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Original Article

Low Light Intensity, Inorganic Fertilizer Application and the Leaf Life Span of *Quercus acutissima* and *Q. serrata* seedlings (Fagaceae)*

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Abstract

Leaves of *Quercus acutissima* and *Q. serrata* seedlings were observed from the time of unfolding to leaf fall to determine the effects of low relative light intensity (RLI) and additional inorganic fertilizer application to leaf life span (LLS). Seedlings of both species grown under low RLI (25%, 12%, 6% and 3%) retained leaves longer and the LLS increased significantly ($p<0.01$) as RLI decreased. Although it has been reported that leaf nitrogen content negatively correlated with LLS (Reich and Walters, 1992), and it was predicted that the artificial addition of nitrogen would shorten LLS (Kikuzawa, 1995), additional inorganic fertilizer did not decrease the LLS of *Q. acutissima* and *Q. serrata* seedlings significantly ($p<0.01$). Fertilizer application promoted leaf production which led to self shading. Self shading may have reduced photosynthetic rates in shaded leaves extending the mean LLS of fertilized seedlings longer than expected. Although there may have been an increase in photosynthetic rate due to fertilizer application self shading may have offset this increase. Comparatively, *Q. acutissima* had a longer LLS than *Q. serrata* seedlings under all treatments.

Key words : Inorganic fertilizer application, shading treatment, *Quercus* seedlings, Leaf Life Span

Introduction

It is important to know what would shorten or prolong leaf life span (LLS) because productivity is to some extent determined by the length of time a leaf is in existence. Chabot and Hicks (1982) suggested that leaf life span is determined by the balance betweeen the carbon gain of a leaf during the season favorable for photosynthesis and the costs to construct a leaf and maintain it during the season unfavorable to photosynthesis. They proposed that the optimum leaf life span is the period

* ジョージ・バニュス・玉泉幸一郎・齋藤　明：ブナ科コナラ属のクヌギ (*Quercus acutissima*) とコナラ (*Quercus serrata*) の葉の寿命の庇陰と施肥に対する反応

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necessary to maximize the net photosynthetic gain of a leaf. According to Kikuzawa (1995), however, this suggests that the leaf life span should be the period extending from leaf birth to the time when the instantaneous net photosynthetic rate of the leaf is zero or until no more positive carbon gain is possible from the leaf. While this may be plausible, the model gives no explanation why leaf life span becomes short even when conditions are still physiologically favorable for the leaf. Kikuzawa (1995), then suggested that it is the photosynthetic rate of the whole plant and not the photosynthetic rate of a single leaf which should be maximized.

Kikuzawa (1995) proposed that the time which maximizes the carbon gain of the whole plant over time (t) is the optimum leaf longevity, with the formula:

$$F=G/t$$
$$=(1/t)\left\{\int_0^t p(t)\,dt-\int_0^t m(t)\,dt-C\right\}$$

where, G is the carbon gain after subtracting the construction cost (C) and the maintenance cost [$m(t)$] from the photosynthetic gain [$p(t)$]; while (F) is the function which should be maximized, and the time (t) which maximizes this function is the optimum leaf life span.

With this model, it is predicted that as the maximum photosynthetic rate increases, or the rate of photosynthesis itself becomes high, LLS becomes shorter; while, LLS becomes longer as the leaf construction cost increases (Kikuzawa, 1995).

Based on these predictions, changes in the LLS of seedlings of two decidous species, *Q. acutissima* and *Q. serrata*, grown under low relative light intensity (RLI) and additional inorganic fertilizer application were examined. This was based on the assumption that low RLI could decrease the photosynthetic rate in seedlings while additional fertilizer may increase it. Faced with possible significant changes in the global climate, it has become even more important to determine how LLS may be influenced by these two important factors.

Methods

Seeds of *Q. acutissima* and *Q. serrata* were collected in autumn of 1993 from the seed orchards of Kyushu University, overwintered and planted in March of 1994 in cement pots (1 meter in diameter, 1 meter in height) in the Kyushu University nursery. Five of the most robust seedlings growing evenly spaced from each other, almost of the same height, status and date of germination were selected from each pot. The rest of the seedlings were culled in May of 1994. Thereafter, observation was made until January, 1995.

A set of four pots each for every species were enclosed with a black net that allows 50% light penetration. Peices of this net were used to decrease relative light intensity to 25%, 12%, 6% and 3% RLI. The nets were held by a frame structure built around

the pots. One pot for each species was left without a net cover as the shading treatment control. All seedlings under the shading treatment, including the control, were fertilized with the Horticulture Cooperative IB chemically synthesized fertilizer (10:10:10 NPK + minerals) at the rate of 10 g per seedling. Fertilizer was applied to ensure adequate growth under low RLI.

Another set of four pots with five seedlings each were grown under full sunlight. The same inorganic fertilizer provided seedlings under the shading treatment was applied at the rate of 10 g, 20 g, 40 g and 80 g per seedling for each fertilizer treatment respectively. Five seedlings for each species grown without fertilizer served as the fertilizer treatment control.

Daily observations were made on the emergence of each leaf. Every new leaf that emerged was labeled. Leaf senescence was recorded at the onset of browning. Leaves were considered dead after abscission. Liter was collected daily. Leaf life span (LLS) was defined as the number of days from the day a leaf unfolded to the time it dropped. The Analysis of Variance (ANOVA) was performed to determine the difference in the mean LLS among treatments.

Leaf size was determined from the liter collected because growing leaves were not disturbed, or collected and seedlings were not harvested. The Specific Leaf Area (SLA) in $cm^2 g^{-1}$ or the ratio of the leaf area to its dry weight was also calculated from the liter. Leaf production was evaluated every two weeks, from the number of leaves found in a seedling. The growth in height and diameter was also recorded fortnightly.

Results

Leaf Life Span

There was an increase in the mean LLS of *Q. acutissima* and *Q. serrata* seedlings as RLI decreased (Fig. 1). The mean LLS of seedlings in the control and shading treatments were significantly different in both species (F- test, $p<0.01$). In *Q. acutissma*, the difference between the mean LLS of seedlings grown under different RLIs (25% and 6%; 25% and 3%; 12% and 6%; 12% and 3% RLI) were also significant ($p<0.01$). In *Q. serrata*, the mean LLS of seedlings under decreasing RLI were significantly different from each other except between 12% and 25%; and 3% and 6%.

In *Q. acutissima* and *Q. serrata* seedlings, decreasing RLI delayed the onset of browning and leaf fall (Fig. 2 and 3). For seedlings of both species grown under 3% RLI, leaf fall began by mid to late December resulting in a longer mean LLS per seedling. The LLS of *Q. serrata* seedlings grown under 3% RLI was not longer than the mean LLS of seedlings under 6% RLI. Particularly in *Q. serrata* seedlings under 3% RLI, leaf fall immediately followed senescence which occurred almost simultaneously throughout the seedlings, regardless of the flush order. Thus, recently flushed leaves died almost around the time old leaves died, reducing the mean LLS of the whole

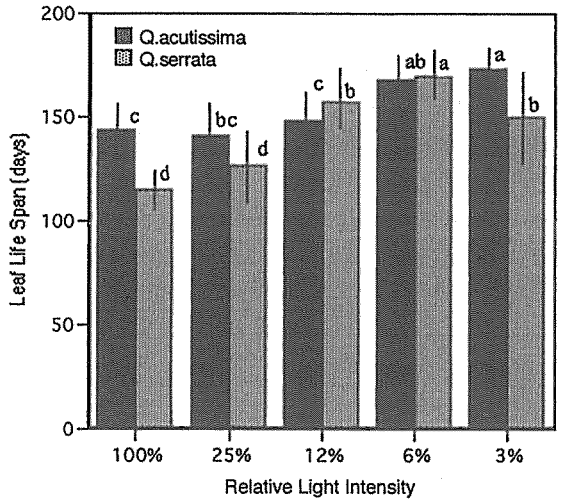

Fig. 1. The mean LLS of *Q. acutissima* and *Q. serrata* seedlings grown decreasing RLI. The LLS increased significantly as RLI decreased in both species. Vertical lines indicate SD, while the characters (a, b..) indicate significant difference ($p<0.05$), Duncan's Multiple Range Test (DMRT).

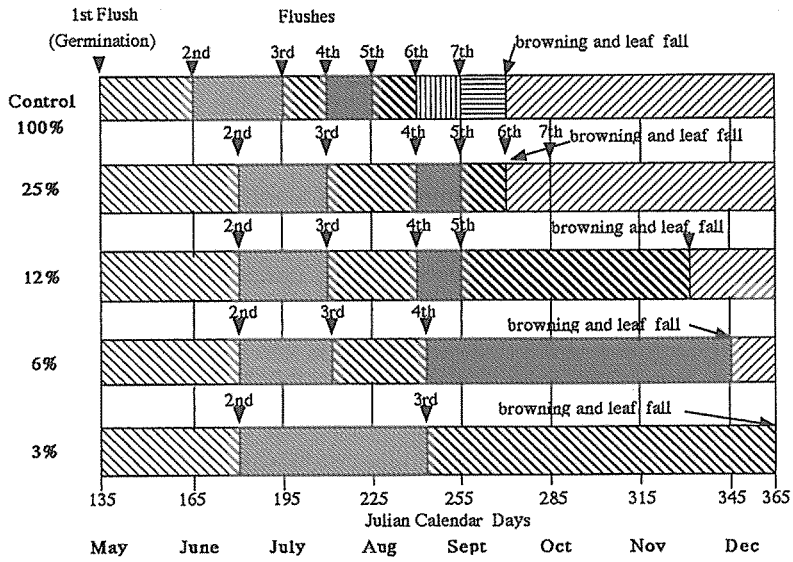

Fig. 2. The leaf production schedule of *Q. acutissima* seedlings under low light intensity treatments

Few flushes were produced by seedlings under 3% RLI. The timing of flushing coincided. The lower the RLI, the later browning and leaf fall (marked by upward diagonal lines) begun in the seedlings.

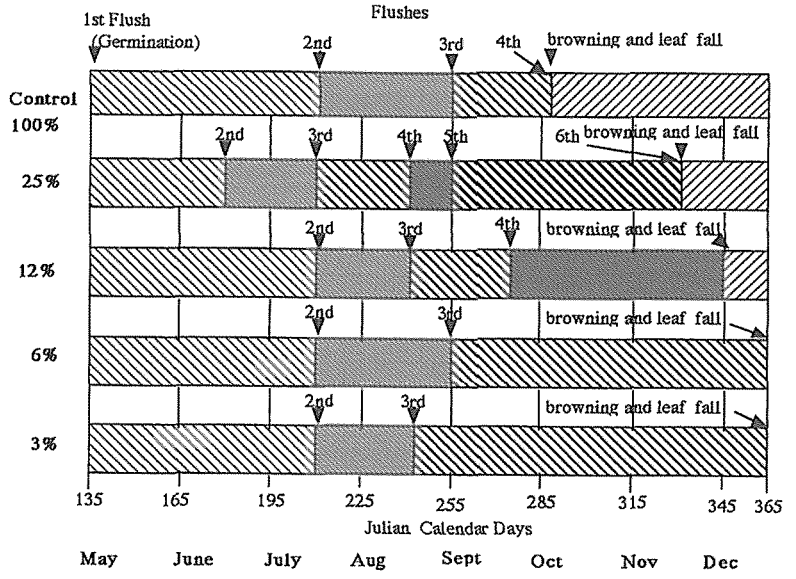

Fig. 3. The leaf production schedule of *Q. serrata* seedlings under low light intensity treatments

Except for seedlings under 25% RLI, fewer flushes were produced by seedlings under low RLIs. Although less consistent, most seedlings produced flushes around the same time regardless of the number of flushes being produced. The lower the RLI the later browning and leaf fall (marked by upward diagonal lines) begun.

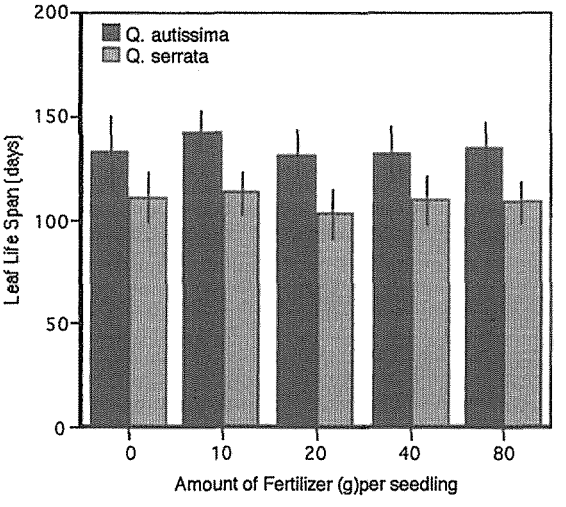

Fig. 4. The mean LLS of *Q. acutissima* and *Q. serrata* seedlings grown under full sunlight with increasing amounts of fertilizer. No significant difference was found between treatments. Vertical lines indicate SD.

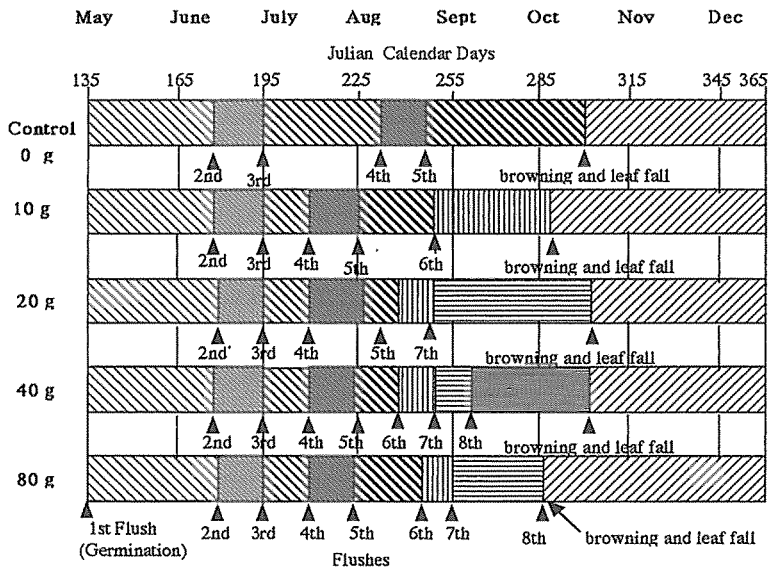

Fig. 5. The leaf production schedule of fertilized *Q. acutissima* seedlings
Seedlings with more fertilizer produced more flushes. Flushing in most seedlings under different treatments coincided, regardless of which flush is being produced at that particular time. For example, while some seedlings were producing the sixth flush, some seedlings were producing the seventh flush. The onset of senescence (marked by upward diagonal lines) did not vary considerably among treatments.

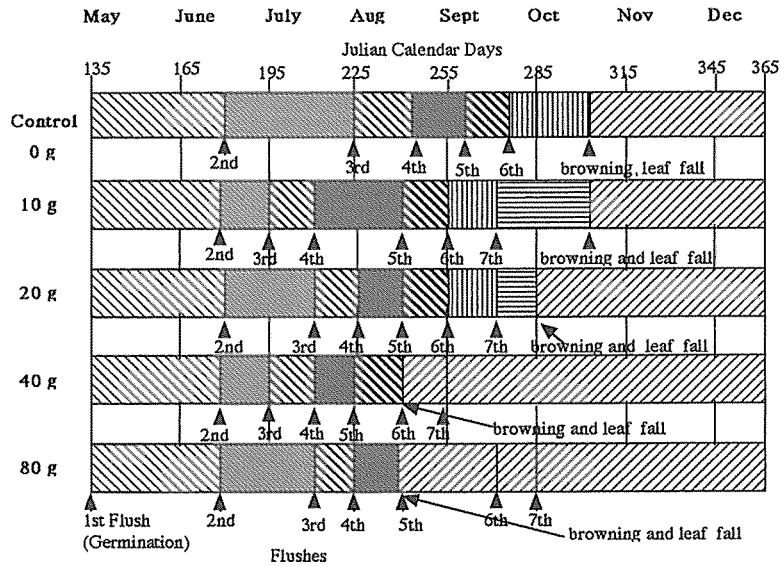

Fig. 6. The leaf production schedule of fertilized *Q. serrata* seedlings
Flushing occurred almost within the same period even though the number of flushes being produced at that particular time varied considerably. Browning and leaf fall (marked by upward diagonal lines) started as early as late August in seedlings with 40 g and 80 g of fertilizer. Even then the sixth and the seventh flushes were produced after senescence begun in earlier flushes.

seedling.

Under full sunlight, there was no significant difference between the mean LLS of both *Q. acutissima* and *Q. serrata* seedlings in the fertilizer treatment control and the fertilizer treatments (Fig. 4). In fertilized seedlings of both species, the timing of flush production was almost synchronous regardless of which number of flush was being produced under different treatments (Fig. 5 and 6). Since seedlings germinated almost at the same time (first week of May), and browning or leaf fall started almost simultaneously in most treatments, the mean LLS among fertilizer treatments did not vary considerably. Moreover, it was observed that under full sunlight leaf senescence in fertilized seedlings occurred from the first to the last flush not simultaneously but chronologically. Thus, there was no drastic difference in the LLS of the leaves that flushed early and those that flushed later within the same seedling.

Number of Leaves, Leaf Area and SLA

In *Q. acutissima* seedlings, the number of leaves declined with decreasing RLI (Table 1). The number of leaves produced by seedlings under 3% RLI was only a third of the number of leaves in the seedlings in the shading treatment control. In *Q. serrata* seedlings, some increase in the number of leaves was observed until 12% RLI. Beyond this, however, leaf number abruptly declined to half the number of the leaves of the seedlings in the shading treatment control.

Q. acutissima and *Q. serrata* seedlings grown under low RLI had a slightly higher mean leaf area than those grown under full sunlight, both in the fertilizer treatment control and the fertilizer treatments. It must be noted, however, that all seedlings in the shading treatment, including the treatment control, were fertilized at the rate of 10 g per seedling. The smaller total leaf area per seedling for those grown under low RLIs could be attributed to the less leaf production of seedlings under low RLIs.

An increase in the SLA was observed with a decrease in RLI. The mean SLA between treatments and the shading treatment control was statistically different ($p<0.01$). The two-fold increase in the amount of fertilizer led to an arithmetic progression in the number of leaves in both species (Table 2). The number of flushes also increased (Fig. 5 and 6). With germination counted as the first flush, *Q. acutissima* and *Q. serrata* had up to eight and seven flushes, respectively, for seedlings with additional fertilizer. Leaves of fertilized *Q. acutissima* seedlings had bigger leaf area than those not fertilized (Table 2). In *Q. serrata*, however, there was less variability in the seedlings' leaf area with fertilization. The increase in the total leaf area per seedling was due to the increase in the number of leaves in fertilized seedlings. The mean SLA of *Q.acutissima* and *Q. serrata* seedlings grown with increasing amounts of fertilizer did not differ significantly from the SLA of the seedlings in the treatment control and from each other.

Table 1. Number of Leaves, Leaf Area and Specific Leaf Area (SLA) of seedlings under Low RLI

Q. acutissima

RLI %	max. leaf no.	*ave. leaf area (cm^2)	total leaf area (cm^2)**	SLA
control (100%)	77ab	26.5	2041	149d
25	96a	26.4	2534	177cd
12	34bcd	29.5	1003	177cd
6	28cd	27.9	781	209b
3	24cd	25.6	614	253b

Q. serrata

RLI %	max. leaf no.	*ave. leaf area (cm^2)	total leaf area (cm^2)**	SLA
control (100%)	41bcd	9.5	390	152d
25	57bc	13.2	752	162cd
12	65ab	9.8	637	196c
6	17d	10.7	182	181c
3	22cd	13.8	304	206b

Note
* indicates significant difference ($p<0.05$) between species
a, b... indicates Duncan's Multiple Range Test characters
** total leaf area is estimated from the mean maximum leaf number and the mean leaf area per treatment.

Table 2. Number of Leaves, Leaf Area and Specific Leaf Area (SLA) of seedlings under fertilizer treatments

Q. acutissima

Amt. of Fertilizer (g)	*max. leaf no.	*ave. leaf area (cm^2)	total leaf area (cm^2)**	*SLA
control (0)	20	14.5c	290	136
10	50	21.5b	1075	125
20	65	23.9b	1554	161
40	135	23.2b	3132	146
80	145	27.4a	3973	136

Q. serrata

Amt. of Fertilizer (g)	*max. leaf no.	*ave. leaf area (cm^2)	total leaf area (cm^2)**	*SLA
control (0)	50	7.1de	355	165
10	116	8.6de	998	168
20	156	8.7de	1357	168
40	301	6.9e	2077	172
80	310	8.9d	2759	157

Note
* indicates significant difference ($p<0.05$) between species
a, b... indicates Duncan's Multiple Range Test characters
** total leaf area is estimated from the mean maximum leaf number and the mean leaf area per treatment.

Discussion

In both species, the mean LLS per seedling increased with decreasing RLI. This is in agreement with the findings reported by Reich and Walters (1992) on the work of Nilsen et al. (1987) and Schoettle (1990) which found increased leaf longevity with shading in the drought-deciduous shrub *Lotus scoparius*.

Referring to Kikuzawa's prediction (1995) that LLS will shorten as photosynthetic rates increased and with an increase in the maximum photosynthetic rate, it is thought that low RLI reduced the rate of photosynthesis enough to prolong LLS in both *Q. acutissima* and *Q. serrata*. A longer LLS under low RLI may have been necessary for the leaves to amortize the leaf construction cost under less photosynthetic production.

The LLS of the seedlings in both species, however, did not increase such that leaves could be retained throughout winter. Although changes in LLS was observed, the effect of low RLI was not enough to change both species' deciduous habit. In fact, even though leaf death started very late in *Q. serrata* at 3% RLI, it proceeded and was completed quickly.

Apparently, even though leaves were retained longer, there was a limit to the time in which LLS could be prolonged. Less production of leaves in seedlings under low RLI, even with adequate fertilization (10 g), seem to imply that leaves that can not pay back for its production cost were never produced at all.

Under full sunlight, on the other hand, increasing rate of fertilizer application did not shorten the mean LLS of *Q. acutissima* and *Q. serrata* seedlings. Reich and Walters (1992), reported that photosynthetic rate negatively correlated with leaf longevity. Furthermore, Kikuzawa's analysis (1995) predicted that as maximum photosynthetic rate increases, leaf life span shortens because the more favorable conditions are to photosynthesis, the sooner it is for the leaf to pay back for its construction cost, thus, eliminating the need for a long leaf life span. Furthermore, since leaf longevity is negatively correlated with leaf nitrogen content, (Reich and Walters, 1992), according to Kikuzawa (1995) the artificial addition of nitrogen should shorten leaf longevity. This, however, was not observed in the study.

Reich and Walters (1992) reported findings of other researchers that LLS either increased or decreased with increasing nutrient availability. Reich and Walters (1992) mentioned that the relationship between LLS and nutrient availability differed between natural stands and recently fertilized ones, where natural stands showed increased leaf retention, while fertility led to shorter LLS. Harper (1989) observed that adding fertilizer to a natural population of *Carex arenaria* growing in Anglesey dunes dramatically accelerated the rate at which the older leaf cohorts died. Fertilizer application in both *Q. acutissima* and *Q. serrata* seedlings led to more flushes. Although, it was initially believed that additional flushing will shorten the average LLS of

seedlings, it did not. This was probably because leaf production was not considerably prolonged by fertilizer application, instead the period between flushes shortened in seedlings growing with more fertilizer, allowing more flush production over the same period.

The production of more leaves, induced by the additional fertilizer, may have promoted self shading within the crown of the seedlings growing with additional fertilizer (40 g and 80 g). Self shading may have reduced photosynthetic rates in shaded leaves. Thus, similar to the prolonging effect of decreasing RLI on the LLS of seedlings under low RLI, the observed LLS of fertilized seedlings were longer than expected. Self shading may have offset any increase in photosynthetic rate from additional fertilization..

Comparatively, *Q. acutissima* seedlings had a longer LLS than *Q. serrata* seedlings under both full sunlight and shading (Fig. 1 and Fig. 4) treatments. Other aspects of phenology like leaf emergence pattern, leaf size and phyllotaxy may have influenced the LLS of the two species.

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ブナ科コナラ属のクヌギ（*Quercus acutissima*）とコナラ（*Quercus serrata*）の葉の寿命の庇陰と施肥に対する反応

ジョージ・バニュス・玉泉幸一郎・齋藤　明

要　　約

ブナ科コナラ属のクヌギ（*Quercus acutissima*）とコナラ（*Quercus serrata*）の葉の寿命の可塑性を明らかにするために庇陰処理と施肥処理を行い，展葉から落葉までの着葉期間の変動について研究した．庇陰処理においては両樹種ともに相対照度（RLI）が低いほど着葉期間が長く，葉の寿命（LLS）は長くなった．これに対し，施肥処理では，施肥処理間に差が認められなかった．従来の報告では，光合成速度とLISは反比例の関係にあり，葉の生産性が高いとLISは短くなるとされている．庇陰処理においては，RLIが高いほど光合成速度が高くなり生産性が維持されたためにLLSは短くなったと考えられた．一方，施肥処理においても，施肥により光合成速度が高まりLLSが短くなると予想されたが，その効果はなかった．その原因として，施肥により多量の葉が生産されたために相互庇陰を起こし，このことによる生産性の低下が施肥による増大分を相殺することになり，結果的にLLSが短くならなかったと推測された．樹種間でLLSを比較すると，ほとんどの処理においてコナラがクヌギよりも短くなった．このことから，コナラの方が単位葉面積の生産コストに対する生産性が高いことが予想された．

キーワード：肥料，庇陰処理，コナラ属，葉の寿命