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PARK, Seok-Gon

Institute of Tropical Agriculture, Kyushu University | Division of Forest Resources and
Landscape Architecture, Sunchon National Univ

MATSUMOTO, Masaru

Institute of Tropical Agriculture, Kyushu University

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A Study on the Effects of Light Conditions on the Longevity and Characteristics of *Daphniphyllum macropodum* Leaves

Seok-Gon PARK^{1,2*} and Masaru MATSUMOTO³

Institute of Tropical Agriculture, Kyushu University, Hakozaki, 6–10–1, Fukuoka 812–8581, Japan
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The aim of this study was to investigate the effects of light conditions on the longevity and characteristics of *Daphniphyllum macropodum* leaves by determining the number of leaves, leaf area, shoot length, leaf thickness, leaf mass per area (LMA), and chlorophyll content (SPAD value) of *D. macropodum* leaves from three individual trees growing under different light intensities. Measurements were made each month from February to November 2014. Shoots growing under weak light intensity had a larger number of leaves, broader leaf area, and longer leaf longevity. Under this condition, self-shading is unavoidable as the leaves overlap each other. The trees appear to increase their light-receiving capacity by enhancing shoot growth in the internodes, which broadens the interval between the leaves and reduces self-shading. By contrast, *D. macropodum* plants growing with sufficient light had thicker leaves and higher LMA and SPAD values, which reflected a strategy for increasing the photosynthesis rate. Leaf longevity in this case was relatively short. A strategy of early shedding of the old leaves (after reabsorption of nutrients) and forming new leaves rather than retaining the old leaves is more beneficial in terms of photosynthetic productivity. These large differences in leaf longevity and characteristics can be seen as an adaptation to differences in light intensity.

Key words: Adaptation strategy, Leaf phenology, Light-receiving rate, Photosynthesis rate, Self-shading

INTRODUCTION

Daphniphyllum macropodum MIQ., known in Japan as the Yuzuri-Ha Tree, gets its common name from its characteristic loss of year-old leaves and their immediate replacement with new leaves in the spring. As its name suggests, leaf longevity of *D. macropodum* is short, similar to that seen in broad-leaved deciduous trees, but it is not a deciduous tree. Broad-leaved deciduous trees growing in temperate climate regions shed their leaves just before the winter season, when photosynthesis is not favored, which suggests that all broad-leaved deciduous trees would have similar leaf longevity. However, their leaf longevity varies substantially. In Hokkaido, Japan, leaf longevity of *Alnus hirsute* was as short as 80 days, while that of *Quercus crispula* and *Fagus engleriana* was two times longer, at 160 days (Kikuzawa, 2005). By contrast, leaf longevity of broad-leaved evergreen trees is relatively long. For example, leaf longevity of broad-leaved evergreen trees in Chiba prefecture, Japan varied from 1.5 years to 4.3 years.

The reason why leaves differ in their longevity is not known. Kikuzawa (2005), who explored the ecological meaning of leaf longevity, reported that the goal of acquiring maximum carbon determines the leaf longevity, because the leaf is the organ that fixes atmospheric carbon. Once a leaf is created, its photosynthesis ability naturally diminishes due to aging as times progresses. Because of this weakened photosynthetic capacity, replacing an old leaf with a new leaf, rather than keeping it, can enhance the photosynthesis rate of the plant

(Kikuzawa, 1991). Thus, a change in leaf longevity and in leaf phenology in response to photosynthesis can be viewed as an adaptation strategy.

The *D. macropodum* tree is typically observed in the understory of broad-leaved evergreen forests, where it experiences a weak light environment and shows a relatively slow growth rate (Park and Matsumoto, 2017). However, it is also often observed in the canopy layer in its habitat in Korea (Park *et al.*, 2015). It is also a popular garden tree, and it grows well in sunny to shady sites, indicating that it tolerates quite a large range of light intensity for its growth. As suggested by Kikuzawa (2005), maximizing the amount of carbon acquisition determines leaf longevity. Therefore, the leaf longevity of *D. macropodum*, as well as the structure, shape, and arrangement of the leaves, is expected to show large differences according to the light conditions under which the tree grows. This study examines the longevity and the characteristics of the leaves of *D. macropodum* growing under different light intensities and discusses adaptation strategies operating at the individual tree level.

MATERIALS AND METHODS

Research site overview and plant materials

A campus and farm at the Sunchon University located in Suncheon City, Jeollanam-do, South Korea were selected as the research site. We chose three *D. macropodum* trees at the research site as the test plants. Two individual trees (Ind. 1 and Ind. 2) were located behind a south-facing five-story building (approximately 16 m high) on the campus of Sunchon University. The third tree (Ind. 3) was located in front of a south-facing building on the farm. Consequently, the two *D. macropodum* trees located on the campus

¹ Division of Forest Resources and Landscape Architecture, Sunchon National Univ., Sunchoen (57922), Korea.

² Institute of Tropical Agriculture, Kyushu University

* Corresponding author (E-mail: eco-research@hanmail.net)

Table 1. General physical overview of each *Daphniphyllum macropodum* individual (Ind.) examined in this study

Plant material of <i>D. macropodum</i>	Ind.1	Ind.2	Ind.3
Location(GPS)	N34°96'95.99" E127°48'22.63"	N34°96'95.70" E127°48'23.57"	N35°00'19.28" E127°50'75.70"
Tree height (m)	3.0	2.7	7.5
Slope (°)	2	1	5
Canopy openness (%) †	20.3	37.5	58.5
Relative PPFD (%) †	20.7	40.5	83.2

†: Canopy openness and photosynthetic photon flux density (PPFD) were estimated from hemispherical photographs taken at the top of individual trees. "Gap Light Analyzer" software (Frazer *et al.*, 1999) was used to calculate relative PPFD.

(Ind. 1 and Ind. 2) experienced low relative photosynthetic photon flux density (PPFD) values of 20.7% and 40.5%, respectively, where PPFD is a criterion of light intensity. By contrast, the *D. macropodum* tree on the farm (Ind. 3) had a relatively high PPFD of 83.2%. The heights of these trees were between 2.7 and 7.5 m. The trees had multiple shoots and all showed good growth (Table 1).

Investigation and analysis method

We conducted monthly investigations from February to November in 2014 on the longevity and characteristics of the leaves of *D. macropodum* growing under different light conditions. We selected six shoots from each of the three *D. macropodum* individuals (a total of 18 shoots) and attached marking tape to each leaf to enable continuous follow-up. We counted the numbers of leaves on each shoot and divided the leaves between those created in the current year (current-year leaves, 2014) and those from the previous year (one-year-old leaves, 2013). We measured leaf area, chlorophyll content, leaf thickness, and weight per leaf area of the current-year leaves from April to November 2014. We estimated the leaf area based on a regression equation by measuring the major and minor axes of each leaf as described previously (Park and Matsumoto, 2017). The leaf area was measured for 60 leaves from each *D. macropodum* individual. We measured the chlorophyll content and leaf thickness of the same leaf used for the area measurement. Chlorophyll content was measured as the SPAD value using a Minolta chlorophyll meter (SPAD-502, Japan) and the leaf thickness was measured with a digital micrometer (Mitutoyo 293-821, Japan). The shoot length was measured only for the shoots that had grown in the current year (2014). We collected ten leaves from each *D. macropodum* individual every month, and we measured the leaf area and dry weight to compute the leaf mass per area (LMA, g/m²).

We conducted one-way analysis of variance and post-hoc analysis (Bonferroni test) on the leaf area, leaf thickness, LMA, shoot length, and SPAD value at a 5% significance level to determine the statistical significance of the effects of light condition of the measured data. IBM SPSS Statistics (ver. 21) software was used for statistical analysis.

RESULTS AND DISCUSSION

The number of leaves on each shoot in February and March was larger for the first *D. macropodum* individual (17 for Ind. 1) than for the other two individuals (15.5 for Ind. 2 and 11.8 for Ind. 3) (Fig. 1). The situation was similar for the leaves generated in the current year. In Ind. 1, the total number of leaves in April was double that of the one-year-old leaves, as the same number of new leaves were generated. The one-year-old leaves began to fall in August and over half the leaves had fallen by September. In other words, the current-year leaves and the one-year-old leaves coexisted on a shoot from Ind. 1 for a considerable time. By contrast, Ind. 2 and Ind. 3, which grew under high relative PPFD, showed a different trend. Ind. 2 began to shed one-year-old leaves in April and the total number of leaves was halved by May. Ind. 3 shed most of its one-year-old leaves in April, and these were replaced by the current-year leaves. In general, tree species like *D. macropodum* that have a flush-type leaf unfolding in springtime also have flush-type leaf fall (Kikuzawa, 2005). This is because mineral nutrients and carbohydrates are reabsorbed from the leaves before the leaves fall to provide nutrients for the unfolding leaves (Nitta and Ohsawa, 1997). That is, the unfolding leaves become sinks for nutrients and the falling leaves become a source of these nutrients. Here, the timing of leaf unfolding and falling coincides.

In this study, the longevity of leaves was defined as the time when more than half of the one-year-old leaves had fallen. The leaf longevity of Ind. 1 was 510 days, while that of Ind. 2 and Ind. 3 was shorter, at 390 days and 360 days, respectively. Therefore, even within the same species, the response of leaf phenology and longevity to the light condition showed a large difference. Leaf longevity has been negatively correlated with photosynthesis rate. Within the same species, leaf longevity tends to decrease with stronger light intensity and higher photosynthesis rate (Kikuzawa, 1989). According to Kikuzawa (1989), *Daphniphyllum teijsmannii* has only two-year-old leaves on shoots that experience strong light intensity, whereas four- and five-year-old leaves were common on shoots growing under weak light intensity, which was identified as a condition that increased leaf longevity. Increases in leaf longevity in an environment with limited light will compensate for the low pho-

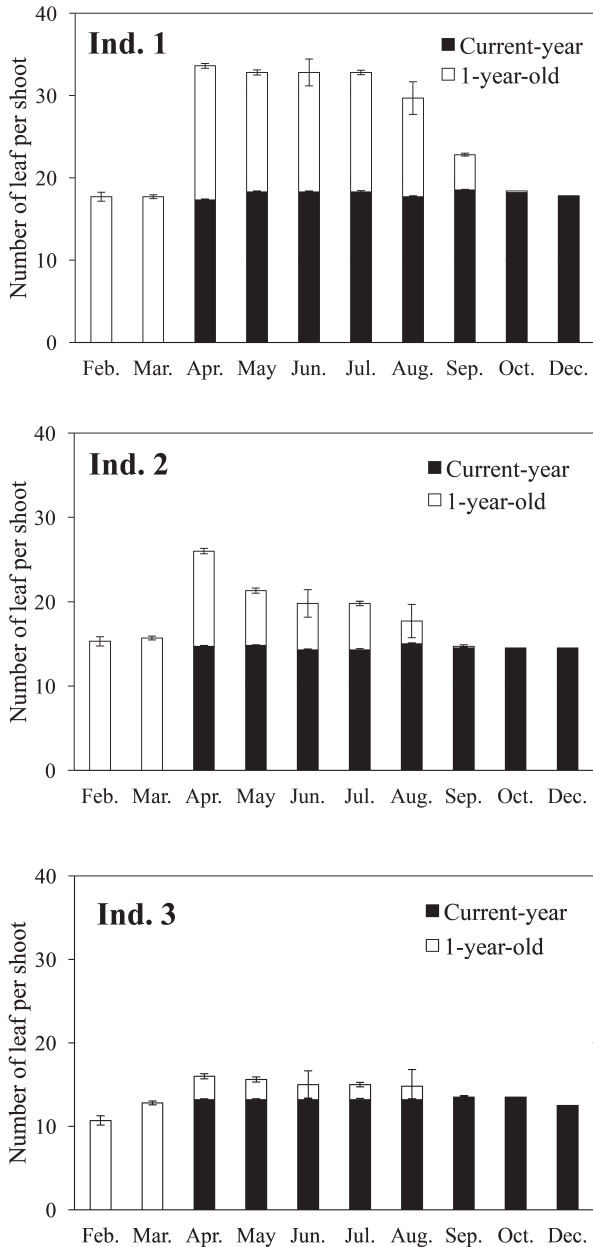


Fig. 1. Seasonal changes in the number of leaves per shoot of *Daphniphyllum macropodum* according to the prevailing light condition. Ind. 1–3 indicate *D. macropodum* individuals. The error bars indicate standard error.

tosynthesis capacity. Other studies that have compared diverse plant groups have reported a negative correlation between leaf longevity and photosynthesis capacity (Chabot and Hicks, 1982). At an individual level, the longevity is shorter for leaves under shade. However, if all the leaves of an individual tree are under shade, the overall leaf longevity of the tree increases (Hikosaka and Hirose, 2001; Kikuzawa, 2005). The results of our study clearly demonstrate this relationship.

As new leaves unfold in flushes and become fully grown in April, the leaf area does not show much change (Fig. 2). The leaf area of Ind. 3, whose relative PPFD was the highest of the three individuals, was significantly smaller than that of Ind. 1 and Ind. 2. This tendency was similar to that observed for shoot length (Fig. 3A).

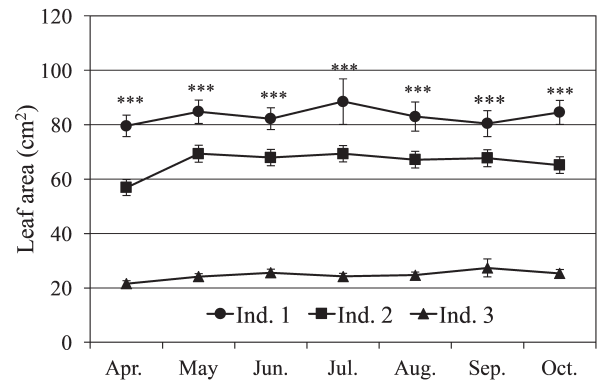


Fig. 2. Seasonal changes in the leaf area of *Daphniphyllum macropodum* according to the prevailing light condition. Ind. 1–3 indicate *D. macropodum* individuals. The asterisk (***) above the line indicate statistical differences at the 0.1% level by Bonferroni test. The error bars indicate standard error.

The LMA of *D. macropodum* was 148.1 g/m^2 , which is similar to that reported for *Camellia japonica* (142) and *Quercus glauca* (139) and considerably larger than the reported LMA for broad-leaved deciduous trees, such as *Fagus engleriana* (82) and *Acer pictum* subsp. *mono* (22) (Kikuzawa, 2005; Park and Matsumoto, 2017). The leaves of *D. macropodum* are relatively thick and broad, and the leaves unfold in a flush in April. As a result, the leaves block the light and diminish the photosynthesis rate. To avoid this type of self-shading, many broad-leaved evergreen trees show simultaneous leaf creation and leaf fall in the springtime (Nitta and Ohsawa, 1997). The leaf thickness (Fig. 3B), LMA (C), and SPAD value (D) increased with higher relative PPFD. This is consistent with the findings of Chung *et al.* (2011), who analyzed growth and development in *D. macropodum* habitats according to the prevailing light conditions.

Leaf longevity and LMA are positively correlated (Koike, 1988). Broad-leaved evergreen trees with thick leaves have longer leaf longevity when compared with broad-leaved deciduous trees (Kikuzawa, 2005). A steady provision of carbon dioxide is required to increase the photosynthesis rate by increasing the surface area of the mesophyll cells and chlorophyll (Terashima *et al.*, 2001). That is, a small cell size within the leaves can increase LMA. Moreover, leaves are thickened as the ratio of the cuticle layer increases to protect the plant from animals (Kursar and Coley, 1992). The leaves of the species with these kinds of characteristics tend to have greater longevity (Koike, 1988; Kikuzawa, 2005). This positive relationship between leaf longevity and LMA persists among different tree species; however, in our opinion, this relationship does not hold among *D. macropodum* individuals experiencing different light conditions. The *D. macropodum* individual growing under insufficient light had intermittent leaves that did not overlap with each other and it retained its leaves for a long time. By contrast, the *D. macropodum* individuals growing in a site with sufficient light had more pali-

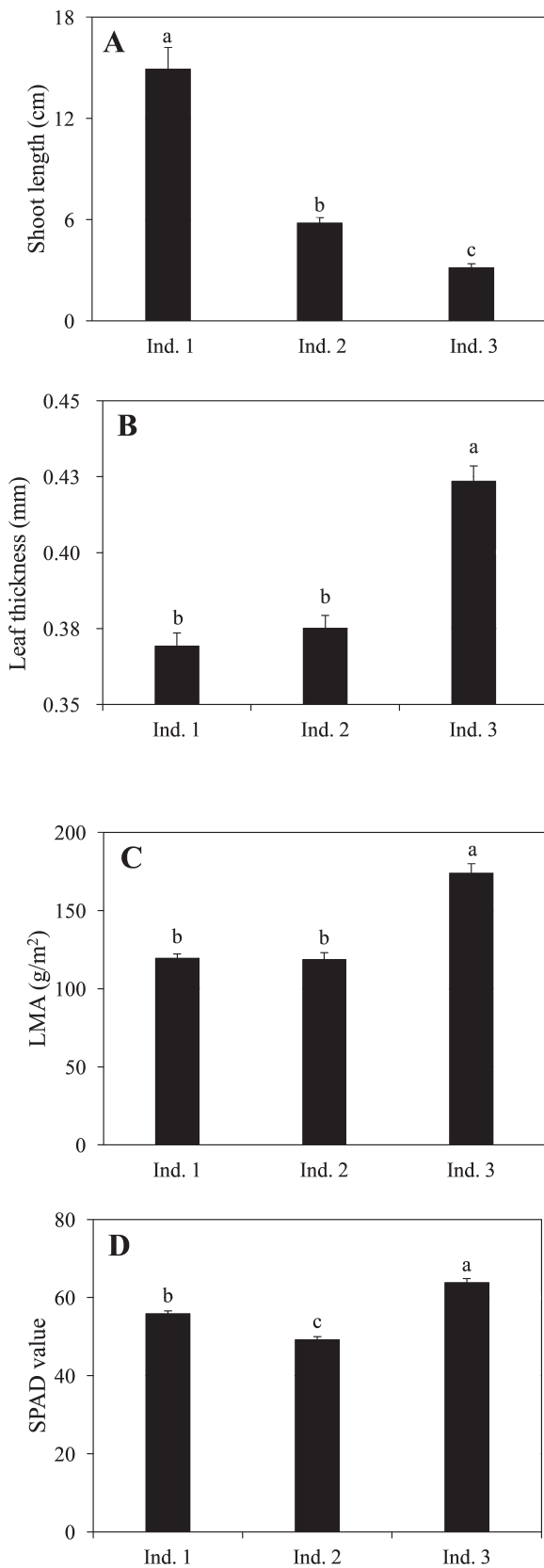


Fig. 3. Shoot length (A), leaf thickness (B), LMA (C), and SPAD value (D) of *Daphniphyllum macropodum* according to light condition. 1–3 are the individual number of *D. macropodum*. Different letters (a–c) within a graph indicate statistical differences at the 5% level by Bonferroni test. The error bars indicate standard error.

sade tissue (i.e., greater leaf thickness) and chlorophyll content (SPAD value) in their leaves, and this increased the photosynthesis rate. However, these leaves had a short longevity. Our opinion is that the longevity of *D. macropodum* leaves at the individual tree level is determined by the cost of forming and maintaining those leaves (photosynthate, nitrogen, and water) and the productivity of the leaves (photosynthesis rate). If a one-year-old leaf gets older and the maintenance cost (consumption) exceeds its photosynthate production (benefit), then shedding of that leaf would be beneficial in terms of the plant's carbon economy.

D. macropodum is recognized as an understory tree that grows under the crown layer and shows strong shade adaptation (Park and Matsumoto, 2017). Under those conditions, light becomes the limiting factor for photosynthesis. For this reason, *D. macropodum* must retain its broad leaves long after its flush-type leaf unfolding in the springtime. This creates a situation where leaves inevitably overlap and diminish the amount of light received. The tree is able to overcome this by growing long shoots, thereby widening the intervals between the leaves and minimizing the self-shading. This strategy enables adaptation in the poor light environment under the crown by maximizing the photosynthesis rate. By contrast, trees in sites with sufficient light do not have to broaden their leaf areas, nor is self-shading a concern. Increasing the photosynthesis rate by increasing the content of palisade tissue and chlorophyll in the leaves is more beneficial. The leaves will also require additional thickness of the cuticle layer, as this layer prevents water loss and protect the leaves from animals. Therefore, *D. macropodum* appears to adopt a survival strategy whereby it increases its adaptability by changing the shape, structure, and arrangement of its leaves according to the prevailing light condition.

CONCLUSIONS

The leaf phenology of *D. macropodum* showed large differences depending on the prevailing light intensity where the plant was situated. Leaf longevity decreased with increasing light intensity. *D. macropodum* situated in a site with weak light intensity had a larger leaf area and longer shoots, which minimized self-shading. By contrast, *D. macropodum* situated in a site with sufficient light had thicker leaves and higher LMA and SPAD values, which can be considered to reflect a strategy aimed at increasing the photosynthesis rate. A *D. macropodum* tree situated in a site with sufficient light does not need to retain the previous year's leaves, which have diminished photosynthesis capacity. Shedding of the old leaves after reabsorbing the nutrients contained in them will be more beneficial for the carbon economy of the plant. In our opinion, the longevity of *D. macropodum* leaves is determined by photosynthate (benefit) and maintenance (consumption) costs. The changes observed in leaf phenology and leaf longevity in response to light intensity can be seen as an adaptation strategy for growth under different light conditions.

Korea has generally poor conditions for the growth of broad-leaved evergreen trees, so the northernmost limit of *D. macropodum* is at 35°29' latitude with winter temperatures as low as -15°C (Park and Matsumoto, 2017). Further studies on the adaptation strategy for growth under these poor conditions will be required in terms of leaf phenology.

AUTHOR CONTRIBUTIONS

S. G. Park designed the study, performed the histological experiments, analyzed the data and wrote the paper. M. Matsumoto supervised the work, wrote the paper. All authors assisted in editing of the manuscript and approved the final version.

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