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## Patterns of vegetative growth and reproduction in relation to branch orders: the plant as a spatially structured population

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**Abstract** The patterns of vegetative growth and reproduction in relation to orders of terminal branches were examined in the evergreen woody plant, *Eurya japonica*. The branch order number was determined centrifugally. The trunk was given order number 1; branches issuing directly from the trunk were order 2; branches growing on order 2 branches were order 3, and so on. The results of this study show the differential patterns of vegetative growth and reproduction in relation to the branch orders. Lower-order shoots of terminal branches grew more, but produced few flowers. On the other hand, for the higher-order terminal branches, shoot growth was very limited but flowering was more intense. The results show that a tree can be interpreted not as a mere population of equivalent modules but as a spatially structured population. Thus, it is essential to consider the position of modules within the branch system when patterns of vegetative growth and reproduction are examined. It is hypothesized that the difference in the opportunity cost in relation to the branch orders is the main cause of the spatial structure for patterns of vegetative growth and reproduction. Furthermore, for same-order terminal branches, current-year shoot elongation was independent of flowering intensity. These results suggest that this species only invests resources in reproduction that are surplus to its requirements for the functions associated with survival, such as growth and/or storage.

**Key words** Vegetative growth · Reproduction · Spatially structured population · Hierarchical allocation · Opportunity cost

### Introduction

Woody plants have highly developed aboveground structures that determine their light acquisition capabilities and the outcomes of competition for light. The aboveground structures of a tree can be considered as a population of shoots, since the shoot is a modular architectural unit.

Plants partition resources amongst various functions including growth and reproduction, and thus shoot growth may be affected by reproduction. Because the aboveground structures of a tree are determined by the placement of its shoots and shoot placement affects resource allocation and distribution, distribution of reproductive agents and this effect on vegetative growth may not be uniform within the crown or within an individual branch system.

The cost of reproduction at the shoot level has been examined by comparing the current-year elongation between reproductive and non-reproductive shoots (e.g., Tuomi et al. 1982; Delph 1990; Newell 1992; Obeso 1997). However, in these studies, the spatial distribution of reproduction within the crown was ignored, and shoots were selected at random within the crown. Maillette (1982), on the other hand, focused on the effect of crown position on the vertical distribution of flowering buds within the crown. However, she did not consider the cost of reproduction at the shoot level. Thus, little is known about the effects of reproduction on the development of aboveground structures of a tree.

The main purpose of this study was to describe the effects of reproduction on aboveground vegetative growth and the spatial variation in effects within the crown and within a branch. Specifically, patterns of vegetative growth and reproduction in relation to branch orders in *Eurya japonica* (Theaceae) are examined, and the significance of such patterns in maintaining a balance between vegetative growth and reproduction is noted. *E. japonica* is a dioecious and broad-leaved small evergreen tree. This species is capable of reproduction at relatively small sizes (1–2 m tall, personal observation) and ap-

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proaches heights of up to 10 m (Aiba and Kohyama 1996).

## Materials and methods

### Study species

*E. japonica* (Theaceae) is a dioecious and broad-leaved evergreen woody perennial that is widely distributed in Taiwan, China, Japan (Honshu, Shikoku, Kyushu, and Ryu Kyu Islands) and the southern parts of the Korean Peninsula (Oh et al. 1996). *E. japonica* bears plagiotropic branches (having planar leaf arrangements) on vertical stems. Plants flower between late March and early April. Flowers are borne in the leaf axils of shoots. The fruit ripens in autumn and is dispersed by birds. Plants grow from early May until autumn.

### Study area

The study was carried out in a natural forest dominated by *Chamaecyparis obtusa* Endl. at the Kamigamo Experimental Forest Station of Kyoto University (35°04' N, 135°43' E), about 12 km north of Kyoto. At this location, *E. japonica* is a common understory tree. Meteorological records were obtained from the Station. Mean annual precipitation and evaporation were 1,678 mm and 985 mm respectively.

### Sampling procedures

Within the experimental forest, a 20×20m plot was established. In early April 1997, the height and sex of each tree within the plot was recorded. Three male and five female trees, 1.5–2.5 m tall, were randomly selected. The order numbers of branch and twig were determined. The trunk was given order number 1; branches issuing directly from the trunk were order 2; branches growing on order 2 branches were order 3, and so on (Fig. 1). At the start of the study 40 male and 41 female second-order branch systems for the sampled trees were selected from the upper parts of the crown. Two-dimensional diagrams were drawn to describe the branching structure of each sampled second-order branch system. Because *E. japonica* bears plagiotropic branches (having planar leaf arrangements) on vertical stems, all shoots within a second-order branch system are on a nearly horizontal plane. The position of each leaf, flower, and fruit was also indicated on the diagram using symbols (Maillette 1982). At regular intervals (every month during the growth period and every 2 months during the rest of the year), additions and losses of the branching structure were also indicated on the diagrams. To analyze patterns of vegetative growth and reproduction in relation to the branch order, the order number (centrifugal ordering, not centripetal) of each terminal branch was determined from the branching structure diagrams. In this paper, the terminal branch was defined as each terminal, unbranched segment of a branch (Fig. 2), which is equivalent to the first-order branch in centripetal ordering systems, such as the Strahler system (see Borchert and Slade 1981). The lengths of current-year shoots produced on the terminal branches were measured. The number of flowers produced on the terminal branch was used as an estimate of flowering intensity.

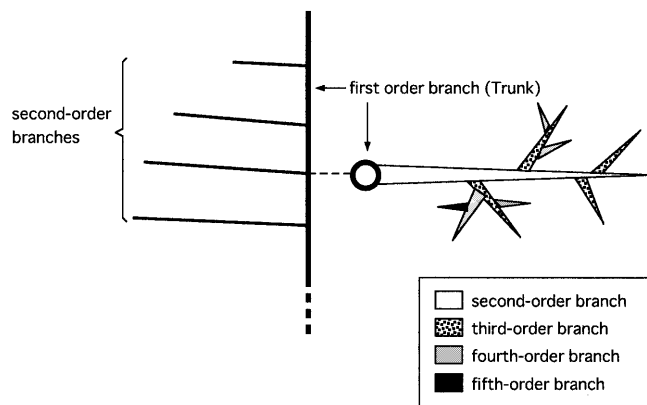
### Statistical analysis

Analysis of covariance (ANCOVA) was used to relate the gradients in current-year shoot length to gradients of flowering intensity (number of flowers) within each order of the branch (see Ackerly 1992; Sokal and Rohlf 1995). The ANCOVA model was constructed with the order of the branch as a factor, and flowering intensity as a covariate. The interaction between the order of the branch and flowering intensity was used to test for differences in slopes among orders of the branch. If current-year shoot length gave consistently

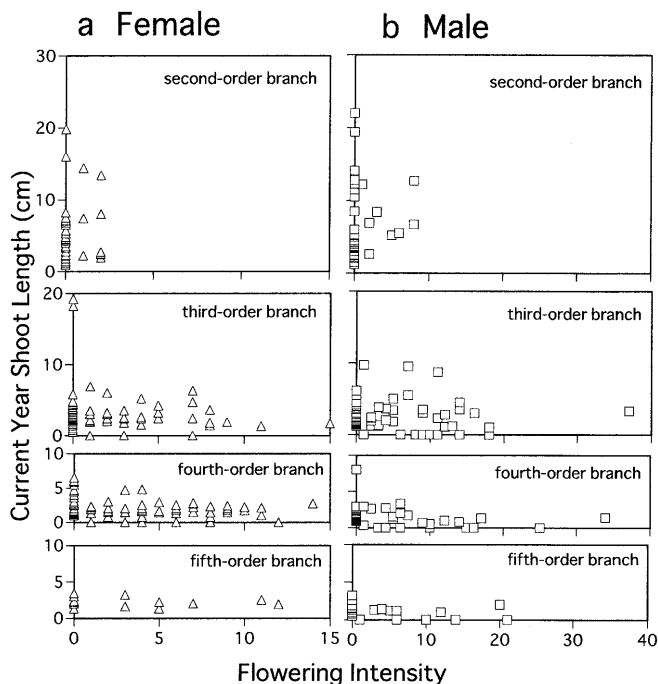
parallel gradients of flowering intensity, then there would be a significant covariate effect in the ANCOVAs. A significant interaction term, on the other hand, would indicate that the slopes of the relationships vary among orders of the branch. If there was no significance in the covariate analysis, then the differences between shoot length and flowering intensity for the different orders of branches were evaluated using analysis of variance (ANOVA).

## Results

Relationships between flowering intensity (number of flowers) and current year shoot length for both male and female plants and for each order of branch are shown in Fig. 2. The gradient of current-year shoot length in relation to flowering intensity was not significantly different



**Fig. 1** Diagrams of the branching structure of *Eurya japonica* and branch ordering in this study. *Left* Side view of the crown; *right* upper view of the two-order branch system



**Fig. 2** Relationship between current-year shoot length and flowering intensity, for **a** female and **b** male at terminal branch level

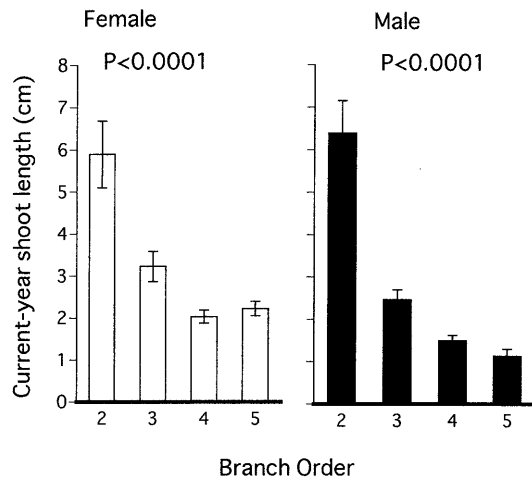
**Table 1** Results of analysis of covariance of shoot length with flowering intensity as a covariate and the four terminal branch orders as random factors. A significant interaction term between branch order and the covariate ('among slopes') indicates that the slope of the relationship between the shoot length and the covariate was different on different terminal branch orders. A significant covariate term indicates that there was a significant correlation between shoot length and the covariate

Source of variation	MS	F	P
<b>Female</b>			
Among	118.94		
Within	7.29		
Covariate	17.8	2.46	0.12
Deviation from common slope within groups	7.24		
Among slopes	1.31	0.18	0.77
Deviation in each group from its separate slope	7.33		
<b>Male</b>			
Among	230.71		
Within	7.01		
Covariate	8.82	1.26	0.26
Deviation from common slope within groups	7.00		
Among slopes	5.40	0.77	0.51
Deviation in each group from its separate slope	7.03		

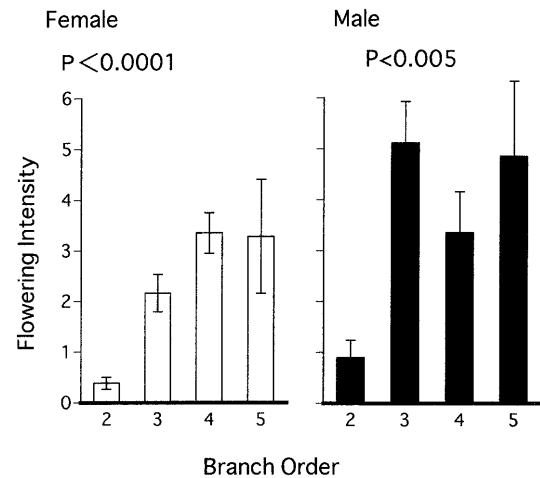
**Table 2** Flowering intensity for male and female, for the terminal segment of each order of branch

Order number of terminal branch	Male			Female			Significance of difference
	n	Mean	SE	n	Mean	SE	
2	40	0.90	0.34	41	0.38	0.12	n.s.
3	67	5.12	0.81	86	2.16	0.37	***
4	57	3.36	0.80	114	3.35	0.40	n.s.
5	13	4.86	1.47	17	3.29	1.13	n.s.

\*\*\* $P < 0.001$



**Fig. 3** Current-year shoot length in each order of terminal branches (mean±SE). The differences between the terminal branch orders were significant for females and males ( $P < 0.0001$  and  $P < 0.0001$ , respectively, ANOVA)



**Fig. 4** Flowering intensity in each order of terminal branches (mean±SE). The differences between the terminal branch orders were significant for females and males ( $P < 0.0001$  and  $P < 0.005$ , respectively, ANOVA)

between the second-, third-, fourth-, and fifth-order branches (see among slopes term of ANCOVA, Table 1). Furthermore, there was no significant flowering intensity covariate effect for current-year shoot length (Table 1), reflecting little correlation between flowering intensity and shoot length (Fig. 2), i.e., shoot length was independent of flowering intensity within the same-order branches for both sexes. For this reason, differences between current-year shoot length and flowering intensity between the orders of branches were examined separately

using ANOVA. The current-year shoot length was shorter for higher-order and tended to be longer for lower-order branches for both sexes (Fig. 3:  $MS = 118.94$ ,  $F = 16.31$  for females;  $MS = 230.71$ ,  $F = 32.90$  for males). In contrast to the shoot length patterns, flowering intensity for the second-order branches was weakest for both sexes (Fig. 4:  $MS = 83.49$ ,  $F = 8.22$  for females;  $MS = 159.32$ ,  $F = 4.44$  for males).

Flowering intensities for male and female plants, and for each order of branch, are shown in Table 2. For the

**Table 3** Total number of flowers, total number of fruits, and fruit set for the terminal segment of each order of branch

	Second order	Third order	Fourth order	Fifth order
Total number of flowers	15	156	331	46
Total number of fruits	10	139	300	43
Percent flowers setting fruit	67	89	91	93

branches of all orders, males had more flowers than females and for the third-order branches the difference in flowering intensity between male and female flowers is significant. For the second-order branches, males have 0.90 and females have 0.38 flowers. For the third-order terminal branches, males have 5.12 flowers, while females have only 2.17. For the fourth order, males have 3.36 flowers, while females have 3.35. For the fifth order, males and females have 4.86 and 3.29 flowers, respectively.

Fruit set for each order of terminal branch is shown in Table 3. About 90% of flowers set fruit for third-, fourth-, and fifth-order terminal branches. Only 67% of flowers set fruit for second-order terminal branches.

## Discussion

The results of this study show the differential patterns of vegetative growth and reproduction in relation to branch order. Lower-order shoots of branches grew up to six times more than shoots of the highest-order branches. In contrast, highest-order branches produced 4–6 times the flowers of second-order branches. Both sexes had similar patterns. In addition, fruit set for the second-order female branches was only 67%, while those of the other orders of branches were about 90%.

Maillette (1982) showed that low-order shoots of silver birch had more growth and bore more buds than high-order shoots, and concluded that it was because high-order shoots were located in the shaded parts of the crown. That is, she suggested that the availability of energy limited shoot elongation in silver birch. However, in *E. japonica*, flowering intensity is greater in higher-order branches (Fig. 4), although lower-order shoots had more growth than high-order shoots. Thus, the results for *E. japonica* contradict the hypothesis that only the availability of energy for each shoot limits vegetative growth, and suggests that resource allocation patterns are differentiated in relation to the positions within the branch system.

The efficiency of investment in reproduction is determined by the balance between the potential benefit to fitness to be gained from investment in reproduction and the costs of the investment. The latter includes lost opportunity costs (Chapin et al. 1990; Dill et al. 1990). The difference in the opportunity costs in relation to branch order and its predictability seems to be the main cause of the spatial patterns of vegetative growth and reproduction. An investment in reproduction rather than vegetative growth has a potential cost to the long-term health

and fitness of the plant. The reduction in vegetative growth during the reproductive phase causes a loss to the plant in terms of lost opportunities for light acquisition via photosynthesis. The second-order branches are the main axis of a branch system by definition and so the terminal growth of the second-order branches is of considerable importance for the expansion of a branch and, thus, the crown system. For example, a lateral bud on a second-order branch may expand to produce a third-order branch and bear lateral buds which, in turn, may contribute to fourth-order branches. Thus the opportunity cost of reproduction for the lower-order branches is relatively high when compared to higher-order branches. Consequently, there is a predictable gradient in the opportunity cost of reproduction as branch order increases. Two internal constraints in developing the branch system increase the predictability of the opportunity cost in relation to branch orders. First, the transition from one branch order to another is one-way, lower order to higher order (Harper 1980). Second, a bud cannot select its position. It is connected to its mother shoot and, thus, cannot move around like a mobile animal.

In spite of such internal constraints, the position within the crown and branch system has not been considered in studies of interactions between vegetative growth and reproduction: reproductive and non-reproductive branches have been sampled at random from the crown (e.g., Tuomi et al. 1982; Delph 1990; Newell 1992; Obeso 1997). Such sampling procedures would reflect the premise that a tree is a mere population of equivalent modules. However, the tree is a spatially structured population of modules for which there are hierarchical patterns of interaction. Thus, it is essential to consider the position of modules within the branch system when patterns of vegetative growth and reproduction are examined.

Also, in previous studies the reduced growth of the reproductive branches has been interpreted as a consequence of the competition for limited resources between vegetative and reproductive functions. However, this study suggests that reproduction in *E. japonica* may be preferentially allocated to or restricted to higher-order branches, perhaps due to the differences in opportunity costs in relation to branch orders. Considering the same-order branches, the length of current-year shoots is independent of flowering intensity for both sexes (Fig. 2). A similar hierarchical investment pattern was found in *Quercus robur* (Crawley 1985, 1997). For long-lived, polycarpic species like trees, it seems that survival is more important than reproduction in any given year. Whether the pattern observed is a result of a resource, a

plant growth substance, or combination-based control needs further elucidation.

When same-order terminal branches were compared between the sexes, the mean flowering intensities of males were greater than those of females for branches of all orders (although there was a significant difference for the third-order branches only; Table 1). Several authors have found similar patterns in dioecious plants (Bawa 1980; Bawa et al. 1982; Bullock 1982; Cavigelli et al. 1986; Allen 1986). Lower flowering intensity for females may be a means by which the resources allocated to reproduction are regulated to match the resources available.

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