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Original Article

Plasticity in the Branching Characteristics of four year old *Quercus acutissima* and *Q. serrata* Seedlings in Response to Low light Intensity and Additional Fertilizer*

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Abstract

The branching characteristics of *Q. acutissima* and *Q. serrata* seedlings grown for four years under shade and under full sunlight were compared to determine the plasticity of the crown architecture to low Relative Light Intensity (RLI) and additional inorganic fertilizer. The primary branching pattern reflected the phyllotaxy of both species, specifically, branches originated from lateral buds on every leaf on the rosette of 4 to 5 leaves at the end of a stem in *Q. serrata* and from any of the spiral of 4 to 12 leaves from a single stem in *Q. acutissima*. The bifurcation ratio was lower and more constant in *Q. serrata* (5.7), than in *Q. acutissima* (8.5). Based on previous findings that bifurcation ratio is inversely proportional to shade tolerance, a lower bifurcation ratio in *Q. serrata* may indicate greater shade tolerance. The difference in the degree of variability in the bifurcation ratio between the two species may be due to the constancy in the branching pattern of *Q. serrata* and the less deterministic branching in *Q. acutissima*. In *Q. serrata*, the rosette branching pattern and the number of branches produced from an existing growth module remained mostly the same under any condition. On the other hand, branches in *Q. acutissima* did not originate from every leaf on the stem, instead, branches were produced from any of these leaves, providing more variability in the degree and pattern of branching. In *Q. serrata* the mean branch length under shade was significantly ($p < 0.0001$) longer than those of seedlings grown under full sunlight with no fertilizer and with 10 g of fertilizer. Compared to seedlings grown under full sunlight with 10 g of fertilizer, the mean branch length of *Q. acutissima* seedlings was longer under Low RLI but was shorter under Very Low RLI. Although not statistically significant, Heavy Fertilizer and Low RLI treatments decreased the mean branch angle in *Q. serrata*, while Heavy Fertilizer treatment slightly increased the mean branch angle in *Q. acutissima*. The mean interbranch length of *Q. serrata* and *Q. acutissima* seedlings

* ジョージ・バニユス・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*) の分枝形態の低照度と施肥に対する反応

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grown under shade were longer than those of seedlings grown under full sunlight. However, this was significant ($p < .0001$) only between seedlings in the control (no fertilizer) and those under Low RLI. Variation in the branching characteristics such as the bifurcation ratio, the branch length, interbranch length observed in seedlings under shade and additional fertilizer were species specific. This may be due to the strong influence of leaf phyllotaxy on each species' branching pattern.

Key words : Branching pattern, Low Light Intensity, Fertilizer, *Quercus* seedlings, phyllotaxy

Introduction

Some of the most important physiological processes, like photosynthesis, respiration and transpiration, take place in the crown (Baldwin and Peterson, 1997). As such, crown architecture, which determines leaf display, distribution and canopy density closely links to productivity (Ceulemans *et al.*, 1990). Consequently, the branching pattern, defined here as the way in which new modules are added as the tree grows, directly affects plant physiological functions (Fisher, 1990) because branches form the skeleton of the crown.

Branching of modular organisms, like trees, follow certain rules of growth (Waller, 1986). These rules have been described mathematically and simulated even without reference to real organisms. In nature, however, patterns of branching are subject to constraints, thus limiting the range of the tree architectural designs possible. Aside from supporting the weight of leaves, branching must ensure that the position of leaves or photosynthetic organs maximizes production.

Genetically determined factors, like apical dominance, phyllotaxis, allocation, inflorescence, ageing and abscission, influence the way in which branching occurs. Kikuzawa (1996) wrote that phenology is linked to tree architecture because the difference in the timing of leaf emergence results to a difference in shoot growth.

Environmental factors like the availability of light, water and nutrients, or photoperiod and temperature also influence branching because they influence the amount and timing of growth. Citing the work of other authors, De Castro and Fetcher (1998) reported that radiation is usually the most important factor influencing the growth and development of plants when nutrients or water are not limiting.

This study investigated the changes in the branching pattern of the seedlings of two *Quercus* species under low light intensity and additional fertilization. Information on the plasticity in the branching pattern of species belonging to the same genus will provide insights on the different strategies employed by seedlings to adapt to life under forest canopies.

Methods

The crown architectures of *Q. acutissima* and *Q. serrata* were studied by comparing the branching pattern of seedlings grown for four years under shade and under full sunlight (Table 3.1). These seedlings were planted in cement pots (1 meter in height and diameter) in the Kyushu University Forestry Nursery, South Western Japan, March, 1994 and harvested April, 1998. There were two shading treatments, Low RLI and Very Low RLI treatments. Under the Low RLI treatment, seedlings were grown under the shade of a black nylon net cover to reduce light to 12~25% RLI. Under Very Low RLI treatment, seedlings were grown under a net cover which reduced light to 3~6% RLI. Fertilizer was applied at the prescribed rate of 10 g per seedling to induce adequate branch production under shade. Horticulture Cooperative IB chemically synthesized (10:10:10 NPK + minerals) fertilizer was applied once, before every growing season for three years to seedlings under shade.

For seedlings grown under full sunlight, the same inorganic fertilizer used in the shading treatment was applied with the same frequency to seedlings under two fertilizer treatments, Normal and Heavy Fertilizer treatments. Under the Normal Fertilizer treatment, fertilizer was applied at the same rate (10 g per seedling) provided seedlings under the shading treatments. Under the Heavy fertilizer treatment, seedlings were provided with 2 to 8 times more than the prescribed amount of fertilizer (20 g to 80 g per seedling). Excessive fertilizer application was done to promote prolific branch production to facilitate the observation of the branching patterns of each species. Seedlings grown with no fertilizer under full sunlight served as the overall control.

A total of 14 and 12 seedlings of *Q. acutissima* and *Q. serrata*, respectively, were

Table 1. Treatments and the corresponding rate of fertilizer application and Relative Light Intensity (RLI).

| Treatments | RLI (%) | Rate of Fertilizer (g/seedling) |
|------------------------------|----------|------------------------------------|
| Control | 100 | 0 |
| Normal Fertilizer (NFert) | 100 | 10 |
| Heavy Fertilizer (HFert) | 100 | 20 to 80 |
| Low RLI (LRLI) | 12 to 25 | 10 |
| Very Low RLI (VLRLI) | 3 to 6 | 10 |

harvested before the first flush of leaves emerged in April, 1998. The seedlings were between 40 to 260 cm in height and 4 to 37 mm in trunk base diameter at the time of harvest.

Branch morphometrics

For each seedling, the stoutest vertical axis was identified as the trunk. Branches arising from the trunk were labeled. The branch length, branch angle, base diameter and the height of each lateral branch from the ground were measured. Branch angle was defined as the angle of inclination of the branch from the trunk, with the vertical at 0 and horizontal at 90 degrees. The interbranch distance was computed as the distance between consecutive branches in the trunk. Since branching in *Q. serrata* occurred in whorls, following the rosette formation of leaves, the interwhorl distance was also determined.

Bifurcation ratio

Branching topology, which explain the arrangement and the connection between units of construction in the architectural scheme was evaluated through the bifurcation ratio. Although, more recent studies reported the limit in its usefulness (Fisher, 1990) the bifurcation ratio was used in this study, to examine the degree of branching from one order of branching to the next in the seedlings under different conditions. The Horton's system(1945) of numbering river drainage systems as it applied to branching was used to determine the bifurcation ratio (Kempf and Pickett, 1981, citing Whitney, 1976):

$$R_b = \frac{(\sum_1^t N_o) - N_t}{(\sum_1^t N_o) - N_1}$$

where N_o is the number of branches of order 0, N_t the number of branches of the highest order, t , and N_1 is the number of branches of the first order.

The bifurcation ratio is an indication of the number of branches originating from one branch. Whitney (1976) described two extremes in the branching continuum, symmetrical and asymmetrical branching. Branching which occurred with symmetrical dichotomy yielded a lower bifurcation ratio, while asymmetrical branching, characterized by a series of lateral branches or short shoots originating from a long shoot, yielded high bifurcation ratios. According to Whitney (1976), citing Leopold (1971), these two extremes represented the attempt to avoid leaf overlap (asymmetrical branching) and the necessity to minimize investment on non-photosynthetic structures (symmetrical branching). Whitney (1976) reported that bifurcation ratio is inversely correlated with the degree of shade tolerance.

Results

Branching and Leaf Phyllotaxy

Branches in the two *Quercus* species, as observed in most seed plants (Fisher, 1990), originated from lateral buds. Since these buds originated from existing leaves, the primary branching pattern of both species was determined by their leaf arrangement or phyllotaxy, the number of leaves per cohort and the timing of leaf emergence of each species. *Q. serrata* seedlings produced a shoot with a cohort of 5 to 7 leaves which emerged and unfolded simultaneously in every flush. This shoot represented one unit of growth or a module (Fig. 1).

One module in the *Q. serrata* seedling consisted of a stem, with 2 to 3 leaves alternately arranged on it and a rosette of 3 to 5 leaves at the end of this stem. In each succeeding flush, a new module on every leaf on the rosette, and an apical module is produced. Branching occurred as modules were added to almost every leaf on the whorl of existing modules, with the stems thickening to support new growth. Lateral modules flushed almost simultaneously with the apical shoot (or module) of the main axis, resembling sylleptic branching. There were more leaves on the stem of every module at the higher portions of the trunk in fertilized seedlings. Branches originating from leaves on the stem itself were also more numerous in this part of the crown.

In *Q. acutissima*, an apical or a lateral bud produced a cohort of 4 to 12 leaves on a single stem. The stem and the leaves represented one module (Fig. 2). Leaves unfolded a few at a time, taking almost the time for the next bud burst of the next flush for all the leaves in a cohort to unfold. Leaves in one cohort were arranged

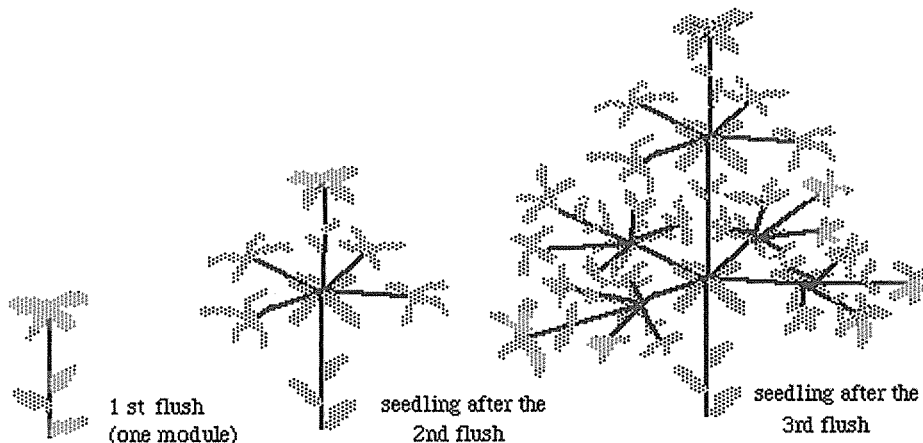


Fig. 1. The branching pattern of *Q. serrata* seedlings. A module is composed of a stem with 2 to 3 leaves on it and a rosette of 3 to 5 leaves on top. Every flush, an apical module and lateral modules are added to each leaf on the rosette of leaves at the end of the stem.

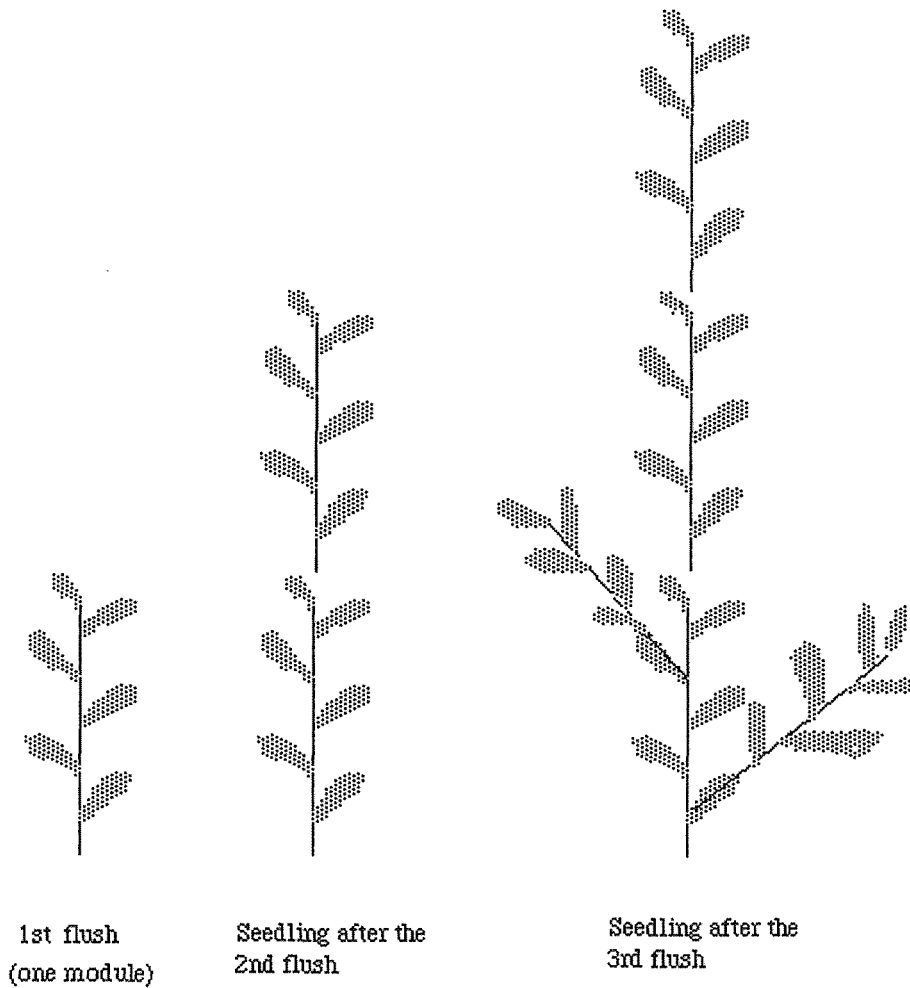


Fig. 2. The pattern of branching in *Q. acutissima* seedlings. A module is composed of a stem and 4 to 12 spirally arranged leaves on it. A module is added apically as flushes are produced. Lateral modules emerge from any of the leaves on existing modules.

spirally on a stem, the long axis of the module. The number of leaves in one module varied. New modules were initially added apically as flushes were produced. Later, lateral modules, which became branches, emerged from lateral buds on the spiral of leaves on the thickened stem which served as the parent axis. Delayed lateral branching in *Q. acutissima* resembled proleptic branching. It was easier to predict branching and the number of branches in *Q. serrata* seedlings because modules were always produced on the buds originating from almost every leaf on the rosette of leaves at the end of each stem of each module on every flush. In *Q. acutissima*, however, it was difficult to predict in which of the 4 to 12 leaves on the stem will new

Table 2. Bifurcation ratio, the highest branch order and the percentage of unbranched shoots from the main axis or the trunk of *Q. serrata* and *Q. acutissima* seedlings.

| | Bifurcation ratio | | Highest Branch Order | | % unbranched shoots | |
|---------|-------------------|----------------------|----------------------|----------------------|---------------------|----------------------|
| | <i>Q. serrata</i> | <i>Q. acutissima</i> | <i>Q. serrata</i> | <i>Q. acutissima</i> | <i>Q. serrata</i> | <i>Q. acutissima</i> |
| Control | 5.1 | 14.2 | 3 | 3 | 60 | 96 |
| N Fert | 5.8 | 8.1 | 4 | 4 | 45 | 53 |
| H Fert | 7.6 | 7.0 | 4 | 5 | 43 | 44 |
| LRLI | 4.9 | 4.0 | 4 | 5 | 39 | 22 |
| VLRLI | 5.3 | 9.3 | 3 | 4 | 70 | 85 |

branches arise.

Topology

Although there was an increase in the bifurcation ratio of *Q. serrata* under Heavy Fertilizer treatment to 7.6, the bifurcation ratio of 5 seemed constant to the species (Table 2). An increase in the number of branches originating also from the leaves on the stem and not just from the rosette of leaves in *Q. serrata* seedlings under the Heavy Fertilizer treatment may be related to the high bifurcation ratio in this treatment.

In *Q. acutissima*, however, the highest value (14, for the control) was twice the least bifurcation ratio (7, for Heavy Fertilizer treatment) under full sunlight. The bifurcation ratio (9.3) under Very Low RLI was highest among fertilized seedlings. The percentage of unbranched shoots emerging from the trunk of *Q. acutissima* seedlings in the control (96%) and under Very Low RLI (85%) accounted for the high bifurcation ratio under these conditions. A decrease in the bifurcation ratio with fertilizer application, especially under the Low RLI treatment, indicated an increase in the branching of *Q. acutissima* seedlings under these conditions.

Higher order branching was observed with the addition of fertilizer in both species. In *Q. serrata*, however, no increase in branching order was found in seedlings under Very Low RLI. Low RLI and Heavy Fertilizer treatments were conditions which promoted higher order branching in *Q. acutissima*.

Branch length

In *Q. serrata* the mean branch length under both shade treatments were significantly ($p < 0.0001$) longer than those of seedlings grown under full sunlight with no fertilizer and 10 g of fertilizer (Fig. 3). In *Q. acutissima*, the mean branch length of seedlings grown under Low RLI was longer (not significant) while the mean branch length under Very Low RLI treatments was shorter (significant, $p < .0005$) than the mean branch length of seedlings under Normal Fertilizer treatment.

In both species, the mean branch length of all fertilized seedlings, regardless of light condition, were longer than those of seedlings grown with no fertilizer

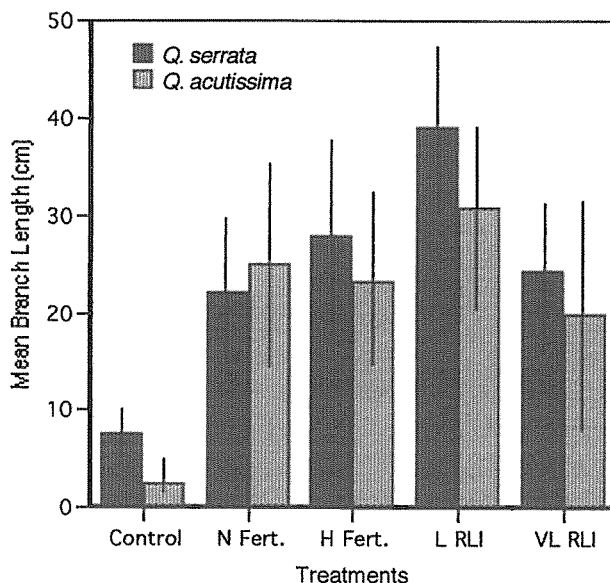


Fig. 3. The mean branch length of *Q. serrata* and *Q. acutissima* seedlings under the control and treatment groups.

($p < 0.0001$).

Branch angle

In *Q. serrata*, a significant increase ($p < 0.0001$) in the mean branch angle of seedlings grown under Very Low RLI compared to that of the control and a mean branch angle smaller (not significant) in the seedlings under Low RLI and Heavy Fertilizer treatments compared to seedlings under Normal Fertilizer treatment were obtained (Fig. 4). Fertilizer application, regardless of light condition, increased the branch angle in *Q. acutissima*, contrary to that observed in *Q. serrata*. However, the difference was significant ($p < 0.0001$) only between seedlings under the control and under the Heavy Fertilizer treatment for *Q. acutissima*.

Interbranch Length

The mean interbranch length of *Q. serrata* seedlings grown under shade were longer than those of seedlings grown under full sunlight. The difference between the interbranch length of seedlings in the control and those under Low RLI was significant ($p < 0.0001$). Even though the mean interwhorl length increased with fertilizer application regardless of light condition, the increase was not found significant except between the control and seedlings under the Heavy Fertilizer treatment ($p < 0.0001$).

The mean interbranch length of *Q. acutissima* seedlings grown under shade

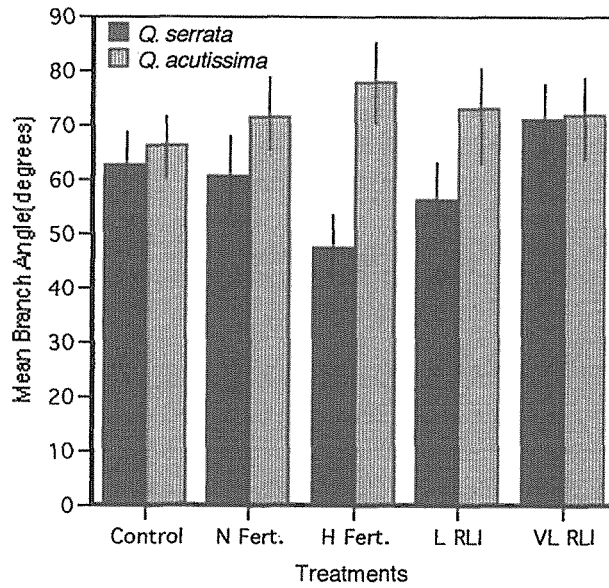


Fig. 4. The mean branch angle of *Q. serrata* and *Q. acutissima* seedlings in the control and under treatment groups.

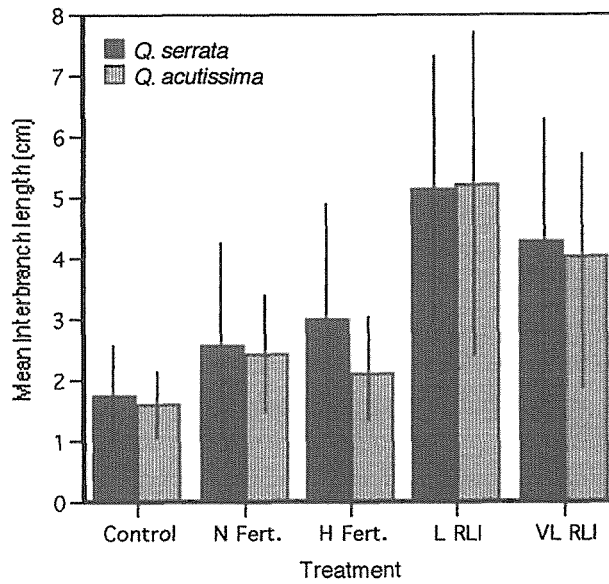


Fig. 5. The mean Interbranch length of *Q. serrata* and *Q. acutissima* seedlings in the control and treatment groups.

treatments were longer (Fig. 5) than those grown under full sunlight but was found significant only between seedlings in the control and seedlings under Low RLI ($p < .0001$), and Very Low RLI ($p < .05$). The mean interbranch length of *Q. acutissima* seedlings under Low RLI was also significantly higher than that of seedlings grown under full sunlight under Normal Fertilizer treatment ($p < .05$).

Discussion

Topology

Bifurcation ratio appeared more constant in *Q. serrata* than in *Q. acutissima*. In *Q. serrata*, the habit of branching in whorls and the number of branches per whorl did not seem affected by the treatments. This may have accounted for less variation in the bifurcation ratio in *Q. serrata*. A lower bifurcation ratio in *Q. serrata* may also indicate greater shade tolerance.

In *Q. acutissima*, the high percentage of unbranched shoots from the trunk of the seedlings under full sunlight with no fertilizer and those under Very Low RLI increased the value of the bifurcation ratio. Branching in *Q. acutissima* approached the topological extreme described by Whitney (1976) as asymmetrical branching or the thin form described by Ford and Ford (1990). Limited growth due to constraints in resource availability under no fertilizer and Very Low RLI treatments may explain the form of branching under these conditions. Under restrictive conditions, a narrow crown may have been most beneficial as Givnish (1990) reported that it is the most mechanically efficient design. A less deterministic pattern of branching in *Q. acutissima*, may also explain the higher and greater variability in the degree of branching among seedlings under different conditions.

Branch Length and Branch Angle

The importance of branch length and angle as determinants of model plant form has been reported (Kempf, 1981). In this study, an increase in the mean branch length under Low RLI in both species may indicate the seedlings' increased investment on lateral extension, one strategy which may enhance leaf display under limited light conditions (12~25% RLI). However, as light became more limiting at 3~6% RLI under Very Low RLI treatment, no further increase in branch length may have been possible.

Although branch length increased inversely with light to a certain degree, changes in the branch angle were not as considerable in both species. Related to this, Fisher (1990) reported that the mean branch angles measured from real *Terminalia* trees approached values optimal for certain functions. As such, artificially combining optimal values of both the branch length and angle produced unrealistic simulations. One reason given was the possible co-evolution of these two parameters such that only

an adjustment in either one is necessary to attain the optimum (Fisher, 1990). Furthermore, changes in these two parameters may have been specific to the species' overall strategy to maximize production within the constraints of genetically determined features like phyllotaxy.

For instance, a smaller mean branch angle in *Q. serrata* seedlings (not statistically significant) under Heavy Fertilizer treatment may have been a strategy to fill up even the space within the crown through more compact branching. Since branches were arranged in whorls in *Q. serrata*, pulling branches closer to each other may have been one way to accommodate as many more branches as can be produced with additional nutrients available. Moreso, compact branching was possible in *Q. serrata* because of its relatively smaller leaf size.

On the other hand, a wider mean branch angle in *Q. acutissima* seedlings under Heavy Fertilizer treatment may have been the species' way to enhance light capture through wider crown spread as more and bigger leaves and branches were produced. Since branches need not originate from fixed points and in fixed numbers within a module, branches were produced in locations where more lateral extension was possible in *Q. acutissima*. Thus, instead of packing a fixed number of new branches within the crown like *Q. serrata*, lateral extension through a wider branch angle may have been more beneficial to *Q. acutissima*.

Some degree of plasticity, based on the changes in the bifurcation ratio, an increase in branch length with Low RLI, and an increase in the interbranch length with shading was observed in both species. However, changes in these parameters were significant mostly between fertilized seedlings, grown with or without shading, and those with no fertilizer (control). Less variability was found between seedlings under shade and full sunlight when grown with the same rate of fertilizer (10 g per seedling). Thus, fertilizer application, rather than shading, brought more significant changes in the branching characteristics of seedlings of both species. Furthermore, variations in the parameters were species specific and may be explained by the strong influence of leaf phyllotaxy on each species' branching pattern.

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ブナ科コナラ属のクヌギ (*Quercus acutissima*) と
コナラ (*Quercus serrata*) の分枝形態の
低照度と施肥に対する反応

ジョージ・バニユス・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*) の分枝形態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、分枝形態の変化について研究した。両種に分枝形態は葉序の様式を反映しており、コナラは茎の先端にロゼット状に配置された葉の葉腋から車輪状に側枝を出し、クヌギは茎上に配置された葉の葉腋から側枝を螺旋状に出した。分枝比はコナラで5.7、クヌギで8.5の範囲で変化し、コナラの反応が小さかった。つまり、環境の変化に対しコナラは車輪状の発生様式を変化させず、しかも側枝数をほぼ一定に保つのに対し、クヌギは側枝の発生する葉腋数を変化させて対応した。これまでの報告例から分枝比の小さいコナラの方が耐陰性の強い種と考えられた。

平均枝長はコナラでは庇陰下で全光下よりも有意に長く、クヌギでは弱い庇陰では長く強い庇陰では短かった。枝の岐出角はコナラでは有意ではないが多施肥と弱い庇陰で小さくなり、クヌギでは多施肥でわずかながら大きくなった。枝間長は両樹種ともに全光よりも庇陰で長くなる傾向が認められた。これらの分岐係数、枝長および枝間長などの枝特性は種に特有であり、特に葉序の影響を強く受けていると考えられた。

キーワード：分枝様式、低照度、施肥、コナラ属、葉序