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Photosynthesis and leaf longevity in alder, birch and ash seedlings grown under different nitrogen levels

T. Koike[1,2] and M. Sanada[2]

[1] *Swiss Federal Institute of Forestry Research, Birmensdorf ZH, Switzerland, and*
[2] *Hokkaido Branch, Forestry and Forest Products Research Institute, Sapporo, Japan*

Introduction

With application of nitrogen fertilizers, photosynthetic rates increase (Field and Mooney, 1986) and the leafy period is prolonged (Linder and Rook, 1984). There is a negative correlation between the maximum photosynthetic rate and its duration (Koike, 1987). However, there is little information about the longevity of individual leaves after nitrogen treatments (Linder and Rook, 1984). We report the relationship between photosynthetic rates and leaf longevity of deciduous broad-leaved tree seedlings in relation to the anatomical characteristics in leaves.

Materials and Methods

One yr old seedlings of alder (*Alnus hirsuta* Turcz.), birch (*Betula maximowicziana* Regel) and ash (*Fraxinus mandshurica* Rupr. var. *japonica* Maxim.) were planted in unglazed pots (diameter: 21 cm) filled with surface soil of the nursery including volcanic ash (Sanada, 1975). As nitrogen fertilizers, ammonium sulfate was supplied 4 times in each pot. Phosphate ammonium (0.2 g) was provided as basal dressing. Until the final supply, total amount of nitrogen in each pot was 5.0, 1.5, 1.0 and 0.35 g. Supplying date and the percentage against the total amount was July 1 40%; July 24 20%; Aug. 20 20%; and Sept. 15 20%, respectively.

Gas exchange rates were determined by an open system with an infrared gas analyzer (URA2S, Shimadzu) in the summer of 1984. Air was stored in an airbag and was humified. The flow rate into the chamber (20 x 18 x 1.8 cm^3) was 66.7 $cm^3 \cdot s^{-1}$. Measurement conditions were regulated strictly with an artificially illuminated chamber (Koike, 1987). Leaf temperature was kept at the optimum temperature of 20°C and was monitored by a copper-constantan thermocouple. After gas exchange measurements, leaf area was determined by an area meter (AAM5, Hayashi). Dry weight of leaves was measured after drying at 85°C for 48 h. Leaf chlorophyll was extracted with 80% acetone. Leaf nitrogen content was determined by a C–N corder (MT 500 W, Yanagimoto). Each measurement was replicated 3–5 times.

Results

The photosynthetic rate at light saturation in each species was increased with increasing nitrogen content (Fig. 1). With increasing nitrogen levels, the dark respi-

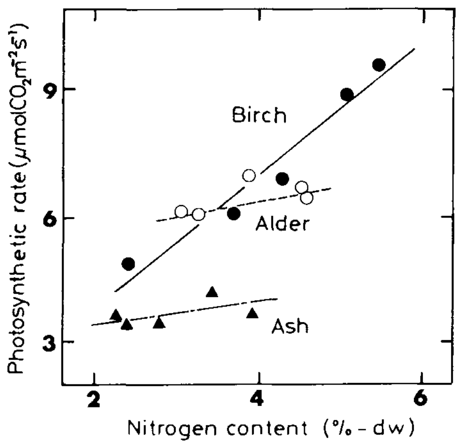

Fig. 1. Relationship between nitrogen content in a leaf and the photosynthetic rate at light saturation at 20°C.

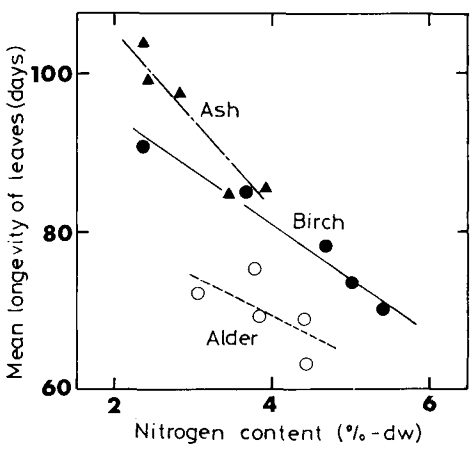

Fig. 2. Negative correlation between the nitrogen content in a leaf and mean longevity of leaves.

ration rate at 20°C in alder and birch was increased but was lower in ash. The apparent quantum yield of all species was increased with the increasing nitrogen content.

In all species, leaf longevity decreased with an increase in the nitrogen content in leaves (Fig. 2). The chlorophyll content in leaves of all species increased with increasing nitrogen, especially in birch. Small differences in the specific leaf weight in alder and in birch were observed between nitrogen treatments. The leaf thickness in leaves of birch and ash increased with an increase in nitrogen content, as compared with alder leaves. The mesophyll surface area per unit area (A^{mes}/A; see Nobel, 1977) in all species increased with increasing nitrogen content.

Discussion

For all species, photosynthetic rates increased, while the mean longevity of individual leaves decreased with increasing nitrogen content in leaves. Based on the individual levels (Schulze and Chapin, 1987), the leaf longevity was diminished, while the number of newly produced leaves increased (Linder and Rook, 1984). If nitrogen were available, trees could produce new leaves with high photosynthetic capacity and could quickly shed their decaying leaves. These phenomena were reviewed for many species (Field and Mooney, 1986; Schulze and Chapin, 1987). With increasing leaf nitrogen, the A^{mes}/A and leaf thickness increased. These structural changes in leaves seem to increase photosynthetic organs and to diminish CO_2 diffusion resistances.

The leaves containing high nitrogen show high photosynthetic rates, while these leaves were short-lived because they are easily attacked by herbivores (Mooney and Gulmon, 1982). These authors emphasized that there was a positive correlation between leaf longevity and the amount of defense chemicals against herbivores in leaves. In the present study, we found a strong correlation between the cuticle ratio (*i.e.*, the ratio of cuticle layers in a leaf to leaf thickness) and leaf longevity (Fig. 3). Cuticle layers may not only restrict extra-transpiration but also form a support part of leaves.

No relationship between the cuticle ratio and leaf longevity in alder leaves was found. The weak response of alder leaves to nitrogen fertilizer may be attributed to the activity of nitrogen-fixing microorganisms in its root system. Birch, an early successional species, could grow quickly with use of nitrogen. Ash, a gap phase species, hardly seems to respond to nitrogen in soil with volcanic ash (Ootomo and Nishimoto, 1984).

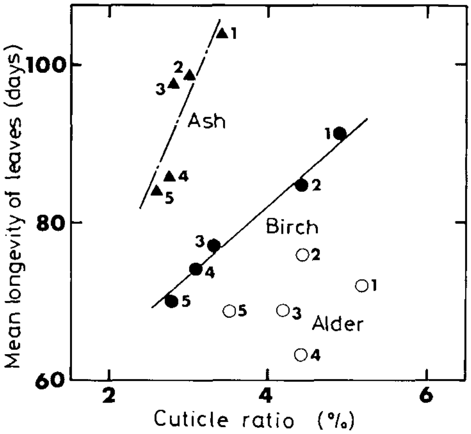

Fig. 3. Relationship between the cuticle ratio and mean longevity of leaves. The definition of 'cuticle ratio' refers to the text. The figures in the diagram show the degree of nitrogen content in a leaf. The higher the numbers, the greater the nitrogen content in leaves.

Acknowledgments

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