike, K. Yazaki, N. Eguchi, S. Kitaoka, and R. Funada

23.1 Introduction

Larch species are broadly distributed in the northern hemisphere, and dominate the landscape especially in the northeastern part of the Eurasian continent where permafrost is well developed (Abaimov et al. 1998, 2000; Kajimoto et al. 2003, 2006). Four species of larch, *Larix sibirica*, *L. gmelinii*, *L. cajanderi*, and *L. kaempferi*, predominate in the eastern Eurasia (Koike et al. 2000a; see Chap. 3). Taxonomy of *Larix* is still somewhat unsettled in the eastern half of Siberia, and particularly in the Far East of the Russian Federation. Although *Larix* in the latter region was not generally classified as *L. gmelinii* in Russia (Abaimov et al. 1998), the larches native to Sakhalin and Kuril Islands have customarily been referred to as *L. gmelinii* by some workers (Kurahashi 1988; Uemura et al. 1994; LePage and Basinger 1995; see also Chap. 3). Therefore, we describe the *Larix* species from Sakhalin and Kuril Islands, and that transplanted in Hokkaido, northern Japan, as *L. gmelinii* hereafter in this chapter.

With the increasing use of forests in this region, growth and regeneration patterns of larch seedlings may become strongly dependent on environmental changes. Moreover, atmospheric CO_2 concentration (hereafter abbreviated as $[CO_2]$) is increasing yearly due to the intensive use of tropical forests and of fossil fuel (IPCC 2007). After COP3 (Kyoto Protocol) (IGBP 1998), it is hoped that biomass productivity of larch forests and other forested ecosystems function as large carbon sink. In this sense, larch species are key plants for moderating $[CO_2]$ based on their photosynthetic productivity.

For prediction of traits in future growth under the increasing $[CO_2]$, it should be noted that values of light saturated photosynthetic rate under a given $[CO_2]$ are similar in larch and birch; but not in Scots pine that photosynthesizes more or less independently of the treated $[CO_2]$ (Koike et al. 2000b). The results show that there may be photosynthetic adjustment for high $[CO_2]$ values in the deciduous trees, but not in the evergreen species. According to these studies, we should evaluate changes in future growth in larch, the dominant species, for predicting potential of atmospheric CO_2 fixation and its possible changes under the warmer climate and increasing $[CO_2]$.

Stomatal conductance (gs) of plants decreases with increasing $[CO_2]$; however, responses of gs to drastic increase in the CO_2 level vary greatly among species

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(Koike 1993; Yazaki et al. 2005). This may be induced by the decrease in the size of vessels or tracheids in xylem at high CO_2 concentration through decrease in water flow (Tyree and Zimmermann 2002; Koike 2003; Watanabe et al. 2008). Therefore, we expect changes in xylem structure in the larch species that grew under the elevated CO_2 level. If xylem structure should change with higher CO_2, a question arises if there is any change in specific gravity of xylem. To evaluate the effect of difference in WUE (water-use efficiency; see Larcher 2003), traits in nitrogen use, and xylem formation under the environment of elevated CO_2 concentration, seedlings of three larch species were raised under different CO_2 and nutrient levels. The species tested were two of the dominant species in Siberia (*Larix gmelinii* and *L. sibirica*) and a species in the maritime region of East Asia (*L. kaempferi*).

23.2 Growth Characteristics of Larch Species

Most larch species in Siberia or eastern Eurasia grow well on fertile soils (Schmidt 1992; Ota et al. 1993; Schulze et al. 1995; Koike and Tabuchi 1994; Abaimov et al. 2000; Koike et al. 2000a, 2000b; Shi et al. 2000). Larch is a typical light demanding conifer, and is characterized by high growth rates, especially in *L. kaempferi* (= *L. leptolepis*; Japanese larch), which originated in central Japan. The growth rate of *L. kaempferi* is the highest among the larch species in the world at midlatitude (Matyssek 1986). It is usually used as a breeding material for the development of high growth species (Matyssek and Schulze 1987, 1988). This species has been widely planted in Korea, northern Japan, and in Europe, and has been used as a breeding material (Koike et al. 2000a).

Larix gmelinii dominates in the forests of Central Siberia in mostly the region between the Yenisei and Lena Rivers (Korotkii et al. 2002). Its distribution also extends into northeastern China (Shi et al. 2000; see Chap. 19). These regions have cold and dry climates, and are characterized by the distribution of mostly continuous permafrost (Schmidt 1992; Abaimov et al. 1998, 2000; Koike et al. 2000b). This species also has been planted through northeastern parts of Eurasian continent, especially in northeast China. *Larix sibirica* is mainly found in areas west of the Yenisei River in Western Siberia, and in regions west of the Lake Baikal, where there is seasonal and discontinuous permafrost (details see Chaps. 1 and 3). In addition, the growth rate of *L. gmelinii* is slower than that of *L. sibirica* (Abaimov et al. 1998, 2000), though its early growth may show an opposite relationship (Martinsson, personal communication).

23.3 Photosynthetic Adjustment at Elevated [CO_2]

Evaluation of the traits in gas exchange was carried out as follows: 1- and 2-year-old seedlings of the three larch species were raised under the conditions of ambient [CO_2] (360 ppm) and elevated [CO_2] (720 ppm) with high (100 mg l^{-1} week^{-1}) and low nutrient (100 mg l^{-1} mo^{-1}) levels (Koike et al. 2000b). Seeds of *L. gmelinii* and *L. sibirica* were collected from a botanical garden in the city of Yakutsk, Northeastern Siberia, and those of *L. kaempferi* were from Uryu Experimental Forest of Hokkaido University at Nayoro, Japan. All treatments were carried out in the phytotron at Forestry and Forest Products Research Institute of Japan. Photosynthesis and transpiration rates of six seedlings of each treatment were simultaneously determined to evaluate WUE with an A/Ci (assimilation rate and intercellular CO_2 concentration) relationship with a portable gas exchange system (LI-6400, NE, USA). Needle area (projected area) was measured with an image analyzer (EPSON, Tokyo, Japan). After the gas exchange measurement, nitrogen content of the needles was determined with a N/C analyzer (NC-900, Shimadzu, Kyoto, Japan) (Koike et al. 2000a).

The light saturated photosynthetic rate (Psat) of all seedlings at high [CO_2] was usually lower than that at ambient [CO_2]. Even though Psat at [CO_2] under which the seedlings had grown was higher at the elevated [CO_2] than that at the ambient [CO_2], the photosynthetic acclimation was found in the needles to the [CO_2] at which seedlings had been grown (Yazaki et al. 2001). A small increase in Psat of the whole crown at elevated [CO_2] was observed. It was considered due to the smaller specific needle area and structural and anatomical change of the needles (Eguchi et al. 2004).

High Psat was only observed at the beginning of [CO_2] treatment as was shown by Coleman et al. (1993) and Lei and Koike (2005). Moreover, Psat measured at the high level of [CO_2] under which the seedlings were grown was almost the same as the value of those grown under the ambient [CO_2] treatment (Fig. 23.1). This photosynthetic adjustment was first recognized for grass species in Alaskan tussock tundra by Tissue and Oechel (1987) and is widely found in several plant species when grown without any special nutrient treatment, i.e., photosynthetic "down regulation" (Koike 1993, 2006; Koike et al. 2000a, 2000b). Therefore, we cannot

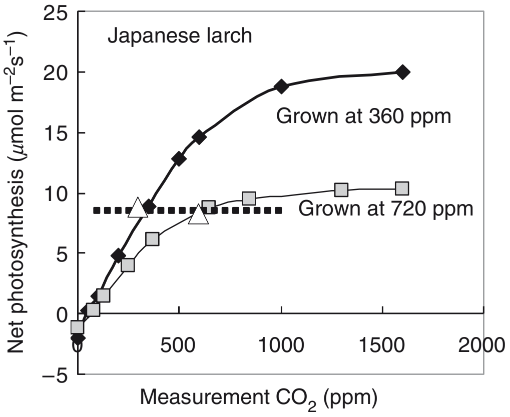

Fig. 23.1 Photosynthetic rate of Japanese larch (*Larix kaempferi*) grown at 360 or 720 ppm as a function of measured CO_2 concentration (Koike, unpublished data)

expect the high CO_2 fixation capacity of larch seedlings at moderate [CO_2] because there are several limitations of root expansion, enzyme level acclimation, extra-accumulation of photosynthates, etc. (Koike 1993; McConnaughay et al. 1993).

23.4 Nitrogen and Water Use Efficiency

At high [CO_2], three larch species (*Larix gmelinii, L. kaempferi, L. sibirica*) showed an increase in nitrogen use efficiency (NUE; net photosynthetic rate at light saturation per unit nitrogen, Larcher 2003). Because of high growth rate, nitrogen concentration of needles is diluted under the elevated [CO_2] (Coleman et al. 1993; Koike 1993). Among the three larch species, no difference in NUE was found (Fig. 23.2a). However, larch species native to Siberia had relatively high NUE. Therefore, photosynthetic rate of the larch in Central and Western Siberia may increase according to the increasing nitrogen deposition as noted by Valentini et al. (2000).

At present, there is low amount of precipitation (ca. 300–500 mm year^{-1}) in Central Siberia (Abaimov et al. 2000; see also Chaps. 1 and 10). With the changes in global climate, the patterns of precipitation are likely to change mainly at higher latitudes, and the direction of change is likely to be substantial reduction (see Chap. 22). How do the larch species respond to future environment of altered precipitation? Based on the analysis of A/Ci curve (Sharkey 1985; Koike et al. 1996), the stomatal limitation (Ls) of seedlings at 720 ppm was larger than that at 360 ppm. The highest Ls was found in *L. gmelinii* and the lowest was found in *L. kaempferi*. The Ls of *L. sibirica* was intermediate between them (Fig. 23.2b). This means that two larch species native to Siberia will be more resistant to desiccation in a future world of enriched [CO_2] through improved water use efficiency (WUE).

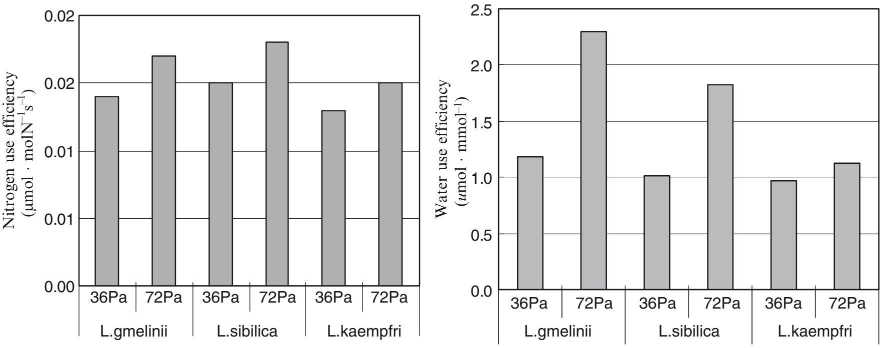

Fig. 23.2 Nitrogen (*left*; (**a**)) and water use efficiency (*right*; (**b**)) in three larch species raised at ambient and elevated CO_2 (after Koike et al. 2000a)

23.5 Xylem Formation

WUE of Siberian tree species increases under the environment of high [CO_2] (Koike et al. 1996). This means that water transport in xylem may decrease at high [CO_2], indicating possible decrease in vessel diameter (Koike 2006; Eguchi et al. 2008). In fact, tracheid size in conifer species decreased at high [CO_2] according to measurements in *L. kaempferi* and *L. sibirica* (Yazaki et al. 2001). Theoretical analysis in conifers also suggests occurrence of the same phenomenon (Roderick and Berry 2001).

Although enhanced [CO_2] may affect physiological and anatomical traits in *L. kaempferi*, tracheids and relative area of the cell-wall did not change in response to the elevated [CO_2] (Yazaki et al. 2004). Namely, there were no obvious differences in the thickness of the cell-wall or the relative area of the cell-wall between the seedlings grown at higher and ambient [CO_2]. Although the cell diameter after growth at the elevated [CO_2] was slightly larger than that after growth at ambient [CO_2], these increases had a minor effect on the relative area of the cell-wall. Therefore, the capacity for carbon fixation through cell-wall synthesis in tree stems may not be increased significantly in *L. kaempferi* that was exposed to elevated [CO_2]. In contrast, elevated [CO_2] affected stem shape by differentially altering shoot elongation and thickening. As the *L. kaempferi* seedlings acclimated to the [CO_2] under growth, increase in the amount of photosynthates gained was smaller than that in Psat in response to high [CO_2] of 720 ppm.

In *L. sibirica*, elevated [CO_2] enhanced stem diameter growth more than height growth, indicating that elevated [CO_2] affects the apical meristem and cambium differently or has different effects on cell division and cell expansion, or both. Changes in tracheid cell morphology in *L. sibirica* seemed to depend on changes in elongation rate of the shoots (Kinsman et al. (1996); Yazaki et al. 2001). Taylor et al. (1994) showed increase in the rate of leaf cell-expansion at elevated [CO_2] in a hybrid poplar. Thus, elevated [CO_2] may affect plant development not only by altering photosynthetic activity, but also by altering apical cell development.

Elevated [CO_2] had no significant effect on either stem height or diameter growth in *L. sibirica* seedlings (Yazaki et al. 2001). However, stem and diameter growth were enhanced by a high nutrient supply, which were also likely to be accelerated by high [CO_2] in the stands of *L. gmelinii* or *L. kaempferi*. (Yazaki et al. 2005). Enhanced [CO_2] increased width of the annual xylem ring and the number of cells in a radial file spanning the ring and tracheid lumen diameter, while it reduced cell-wall thickness (Fig. 23.3).

23.6 Rehabilitation with Larch Species

In the regions of Central and Northeastern Siberia, forest fires occur frequently during the growing season (Abaimov et al. 2000; see also Chap. 4). After a fire, natural regeneration is usually successful in most areas, but it depends on soil moisture

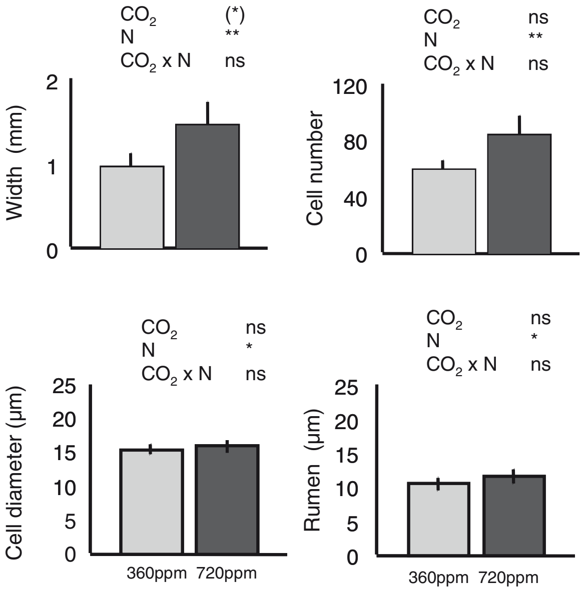

Fig. 23.3 Growth layer width, xylem cell number, cell diameter, and lumen diameter in *L. sibirica* grown at 360 or 720 ppm (after Yazaki et al. 2001)

condition and presence of abundant seed source (Shi et al. 2000; Yazaki et al. 2004) (Fig. 23.4). Based on phytotron studies (Koike et al. 2000b; Yazaki et al. 2005), capacity of CO_2 fixation in larch seedlings may be accelerated during the initial stage of natural regeneration when nutrient is still abundant (Abaimov et al. 2000; Korotkii et al. 2002; Qu et al. 2004).

As regeneration progresses, tree growth may decrease gradually due to competition among roots and shortage of nutrients, especially in the permafrost region (see Chap. 16). Photosynthetic capacity is also strongly regulated by nutrient conditions (Koike et al. 2000a, b; Yazaki et al. 2001). Therefore, the rate of CO_2 fixation in regenerated seedlings may decrease gradually even though [CO_2] may be increasing.

Larch seedlings need a relatively nutrient rich mesic habitat for their maximum growth, but they can survive on infertile volcanic ash soils, because of symbiosis with ectomycorrhiza. Under the enriched [CO_2], photosynthetic capacity of host plants (e.g., larch) may be enhanced when large amounts of photosynthates are translocated to symbiotic microorganisms such as ectomycorrhiza, which in turn supply nitrogen, phosphates, and water to the host plants (Quoreshi et al. 2003; Qu et al. 2004; Yazaki et al. 2004; see also Chap. 21). This symbiotic interaction may play an essential role in the success of forest rehabilitation in infertile soil conditions and is often a reason why larch species should be introduced as reforestation materials.

In northeast China and in Korean Peninsula, *L. kaempferi* has been planted for timber production. In Hokkaido, the northernmost major island of Japan, large

Fig. 23.4 Example of larch regeneration after forest fire in Central Siberia (photo: Koike)

areas of secondary forests of deciduous, broadleaved trees were cut and reforested with *L. kaempferi* during the past century. Recently, the role of the larch ecosystem has expanded from mere timber production to acting as the carbon sink because of its large distribution area in the northern hemisphere and high growth rate.

On the other hand, the *L. kaempferi* plantations in Hokkaido are examples of transplantation of an exotic species from central Japan to a new, local ecosystem. Indeed, *L. kaempferi* has a high susceptibility to shoot blight disease and grazing damage done by voles. Newly introduced species often suffer from several biological and physical problems. In 1954, a hybrid larch that was highly resistant to vole damage was discovered by chance at the Tokyo University Forest located in central Hokkaido.

Based on screening tests, it was found that Dahurian larch (*Larix gmelinii*) originated from the Kurile Islands had a higher resistance to both vole grazing and shoot blight disease, but those from Sakhalin Island did not (Kuromaru 2002; Ryu et al. 2009). In addition, *L. gmelinii* has greater resistance to frost than *L. kaempferi*. Such high tolerance of *L. gmelinii* to low temperature can be attributed to its phenological traits, namely early flush and early shedding of needles. The F_1 hybrid larch was produced by crossing *L. gmelinii* of the Kurile Islands (mother tree), with *L. kaempferi* (father tree). The chloroplast was inherited paternally from *L. kaempferi* (Shmidt et al. 1987) and the other growth characteristics, such as wood density and high resistance capacity, were inherited maternally from *L. gmelinii* (Hokkaido Regional Government 1987; Koike et al. (2000b)).

Recently, this F_1 hybrid larch was used as the planting stock throughout Hokkaido Island because of its high growth rate and high specific gravity of the stem. Most growth traits show intermediate characteristics between *L. gmelinii* and *L. gmelinii*. F_1 larch will be a promising species to fix atmospheric CO_2 more quickly and to moderate global warming because of its high growth rate, high density, and resistance to several damages (Ryu et al. 2009).

23.7 Conclusions

Water use efficiency (WUE) and nitrogen use efficiency (NUE) of three larch species increased with enhanced [CO_2], but the increase in photosynthetic capacity was not long-lasting, which may be due to the effect of nutrient dilution in the plant body and nutrient limitation. The width of the annual ring and lumen size increased with high [CO_2], but no changes were found in the thickness of the cell-wall. Therefore, we cannot expect the naturally occurring larch species to play a role in fixing substantial amount of atmospheric CO_2 to moderate global warming, because they are likely to adapt to the new environment. On the other hand, F_1 (hybrid) larch may serve as a more effective fixer of atmospheric CO_2. Ectomycorrhiza should also be introduced and carefully used to accelerate the growth of larch seedlings, so that they can be effective in forest rehabilitation.

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