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SENESCENCE AND THE PHOTOSYNTHETIC PERFORMANCE OF INDIVIDUAL LEAVES OF DECIDUOUS BROADLEAVED TREES AS RELATED TO FOREST DYNAMICS

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1. INTRODUCTION

Leaf development and senescence are regulated by the specific response of tree species to the environment(1,2). In fact, autumn coloration of late successional species begins from the top part of a crown while early successional species start from the inner part of a crown(3). Based on an analysis of Chl.fluorescence, senescence of leaves starts in mid summer(4). Does the timing of leaf shedding depend upon the specific patterns of trees with different successional characteristics(5)? What about the functional performance of individual leaves during leaf senescence?

To answer these questions, we monitored the time course of the photosynthesis of individual leaves in order to ascertain the timing of inactivation of leaves. We measured the photosynthesis, Chl.fluorescence and nitrogen content in different aged leaves before leaf shedding. We discussed the physiological changes in individual leaves of seral tree species as related to the successional strategy in a forest stand.

2. Materials and Methods

2.1 Plant materials: Leaves of the sunny and shady crown of early successional species, birch (*Betula maximowicziana*; Heterophyllous type) and alder (*Alnus hirsuta*; indeterminant type); late successional species, maple (*Acer japonicum*; determinant type) were used. In mid August, the edge of the sun leaves of the maple turned slightly reddish. Trees were planted in the experimental forest of the Forestry and Forest Products Research Institute (Sapporo; 42°58'N, 141°23'E, 140m a.s.l.).

2.2 Measurements: Photosynthesis of the odd numbered leaves as counted from the base was measured with an infra red gas analyzer(Shimadzu URA2S) under conditions of saturated PPFD(800μmol·m^{-2}s^{-1}), an optimum leaf temperature(20°C), ambient CO_2(340ppm), regulated by a climatized chamber(Koito KG) and flow rate of 83 cm^3·s^{-1}. Relative humidity in an assimilation chamber(20x18x2cm) monitored with a Vaisala humidity sensor(HMP 31UT) was kept at ca.80%. Chl.fluorescence was detected with a fluorometer(Hansatech PEA) in mid August. Chl. content in a leaf was analyzed using 80% acetone extracts. Leaf nitrogen concentration was determined using a C/N corder(Yanagimoto MT 500W). Chl. and nitrogen analysis was carried out in early October.

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3. Results

3.1 Photosynthesis and leaf nitrogen concentration of individual leaves

Except for the first leaves of birch(early leaves), the maximum photosynthetic rate at light saturation(Pns) of alder and birch increased with increasing leaf age then decreased rapidly as the individual leaves aged(Fig.1). The max. Pns of early leaves of birch and maple was maintained over most of the growing season. In maple, there was little difference in Pns between individual leaves. Pns of all leaves unfolded at spring began to decrease in early September irrespective of the green color of the leaves. The younger leaves of birch and alder expanded in July which kept a high Pns of 8 $\mu mol \cdot m^{-2} s^{-1}$ even in early October.

With increasing leaf order, Pns and leaf nitrogen concentration of birch and alder increased(Fig.2). On the contrary, those of maple decreased with increasing leaf order. A positive correlation between Pns and leaf nitrogen concentration was found.

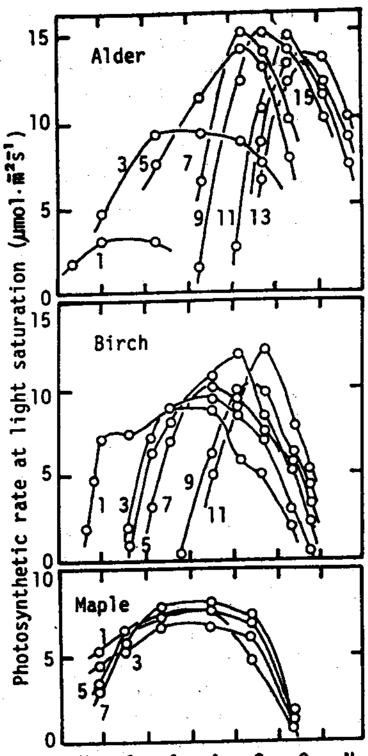

FIGURE 1. Seasonal change in the photosynthesis of individual leaves. Numbers indicate leaf order counted from the shoot base.

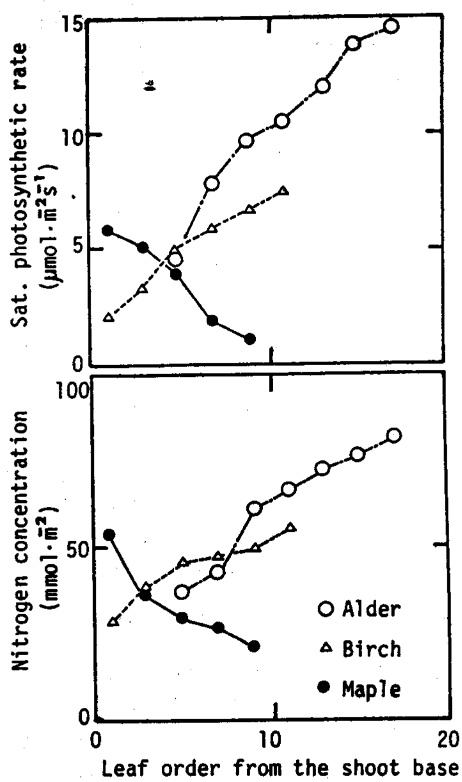

FIGURE 2. Photosynthesis at light saturation and nitrogen concentration of each leaf order. Measurement in early October.

3.2 Chlorophyll content and Chl.fluorescence of sun and shade leaves

Chl. content of alder and birch leaves increased from the bottom part of a shoot to the top(Fig.3). In contrast, Chl. content of maple leaves decreased with increasing leaf order. Except for the older leaves of alder, Chl.b content was more stable than Chl.a. The older leaves of the alder decreased both Chl.a+b. Chl.b of maple leaves was almost constant at 0.1 $mmol \cdot m^{-2}$.

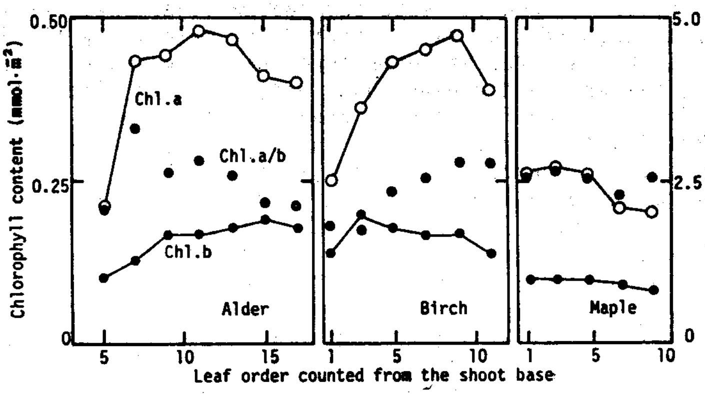

FIGURE 3. Chlorophyll content and chlorophyll a/b ratio determined in early October. Measurement replicated was three times in each.

The Chl.fluorescence curve of sun leaves of alder and birch decreased more rapidly after reaching the peak (P) than with shade leaves (Fig.4). In maple, the curve of sun leaves initially showed higher

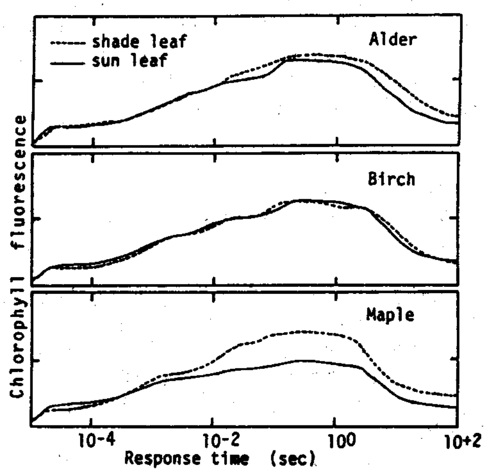

FIGURE 4. Chlorophyll-fluorescence induction kinetics in sun and shade leaves. In maple, autumn coloration started from the top part of a crown in mid August with lower temperature.

values then lower than shade leaves. The difference between sun and shade leaves of birch was the smallest. Despite the green color of the alder leaves, the Chl.fluorescence of shade leaves was higher after the 10^{-2} sec. passed.

4. Discussion

Photosynthetic rate, Chl.content and leaf nitrogen concentration of each species decreased with increasing leaf age(Figs.2,3). Leaf nitrogen concentration may allocate for maximizing the leaf photosynthesis(6,7,8). During senescence, many compounds in leaves, containing nitrogen and phosphorbus, are recycled from the leaf into the stem(1). Alder leaves stay green in color until leaf shedding(3) and showed little response to a supply of nitrogen(9). However, the initiation of senescence in alder leaves was detected with Chl.fluorescence curve(4) irrespective of its green color(Fig.4). The pattern of leaf aging in birch was the same as alder, which may be related to the light environment in the canopy because of the continuously expanding new leaves throughout the growing season. In maple, leaf aging progressed from the outer part of a crown (Fig.2,3,4) because of the severe environment, eg. strong light and large temperature differences. Except for the second flush, the leaf age of maple leaves was the same(3).
Trees indeterminant leaf development produce a high photosynthetic capacity with a short lifespan, which may be advantageous for achieving as long a growth space as possible. Before leaf shedding, little nitrogen in alder was recycled, which may be attributed to the nitrogen fixative microorganism in its root system. In contrast, trees with determinant leaf growth, such as maple, quickly complete shoot elongation and have long leaf lifespans. Most of the nitrogen in maple leaves may translocate to the stem for next growing season. This pattern may confer a competitive advantage to an old forest. In conclusion, the timing of leaf senescence and the photosynthetic capacity and nitrogen recycling are closely related to the successional characteristics of tree species.

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