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Clone Structure and Architectural Development of an Understorey Shrud, *Viburnum furcatum* Blume ex Maxim.

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Abstract The clone structure and architectural development of *Viburnum furcatum* Blume ex Maxim. were examined by trunk analysis. Most clones had one or several trunks produced by recurrent sprouting at the trunk base. Through such recurrent sprouting, this species seems to increase its clone size and to persist on the forest floor for a longer time. Architectural development was not correlated with age but with size. Plants in a canopy gap had a larger, thicker crown than those on the shaded forest floor. The adaptive significance of the crown development of this species was discussed in relation to light environment.

Key words : *Viburnum furcatum,* understorey shrub, clone structure, architectural development, sprouting, canopy gap.

Viburnum furcatum Blume ex Maxim. is one of the most common understorey shrubs in Japanese beech forests (Sasaki, 1970). It produces an orthotropic trunk axis and plagiotropic lateral branches. Tiers of lateral branches spreading into a horizontal direction give the plant a distinctive appearance. Although this species occurs prevalently under the forest canopy, the larger, seed-bearing plants tend to aggregate in small canopy gaps (Hara, unpublished).

The architectural development of woody plants has been studied from the viewpoint of adaptive strategy and ecology after the works of Halle and Oldeman (1970), and Halle *et al.* (1978). The growth pattern and architectural development of woody plants have been studied for several trees (Wilson, 1966; Fisher, 1978; Fisher and Hibbs, 1982; White, 1984), a prostrate shrub (Remphrey *et al.,* 1983) and a liana (Penãlosa, 1983). Pickett and Kempf (1980) compared the branching and leaf display of some forest shrubs and understorey trees in relation to habitat. The growth patterns of some species of *Viburnum* were also studied by Donoghue (1981).

This paper deals with the clone structure and architectural development of *Viburnum furcatum.* Plants growing in both shaded and open habitats were examined.

Methods

Plants growing in a shaded habitat were sampled from an old growth stand dominated by *Quercus serrata* Murray and *Fagus crenata* Blume at Kawatabi, Miyagi Prefecture, Japan. The canopy layer of this forest reached over 15 m in height and was well closed. At this site, 19 clones of *Viburnum furcatum* were sampled in October 1981.

Plants growing in an open habitat were sampled from a small canopy gap in a mature beech forest on a southern slope of Mt. Kurikoma, Miyagi Pref., Japan. This gap had been made by a single canopy tree and its size was about 30 m^2. Five clones of *V. furcatum* were sampled in November 1983.

The plants were brought back to the laboratory, and the growth process of each plants was reconstructed mainly by examination of leaf scars. For aboveground trunks, the diameter of each trunk base and the amount of extension growth of trunks and branches were recorded for each year. If leaf scars did not persist clearly, the amount of extension growth for each year was determined by dissecting the stem transversely and examining the morphological change in the pith and wood near the node.

Results

1. Structure of clones

Samples from the closed stand contained clones of various size. Twelve out of 18 clones had one or two trunks (Fig. 1). Clones having more than three trunks were a few. Clones of larger rootstock usually possessed larger trunks. However, the number of trunks per clone had no correlation with rootstock size. Small clones often showed a

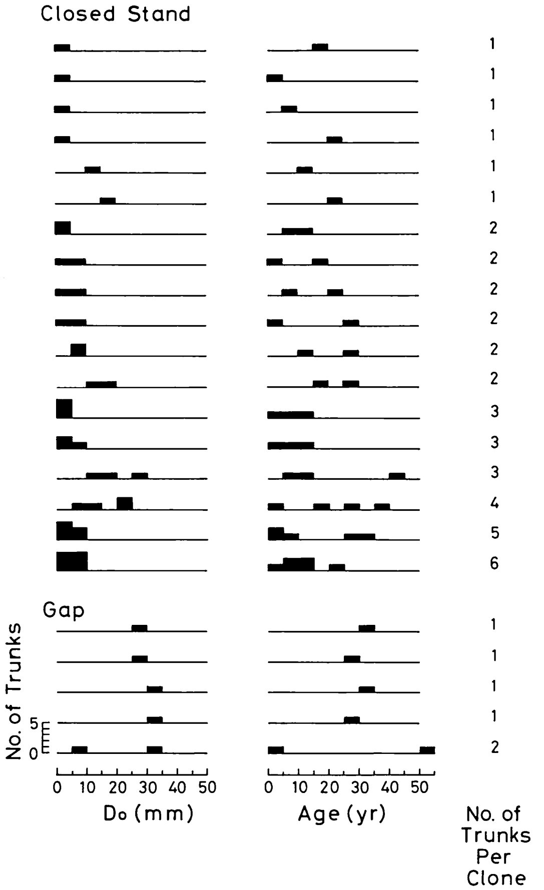

Fig. 1. Diameter class distributions and age class distributions of trunks of each clone. Upper 18 lines show the results for clones in the closed stand, and lower five lines those for clones in the gap. D_0 means diameter at trunk base.

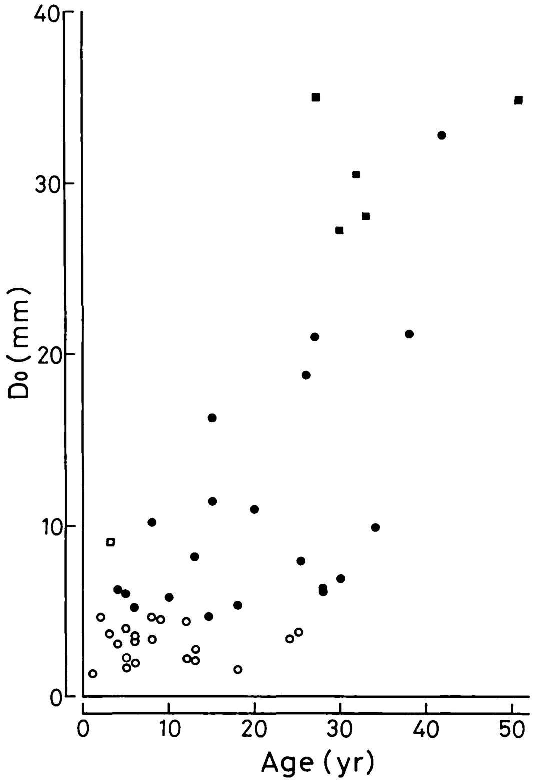

Fig. 3. Relationships between diameter at trunk base (D_0) and age of trunk. Circles indicate trunks in the closed stand and squares those in the gap. Clear symbols indicate plants in the trunk-building phase and solid symbols those in the branching phase. For distinction of the two phases, see text and Fig.5.

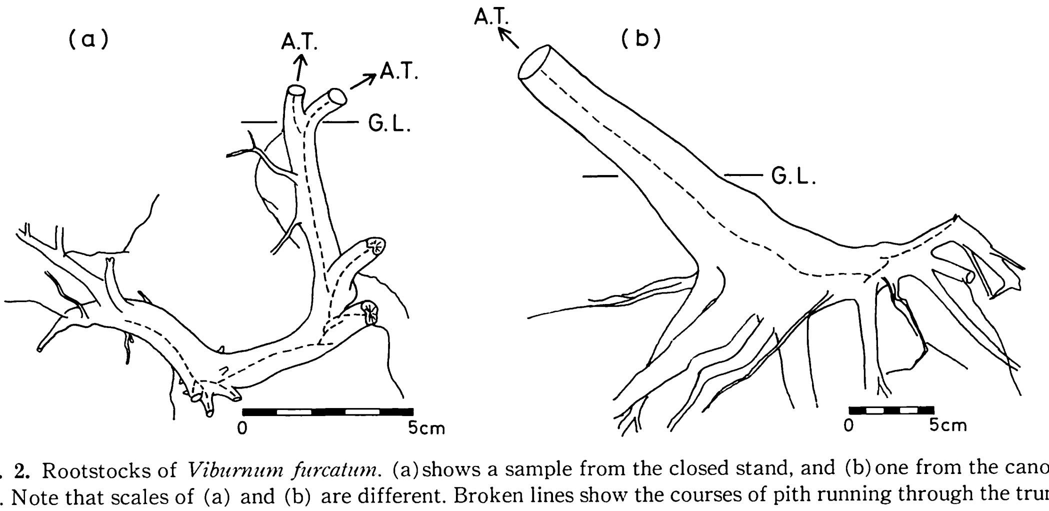

Fig. 2. Rootstocks of *Viburnum furcatum*. (a) shows a sample from the closed stand, and (b) one from the canopy gap. Note that scales of (a) and (b) are different. Broken lines show the courses of pith running through the trunk. G.L. means ground level, and A.T. means above ground trunk.

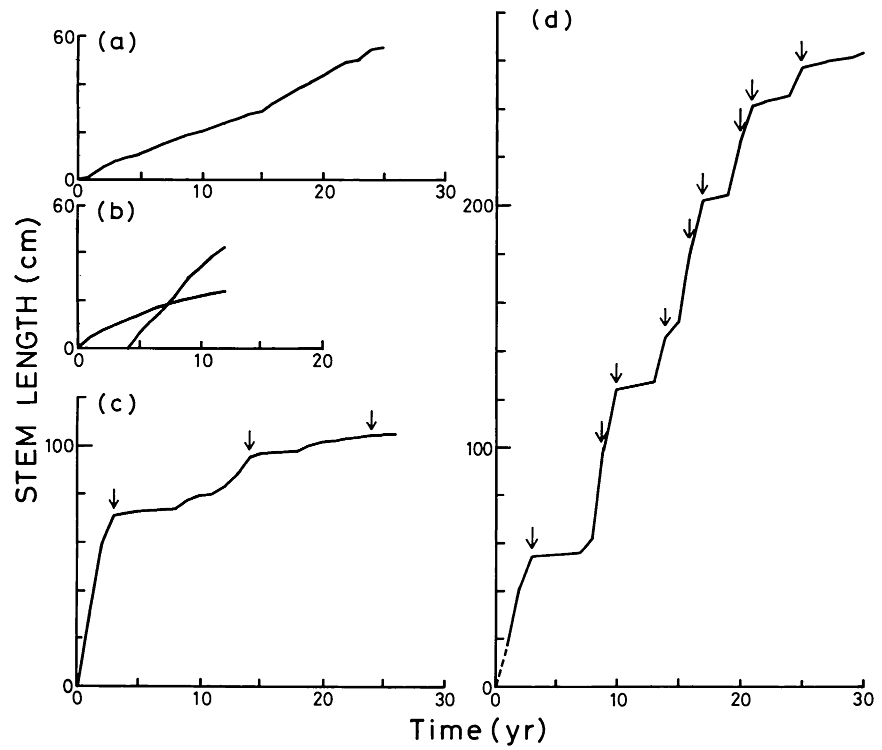

Fig. 4. Growth curves of trunk length reconstructed by trunk analysis. (a), (b) and (c) show results for clones in the closed stand, and (d) those for clones in the gap. Note that the clone shown in (b) has two trunks. Arrows in each figure show the times when lateral branches were produced on a trunk.

creeping form.

A new trunk was usually produced by sprouting at the base of an older one. Dissection of rootstocks revealed that such sprouting had been repeated during the process of clone development (Fig. 2a). Larger clones in a gap also showed signs of repeated sprouting in the past (Fig. 2b). Young seedlings were scarcely observed on the forest floor.

The ages of trunks in one clone showed that sprouting had occurred sporadically in one clone (Fig. 1). The ages of trunks in a gap were concentrated around 30 years, suggesting that the gap had been made at that time.

2. Radial and height growth of trunks

Figure 3 shows the relationship between trunk diameter and age. The correlation was particularly low for samples in the closed stand, indicating that the radial growth rate was variable.

The height growth rate was also variable. It was extremely low for small plants showing a creeping form (Fig. 4a), the mean annual increment being less than 2.5 cm per year.

Figure 4b shows the growth curves for a small clone having two trunks. The annual increments of the older trunk decreased as a function of age, whereas the sprouting new trunk showed mean annual increments twice as large as those of the older one. Also for many other clones, the initial height increment of the younger, new trunk exceeded that of the older one.

Stair-stepped curves were characteristic for large individuals which had branched several times (Fig. 4c). The initial height increment of a sprouting new trunk on a large clone often reached 40 cm per year or more. However, the branching of lateral shoots on a trunk markedly decreased the height increment for more than several years. After the height growth of a trunk had been restored, the next branching caused another decrease. This repeated braching result in the stair-stepped curve.

Larger plants in a gap also showed stair-ste-

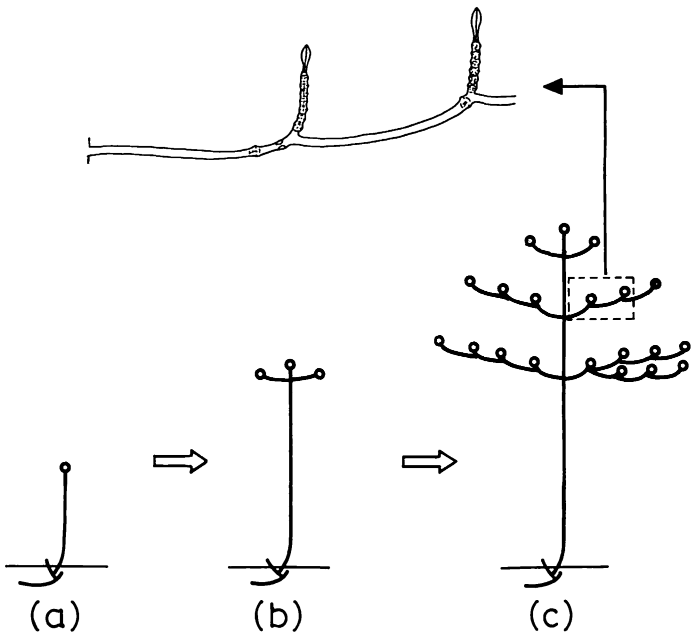

Fig. 5. Schematic representation of the growth of *Viburnum furcatum.*(a):plant in the trunk-building phase. (b): plant in the first year of the branching phase. Plants have one trunk and two tiers of lateral branches. (c):plant in the branching phase, with one trunk and six tiers.

pped curves (Fig. 4d). However, the period of small growth was shorter or sometimes absent in such an open habitat.

3. Production of tiers of lateral branches

In the first phase of growth, an aboveground trunk is unbranched (Fig. 5). After upward growth, the first lateral branching occurs and the first branches are produced. Here, we call the former phase "the trunk-building phase" and the latter phase "the branching phase" after White (1984). Large plants in the branching phase have several or more "tiers" of lateral branches.

The size and age of trunks were compared between the two phases. The size distributions of the two phases nearly overlapped, as shown in Fig. 3. The boundary between the two phases lies at a trunk base diameter of 5 mm and a height of 0.6 m. On the other hand, the age distributions of the two phases overlapped considerably.

The crown development after first branching differed between the closed stand and the gap. In the closed stand, the height growth of a trunk was usually suppressed by lateral branching for a longer time (Fig. 4c). Plants had only several tiers of lateral branches, which had been produced at longer intervals (Fig. 6). On the other hand, in the gap the tiers of lateral branches were produced at shorter intervals (Fig. 6). Plants in the gap had ten or more tiers, which means that plants had thicker crown. The average ages of tiers on one plant were younger than those in the closed stand.

4. Development of tiers of lateral branches

The lateral shoot elongates in a horizontal direction with a long internode length in the first year, but then changes into grow vertically with a short internode length after the second year (Fig. 5). Thereafter, it behaves like a short shoot. A tier of lateral branches is composed of such shoots which have been produced sympodially in successive years.

In addition to the small number of tiers, each tier was poorly developed in closed stands (Fig. 7). The number of shoots per tier nearly exceeded 10, although it increased in proportion to trunk diameter.

In contrast in the gap, the horizontal spreading of a single tier was more vigorous. A large num-

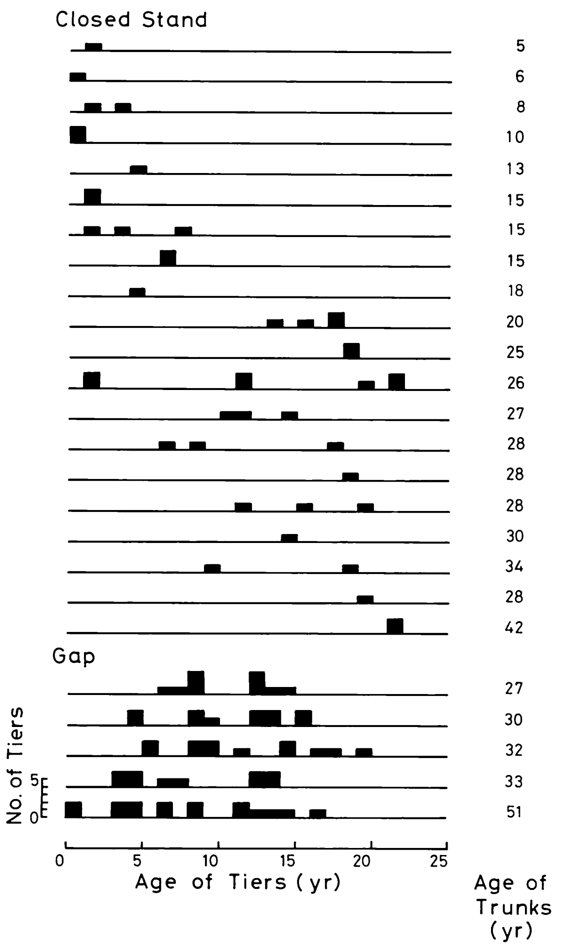

Fig. 6. Age class distributions of tiers for each trunk. Note that each line shows the result for a trunk but not a clone.

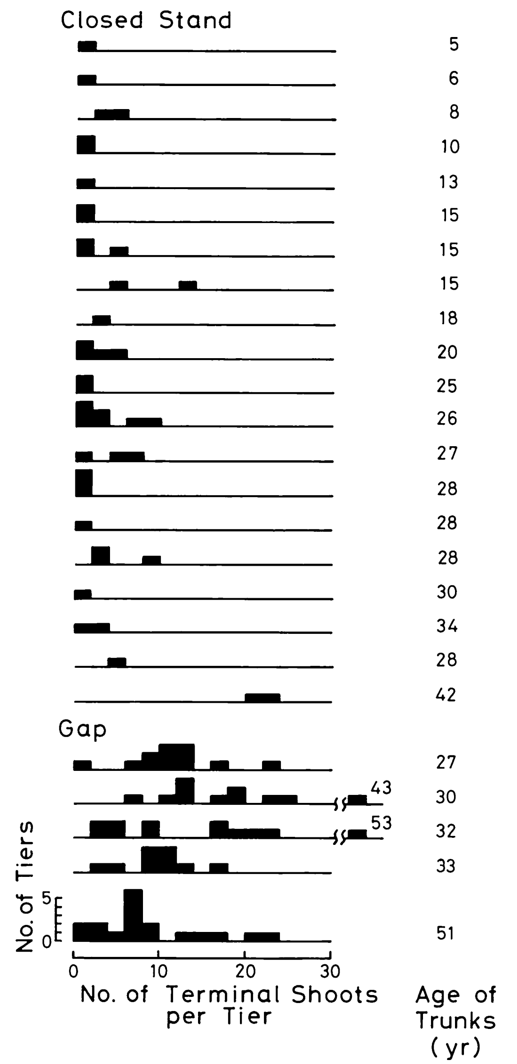

Fig. 7. Class distributions of the number of terminal shoots per tier.

ber of tiers had 10 or more shoots (Fig. 7), and the largest had 53. Consequently, the plants had a relatively large crown.

5. Number of terminal shoots

In the closed stand, the number of terminal shoots per plant increased linealy in proportion to the trunk base diameter (Fig. 8). This increase was mainly brought about by the proportional increase of "short shoots" (defined here as shoots with a current year increment of less than 1.0 cm). "Longer shoots" showed no clear correlation with the trunk diameter.

In the gap, plants had more terminal shoots than expected from the trend in the closed stand, suggesting that the crown form was not similar to that of the closed stand. The number of "longer shoots" was also larger in the gap, indicating more vigorous spreading of the crown. The distribution of these long shoots was confined to the upper half of the crown.

Discussion

1. Sprouting at trunk base

Vegetative reproduction such as sprouting or layering has two important roles in the population dynamics of shrubs; spatial spreading of a clone (Pelton, 1953; Remphery *et al.*, 1983) and survival and long persistence of a clone (Auclair and Cottam, 1971; Tappeiner, 1971; James, 1984). The relatively small number of trunks on one *V.*

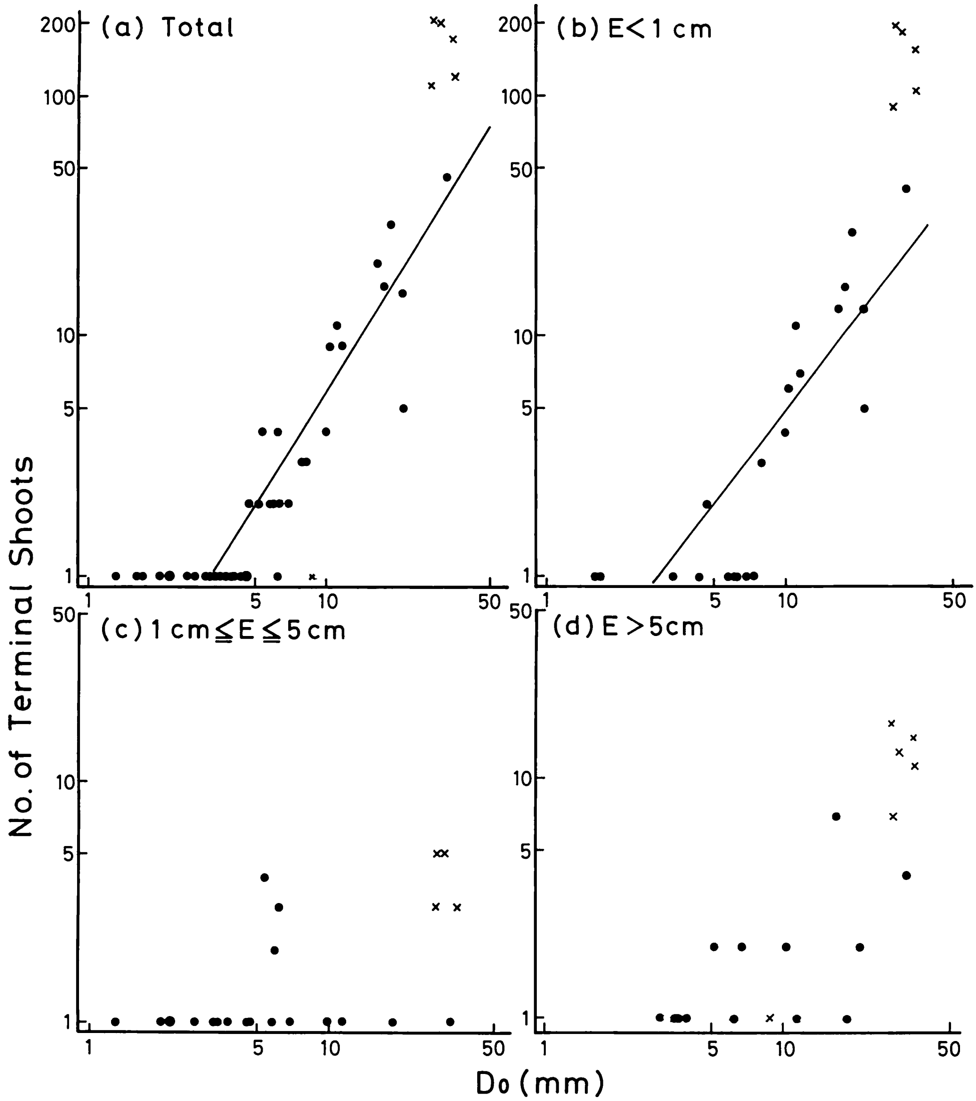

Fig. 8. Relationships between number of terminal shoots per ramet and diameter at the trunk base. (a): all shoots, (b): shoots showing current year growth of less than 1 cm, (c): shoots showing current year growth more than or eual to 1 cm but less than or equal to 5 cm, (d): shoots showing current year growth of more than 5 cm. Dots indicate plants in the closed stand and crosses indicate those in the gap. Regression lines in (a) and (b) were drawn based on data from the closed stand only.

furcatum clone suggests that the latter is more important in this species. Although the age of a trunk rarely exceeded 40 years, the true age of a single clone should be several times larger, because of the recurrent sprouting of the trunks. The lack of young seedlings on the forest floor suggests that establishment of new plants by seeds rarely occurred there.

The large variation of initial growth of trunks, seen in this species is characteristic for shrub species that sprout frequently (Yamanaka and Tamai, 1986). The initial growth of new, sprouting trunk is largely affected by the amount of reserve material in the rootstock, which is perhaps proportional to clone size. Moreover, a younger trunk often showed larger initial growth than an older one. This suggests a gradual increase of clone size through recurrent sprouting and the replacement of older trunks by new ones. This growth habit might be advantageous for clones in an environment such as a forest understorey, where rapid growth of an above-ground trunk is difficult because of the poor light conditions.

2. Architectural development

White (1984) studied the architectural development of *Aralia spinosa* L. and found two successive phases of growth with ramet age, i.e. the trunk-building phase and the branching phase. The branching phase is also a time of sexual maturity and thus fruit production.

In the present study, a similar pattern of architectural development was observed for *Viburnum furcatum*. However, in this species, the architectural development of a ramet was not correlated with age. The length of trunk-building phase was highly variable for each ramet, ranging from several years to more than 20 years. There are some plants which produce no flowers or fruit in the branching phase under shaded conditions (Hara, unpublished data). This difference is considered to be a reflection of the contrasting life history of two species; a pioneer tree growing in an open habitat (e.g. *A. spinosa*) and an understorey shrub growing on a shaded forest floor (e.g. *V. furcatum*).

According to the classification scheme of Halle *et al.* (1978), *V. furcatum* is included within Fagerlind's model. This model is characterized by a monopodial, orthotropic and episodically growing trunk, which produces tiers of modular branches, each branch being sympodial and plagiotropic by apposition. Trees belonging to this model don't become very large and seem to be restricted to the understorey of the forest (Halle *et al.,* 1978).

In terms of photosynthetic activity, the flat, monolayered crown is adaptive to shaded conditions, whereas in contrast, a tall, multilayered crown is adaptive to open conditions (Horn, 1971). From this viewpoint also, the crown development of *V. furcatum* in which horizontal growth occurs prior to vertical growth, is profitable in the shaded understorey of a forest. However, this species shows more rapid vertical growth and more frequent lateral branching in a gap. As a result, they can form larger, thicker crowns rapidly, which are more suitable in open conditions such as those in a canopy gap. This ability of *V. furcatum* to change its crown form according to the light environment seems to be important in enabling it to survive under a forest canopy, to become larger and to produce many seeds in canopy gaps.

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オオカメノキ(*Viburnum furcatum* Blume ex Maxim.)の株構造と樹形発達について

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樹幹解析によりオオカメノキ(*Viburnum furcatum* Blume ex Maxim.)の株構造と樹形発達について調べた．まず株の構造についてみると，1株あたりの地上部幹数は1本から数本のものが多かった．さらに地下部の解析の結果，幹基からの萌芽を繰り返しつつ成長してきた株が多いことがわかった．以上の事から，林床における株の成長と長期生残にとって，このような萌芽が重要であると考えられた．次に地上部の発達についてみると，まず，幹の基部直径が5㎜を越えた時点で，初めて側枝が分枝され，樹冠の側方成長が開始されることがわかった．また，閉鎖林冠下の個体では，樹高成長曲線は階段状となることが多かった．これは主幹上に側枝が分枝されるに伴い，その後，数年間以上，主幹の成長が抑えられることによる．一方，ギャップ内の個体では，このような主幹成長の遅滞する期間は短いか，ほとんど認められなかった．さらに，閉鎖林冠下の個体に比し，ギャップ内の個体は側枝の数が多く，より大きく厚い樹冠を持っていた．最後に，以上のような樹冠発達過程について，その適応的な意味を論じた．