Functional specialization of current shoots as a reproductive strategy in Japanese alder (*Alnus hirsuta* var. *sibirica*)

Shigeaki Hasegawa and Hiroshi Takeda

Abstract: Current shoots, which form the crown of a tree, are specialized in various functions such as crown expansion, reproduction, and assimilation. We examined the temporal and spatial distribution of reproductive shoots in *Alnus hirsuta* Turcz. var. *sibirica* (Fischer) C.K. Schn., assessed their direct and indirect costs of reproduction, and explained their distribution in the crown as the reproductive strategy of a current shoot population. The upper and lower limits to the lengths of current shoots for reproductive growth (flower formation) were 40 and 10 cm, respectively. Reproductive 1-year-old shoots produced fewer shoots in the following year than non-reproductive 1-year-old shoots. In current shoots longer than 40 cm, the increment of reproductive output in the following year by abandonment of reproduction surpassed the decrement of reproductive output in the current year by abandonment of reproduction. This may be one reason for the upper limit of reproductive shoot length. Thus, the current shoot population of *A. hirsuta* var. *sibirica* may be divided into three functionally specialized subpopulations: reproductive, maintenance, and exploratory. This specialization is considered to be a reproductive strategy to maximize their lifetime reproductive success.

Key words: current shoot population, reproductive ecology, functional specialization, cost of reproduction, Japanese alder.

Résumé : Les pousses courantes, qui forment la couronne de l'arbre, sont spécialisées dans diverses fonctions telles que l'expansion de la couronne, la reproduction et l'assimilation. Les auteurs ont examiné la distribution temporelle et spatiale des tiges reproductives chez l'*Alnus hirsuta* Turcz. var. *siberica* (Fischer) C.K. Schn., et ils en ont évalué les coûts directs et indirects de la reproduction, en expliquant leur distribution dans la couronne comme une stratégie de reproduction de la population courante de tiges. Les limites supérieures et inférieures aux longueurs des tiges pour la croissance reproductive (formation des fleurs) sont de 40 et 10 cm, respectivement. Les tiges reproductives âgées d'un an produisent moins de tiges l'année suivante que les tiges âgées d'un an non-reproductives. Chez les tiges courantes de plus de 40 cm, l'accroissement de l'allocation à la reproduction au cours de l'année suivante par abandon de la reproduction dépasse la diminution de l'allocation à la reproduction au cours de l'année courante par abandon de la reproduction. Ceci pourrait expliquer la limitation supérieure de la longueur des tiges reproductives. Ainsi, les populations de tiges courantes du *A. hirsuta* var. *siberica* peuvent être divisées en trois sous-populations fonctionnelles spécialisées: reproduction, maintient, et exploration. On considère cette spécialisation comme une stratégie de reproduction qui maximise la durée de vie de leur succès reproductif.

Mots clés : population des tiges courantes, écologie reproductive, spécialisation fonctionnelle, coût de la reproduction, aulne japonais.

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Introduction

A plant is a collection of subunitary parts, a metapopulation of modules (White 1979; Harper 1980). One can regard the crown of a tree as a population of current shoots, which consists of a young stem that grows from one leaf bud in one growing season and the leaves and buds that it carries

S. Hasegawa[1] **and H. Takeda.** Laboratory of Forest Ecology, Division of Environmental Science and Technology, Graduate School of Agriculture, Kyoto University, Oiwake-Cho Kitashirakawa Sakyo-Ku Kyoto City 606-8502 Japan.

[1]Corresponding author (e-mail: shasegaw@kais.kyoto-u.ac.jp).

(Mailette 1982; Room et al. 1994). Moreover, the current shoot is also considered to be a module in reproduction (Newell 1991; Tuomi et al. 1982). From this viewpoint, studying reproductive ecology of tall trees at the level of the current shoots might have advantages in subsampling of the very large individual (Cooper and McGraw 1988), in detecting cost of reproduction (Obeso 1997), and in demographic analysis of reproduction (Lovett Doust and Eaton 1982).

For trees, local resources are of great importance in determining the probability of reproduction within a crown (Lovett Doust and Lovett Doust 1988; Seki 1994). At the level of the shoot module there is a minimum threshold in shoot size for reproduction (Cooper and McGraw 1988; Obeso 1997), a positive correlation between shoot size and reproductive output (Cooper and McGraw 1988; Tuomi et al. 1982), and negative effects of reproduction on current or future vegeta-

Fig. 1. Current and 1-year-old shoots of *Alnus hirsuta* var. *sibirica*. (*a*) Flowering current shoot (August). LB, leaf bud; LLB, latest leaf bud; FFB, female flower buds; MFB, male flower buds; SL, shoot length; FSL, flower-supportive shoot length. (*b*) One-year-old shoot (August). CS, current shoots; FR, fruit.
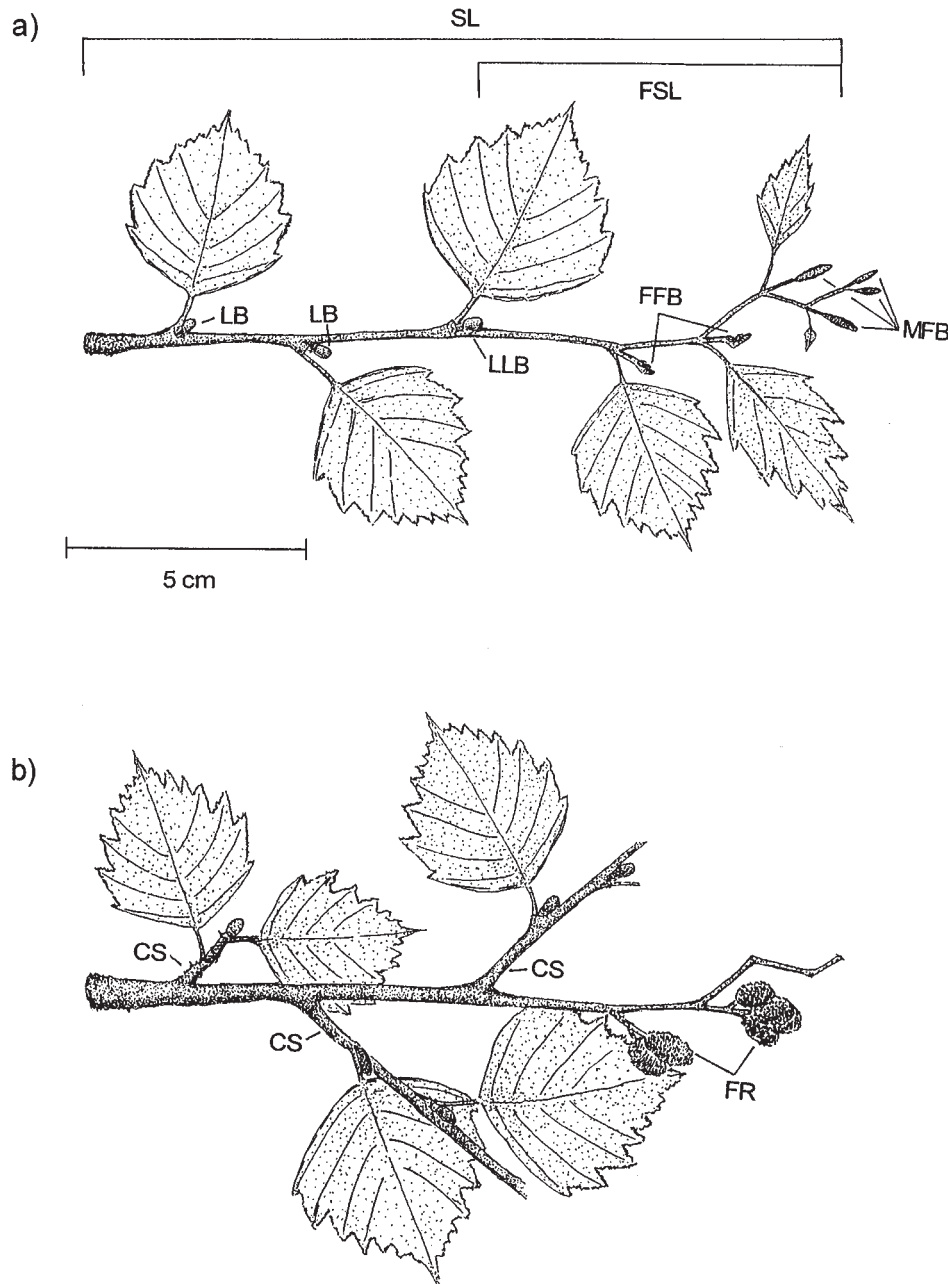

tive growth (Hoffmann and Alliende 1984; Newell 1991; Karlsson et al. 1996). Thus, shoots are semi-autonomous in allocating resources to reproduction. Considering the reproductive success of an individual tree, not all the current shoots in the crown should produce reproductive organs. It is possible that each current shoot in a crown is specialized in some function, such as crown expansion, reproduction, or assimilation, in accordance with crown heterogeneity or more specifically crown requirements. If so, the type of specialization may affect shoot architecture, growth, and reproductive output. From the aspect of evolutionary ecology, a plant's activities must have been selected to maximize its

lifetime reproductive success (Pianka 1983). Thus, current shoots that make up the crown of a tree are expected to be individually specialized in some function so as to increase lifetime fecundity of the individual tree.

Here we propose the hypothesis that each of the current shoots that compose the crown of a tree is specialized in some function to increase the total reproductive output of the individual tree. The specific objectives of this study are (*i*) to measure the seasonal changes of weight of reproductive organs in relation to the phenological patterns of shoot and leaf development, (*ii*) to examine the spatial distribution of reproductive shoots within a crown, (*iii*) to assess the direct

Fig. 2. Seasonal changes in the masses of male flower buds, female flower buds, leaves, and stem per current shoot. Numbers of current shoots are as follows: June, 1101; July, 1005; August, 709; October, 433; and November, 631. Numbers of flowering current shoots are as follows: June, 0; July, 0; August, 2; October, 6; and November, 9. Error bars are SE.
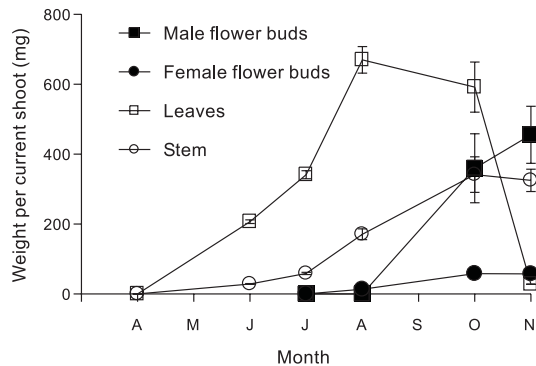
Fig. 3. Seasonal changes in the fruit mass per 1-year-old shoots and stem mass of 1-year-old shoots. Numbers of 1-year-old shoots are as follows: April, 539; June, 212; July, 192; August, 252; October, 141; and November, 175. Numbers of fruiting 1-year-old shoots are as follows: April, 69; June, 25; July, 39; August, 71; October, 14; and November, 12. Error bars are SE.
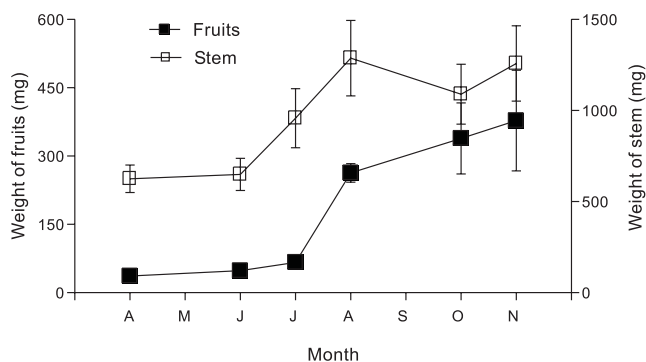
Fig. 4. Leaf display index (LDI; leaf area (cm^2)/shoot length (cm)) of current shoots as a function of current shoot length.
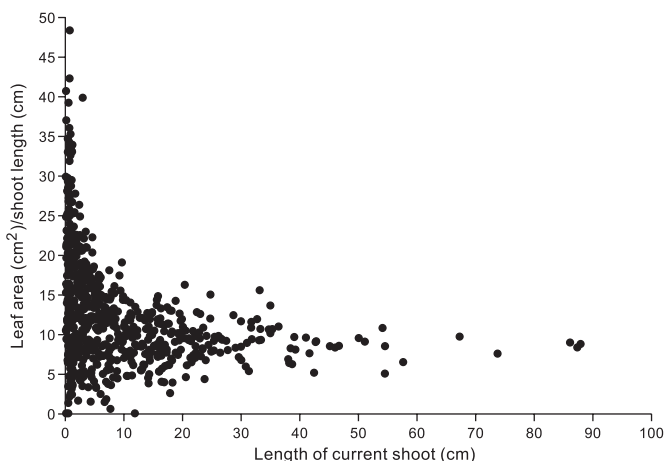
and indirect costs of reproduction at the level of current shoots, and finally (*iv*) to explain the distribution of flowering shoots as the reproductive strategy of the current shoot population.

Materials and methods

Species studied

Alnus hirsuta Turcz. var. *sibirica* (Fischer) C.K. Schn. is a deciduous early successional tree species that is widely distributed in the northern districts and highlands of Japan. Since we were interested in investigating competition between growth and reproduction, we chose *A. hirsuta* var. *sibirica*, as it grows quickly and produces numerous seeds. Bud break begins in late April, and shoot elongation continues until July or August; some vigorous current shoots that are longer than about 60 cm, show a second shoot flush, which occurs in June or July from the leaf bud produced in the current year. In this study, we considered the second flush as a part of the current shoot, and we added the length of first- and second-flush shoots to obtain total shoot length. The length of current shoots ranged from approximately 0.1 to 150 cm. Male and female flower buds develop from early August to November. Flowering shoots normally have both male and female flower buds at their terminal end (Fig. 1). Flower buds overwinter and flowering occurs in mid-April of the subsequent year. Male flowers fall soon after maturation. Fertilized female flowers mature to fruit on 1-year-old shoots. Seeds are dispersed by wind in November.

Study site and sampling methods

The study was conducted in a 30×40 m plot within a secondary forest (approximately 1110 m altitude) at Mount Norikura in the eastern part of Takayama City, Gifu Prefecture, central Japan. *Alnus hirsuta* var. *sibirica* is the only species in the canopy layer in this forest where the canopy trees were about 15 m in height. Diameter at breast height (DBH) of all trees (DBH larger than 5 cm) was measured in November 1995, 1996, and 1997. The total number of trees was 130, 122, 116 in November 1995, 1996, and 1997, respectively. We classified the trees into five size classes according to the 20th, 40th, 60th, and 80th percentile of DBH.

Current and 1-year-old shoots were sampled from one tree selected from each size class in April, June, July, August, October, and November 1995; November 1996; and in November 1997. We divided the crown of the sample tree into three layers equal in crown depth: upper, middle and lower. One branch issuing directly from the trunk was randomly obtained from each layer of the sample tree and top part of the branch (1 m from the top) was used as one sample. All the current and 1-year-old shoots were detached from the sampled branch. We obtained 50–400 current shoots (114 in upper, 256 in middle, 267 in lower layer in 1995; 156 in upper, 354 in middle, 430 in lower layer in 1996; 58 in upper, 91 in middle, 228 in lower layer in 1997) and about 6–100 1-year-old shoots (11 in upper, 62 in middle, 102 in lower layer in 1995; 17 in upper, 84 in middle, 93 in lower layer in 1996; 6 in upper, 27 in middle, 128 in lower layer in 1997). They were dried at 40°C for 5 days soon after they were detached. The lengths of current and 1-year-old shoots were measured to the nearest 1 mm. Since flowering current shoots have flower buds at their terminal ends (Fig. 1), the terminal part of flowering shoots (from the latest leaf bud to the terminal end of shoot) does not function as the supportive tissue of future shoot systems. The length of the node from the latest leaf bud to the terminal end (Fig. 1) is termed the "flower-supportive shoot length." For all flowering shoots, flower-supportive shoot length was also measured to the nearest 1 mm. The number of buds on the current shoot was counted for the samples in November 1995, 1996, and 1997. Leaf area was measured for the leaves of current shoots in 1995. The number of male and female flowers per current shoot and the number of fruits per 1-year-old shoot were counted for the samples in November 1995, 1996, and 1997. The total weights of shoot stem, leaves, male and female flowers, and fruits were measured to the nearest 1 mg for all current and 1-year-old shoots in each shoot sample.

Table 1. Proportion of current shoots bearing no leaf buds as a function of shoot length in 1995 and 1997.

	Shoot length (cm)				
	0–5.0	5.1–10.0	10.1–15.0	15.1–20.0	>20
1995					
No. of shoots bearing no leaf buds	107	18	7	7	5
No. of shoots	292	89	76	73	101
Percentage of shoots bearing no leaf buds	36.6	20.2	9.2	9.6	5
1997					
No. of shoots bearing no leaf buds	175	14	4	2	0
No. of shoots	103	34	22	29	71
Percentage of shoots bearing no leaf buds	62.9	29.2	15.3	6.45	0

Note: The proportion of the current shoots bearing no leaf buds was significantly different among size classes with χ^2 test (1995: $\chi^2 = 42.34$, $P < 0.001$; 1997: $\chi^2 = 127.5$, $P < 0.001$).

Table 2. Distribution of flowering shoots within a crown.

Layer of crown	No. of flowering shoots	No. of non-flowering shoots	Percentage of flowering shoots
1995			
Upper	5	109	4.4
Middle	4	252	1.6
Lower	0	267	0
1996			
Upper	63	93	40.4
Middle	90	264	25.4
Lower	53	377	12.3
1997			
Upper	16	42	27.6
Middle	18	73	19.8
Lower	14	214	6.1

Note: The proportion of flowering shoots was significantly different among the three layers with χ^2 test (1995: $\chi^2 = 11.1$, $P < 0.001$; 1996: $\chi^2 = 56.8$, $P < 0.001$; 1997: $\chi^2 = 26.0$, $P < 0.001$).

Statistical analysis

The morphological traits of current shoots are expressed by the leaf display index (LDI), which is calculated by dividing leaf area on current shoots (cm^2) by shoot length (cm) (Canham 1988). The LDI of current shoots was calculated for each of the shoot samples of August 1995.

A χ^2 test was conducted to compare the frequency of the current shoots bearing no leaf buds among size classes and to compare the ratio of the number of flowering shoots to the number of non-flowering shoots among the following three shoot size classes: shorter than 10 cm (<10), between 10 cm and 40 cm (10–40), and longer than 40 cm (>40).

Nonlinear regression was conducted for the frequency distribution of the length of flowering shoots obtained in November 1996, when a large number of flowering shoots was obtained. Normal distribution ($y = a(\delta\sqrt{2\pi})^{-1} \exp(-(x - \mu)^2/2\delta^2$, where a, μ, and δ are parameters) was applied for the relationships between relative frequency of current shoots and shoot length as regression curve. Parameters were determined by the Levenberg–Marquardt method using SPSS version 7.5.1J for Windows (SPSS, Chicago, Ill.)

Two types of reproductive cost were assessed: direct and indirect (delayed) costs. Direct costs are represented by materials and metabolic energy allocated to produce reproductive organs. Indirect costs are represented by the negative effects of reproductive events on future growth, reproduction, and survivorship (Reekie and Bazzaz 1987; Snow and Whigham 1989; Willson 1983). Direct cost of reproduction was assessed by biomass allocation to reproductive organs per current shoot and per 1-year-old shoot. Indirect cost of reproduction was assessed by the reduction in the number of shoots and shoot growth in the following year. We compared the

number and mean length of the current shoots developed on the fruiting 1-year-old shoots with those of the shoots from non-fruiting 1-year-old shoots, in November 1995 and 1997. A comparison was made by ANCOVA using SPSS with 1-year-old shoot length as the covariant.

We estimated the decrease in reproductive output in the current year and the increase in reproductive output in the following year, when current shoots abandon reproduction. We used the samples from November 1996 that had enough flowering shoots to analyze. We used mass of female flowers as an index of reproductive output. The decrease in reproductive output in the current year was estimated by the regression line between the length of current shoot and the mass of female flowers ($y = 2.2x + 9.0$, $r^2 = 0.17$, $n = 206$, $P < 0.05$). The increase in reproductive output in the following year, RO_{Inc}, was estimated as follows:

$$[1] \qquad RO_{Inc} = RO_{Fr} - RO_{Nonfr}$$

where RO_{Fr} is reproductive output of the current shoots developed on the fruiting 1-year-old shoot and RO_{Nonfr} is reproductive output of the current shoots developed on the non-fruiting 1-year-old shoot. Reproductive output of the current shoots developed on the 1-year-old shoot in the following year was estimated as follows:

$$[2] \qquad RO = NS \times FQ \times MF$$

where NS is the number of the current shoots developed on the 1-year-old shoot, FQ is the frequency of reproductive current shoots, and MF is the average mass of female flowers per reproductive current shoot. NS was estimated by the regression lines between the number of shoots and the length of non-fruiting 1-year-old shoot ($y = 0.14x + 1.1$, $r^2 = 0.59$, $n = 139$, $P < 0.001$). In the fruit-

Fig. 5. Relative frequency distribution of the length of flowering and non-flowering current shoots in the upper, middle, and lower layers of the crown in (*a*) 1995, (*b*) 1996, and (*c*) 1997. Shaded bars, flowering shoots; open bars, non-flowering shoots.
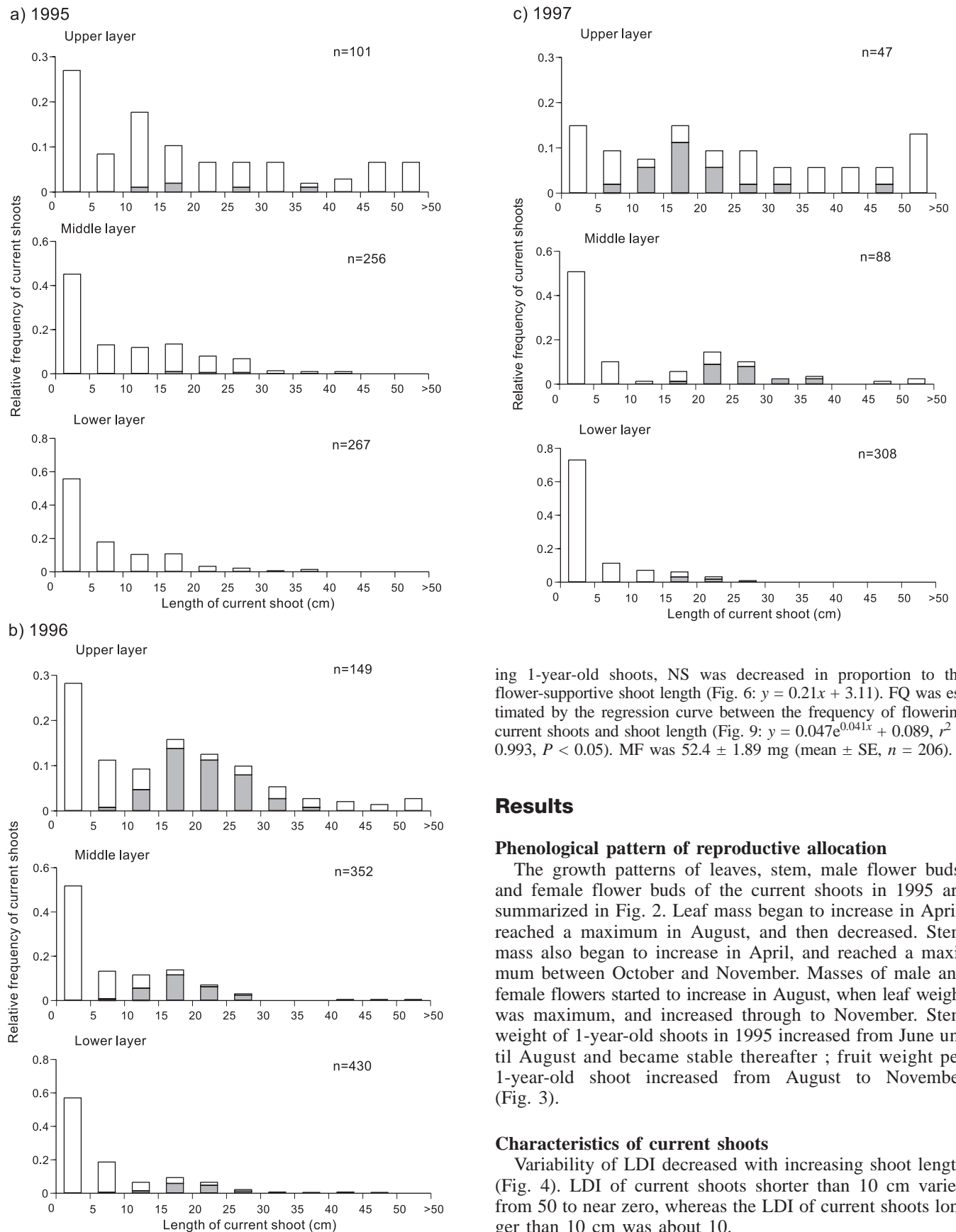
ing 1-year-old shoots, NS was decreased in proportion to the flower-supportive shoot length (Fig. 6: $y = 0.21x + 3.11$). FQ was estimated by the regression curve between the frequency of flowering current shoots and shoot length (Fig. 9: $y = 0.047e^{0.041x} + 0.089$, $r^2 = 0.993$, $P < 0.05$). MF was 52.4 ± 1.89 mg (mean $\pm$ SE, $n = 206$).

Results

Phenological pattern of reproductive allocation

The growth patterns of leaves, stem, male flower buds, and female flower buds of the current shoots in 1995 are summarized in Fig. 2. Leaf mass began to increase in April, reached a maximum in August, and then decreased. Stem mass also began to increase in April, and reached a maximum between October and November. Masses of male and female flowers started to increase in August, when leaf weight was maximum, and increased through to November. Stem weight of 1-year-old shoots in 1995 increased from June until August and became stable thereafter ; fruit weight per 1-year-old shoot increased from August to November (Fig. 3).

Characteristics of current shoots

Variability of LDI decreased with increasing shoot length (Fig. 4). LDI of current shoots shorter than 10 cm varied from 50 to near zero, whereas the LDI of current shoots longer than 10 cm was about 10.

Table 3. Number of flowering and non-flowering shoots and percentage of flowering shoots, as a function of shoot length in 1995, 1996, and 1997.

	Shoot length (cm)		
	0–10.0	10.1–40.0	>40
1995			
No. of flowering shoots	0	9	0
No. of non-flowering shoots	381	222	19
Percentage of flowering shoots	0	3.9	0
1996			
No. of flowering shoots	4	202	0
No. of non-flowering shoots	607	108	15
Percentage of flowering shoots	0.7	65.2	0
1997			
No. of flowering shoots	0	47	1
No. of non-flowering shoots	326	63	17
Percentage of flowering shoots	0	42.7	5.6

Current shoots bearing no leaf buds do not contribute to further shoot extension. The frequency of the current shoots bearing no leaf buds was examined in relation to the shoot length at 5 cm intervals using the samples taken in November 1995 and 1997. The proportion of the current shoots bearing no leaf buds was significantly different among size classes (1995: $\chi^2 = 42.34$, $P < 0.001$; 1997: $\chi^2 = 127.5$, $P < 0.001$) and was higher in the size classes shorter than 10 cm (Table 1).

Distributions of flowering shoots in a crown

There were 206 flowering shoots of 936 current shoots (22%) in 1996, but only 9 of 631 (1.4%) in 1995 and 48 of 454 (11%) in 1997. To examine the distribution of flowering shoots within the crown, we compared the frequency of flowering shoots in three layers of the crown. The proportion of flowering shoots was significantly different among the three layers in each year (1995: $\chi^2 = 11.1$, $P < 0.001$; 1996: $\chi^2 = 56.8$, $P < 0.001$; 1997: $\chi^2 = 26.0$, $P < 0.001$). In each year, the upper crown layer had the highest proportion of flowering shoots, followed by the middle and lower layers (Table 2).

Size distribution of flowering shoots

Using the shoot length as an index of shoot size, shoot length distributions were examined for flowering and non-flowering shoots to determine the relationship between the production of flower buds on the current shoot and shoot size (Fig. 5). The ratio of number of flowering shoots to the number of non-flowering shoots was significantly different among size classes (1995: $\chi^2 = 15.81$, $P < 0.001$; 1996: $\chi^2 = 502.9$, $P < 0.001$; 1997: $\chi^2 = 159.3$, $P < 0.001$; Fig. 5). The ratio of the number of flowering shoots was higher in the 10- to 40-cm shoot size class than in the <10-cm or >40-cm size classes (Table 3).

Nonlinear regression showed that the distribution of flowering shoots was approximated by normal distribution for each canopy layer (upper layer: $\mu = 23.10$, $\delta = 6.14$, $r^2 = 0.96$; middle layer: $\mu = 20.34$, $\delta = 4.52$, $r^2 = 0.99$; lower layer: $\mu = 21.90$, $\delta = 3.91$, $r^2 = 0.99$). The median of the frequency distribution of flowering shoots was almost the same, with approximately 20 cm in each layer.

Fig. 6. Relationship between the proportion of flower-supportive shoot length (shoot length from the terminal – nearest leaf bud to terminal end of shoot) and shoot length in (*a*) 1995, (*b*) 1996, and (*c*) 1997. Proportion of flower-supportive shoot length was arcsine transformed.
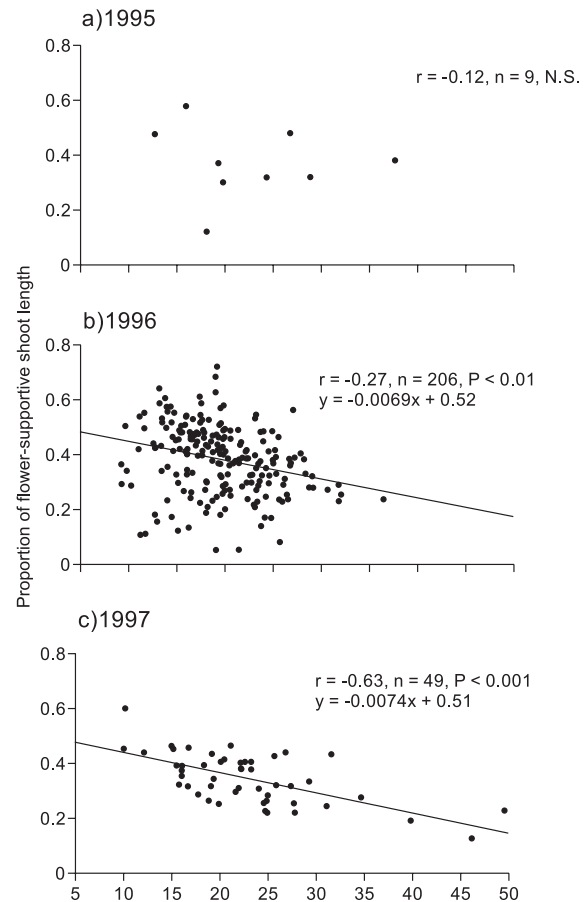
Characteristics of flowering current shoots and of fruiting 1-year-old shoots

The relationship between shoot length and flower-supportive shoot length was examined for all flowering shoots in November 1995, 1996, and 1997 (Fig. 6). The proportion of flower-supportive shoot length was negatively correlated with shoot length in 1996 and 1997, although no significant correlation was found in 1995. These results indicate that flowering shoots develop fewer shoots in the following year than non-flowering shoots and that this negative effect may be weaker in longer shoots than in shorter shoots.

Regression analysis was conducted for the relationship between the mass of the stem and the mass of male and female flowers per current shoot to examine the size dependency of reproductive output at the level of current shoot (Fig. 7). Masses of male and female flowers were significantly and positively correlated with stem mass in 1996 and in 1997. The coefficient of determination between the flower mass and the stem mass was higher in female flowers than in male flowers in 1996 (male: $r^2 = 0.092$; female: $r^2 = 0.31$) and 1997 (male: $r^2 = 0.16$; female: $r^2 = 0.39$).
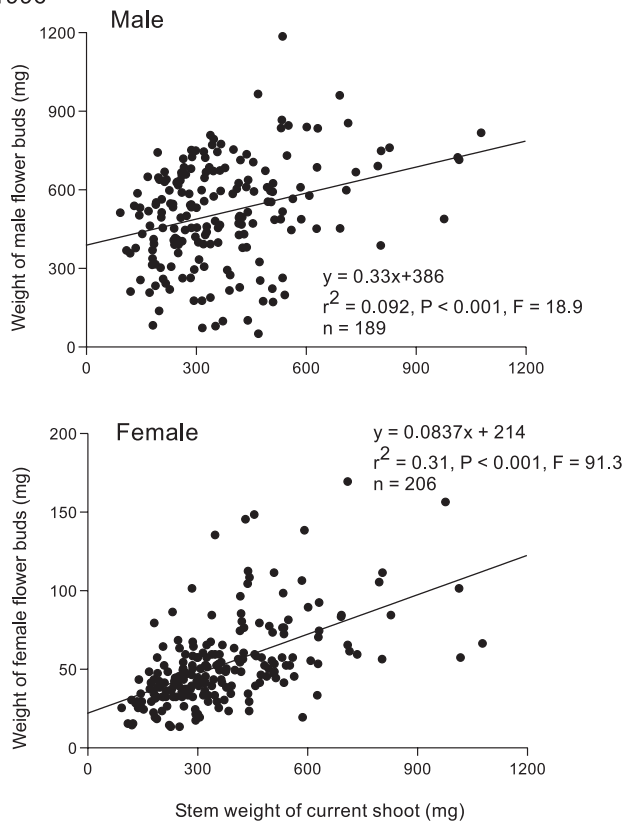
Regression analysis was conducted for the relationship between stem mass and fruit mass per 1-year-old shoot to ex-

Fig. 7. Relationship between the mass of flower buds per current shoot and stem mass of current shoot and the results of regression analysis in (*a*) 1995, (*b*) 1996, and (*c*) 1997.
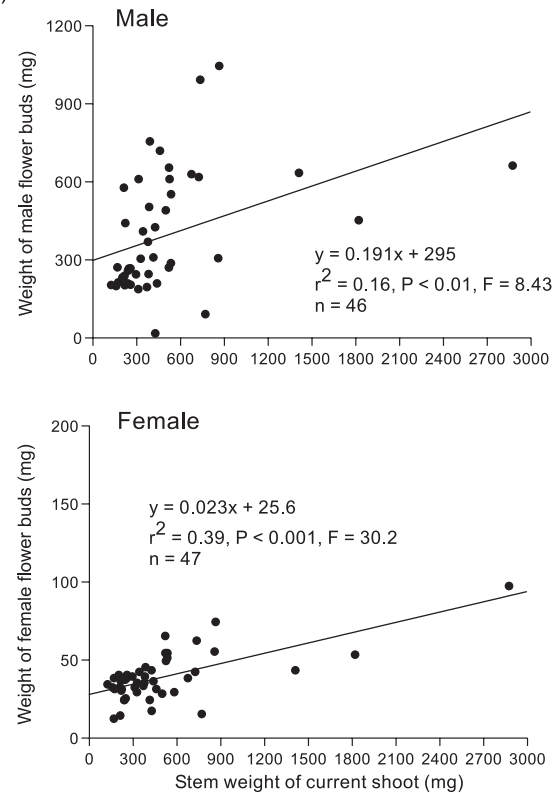

a) 1995
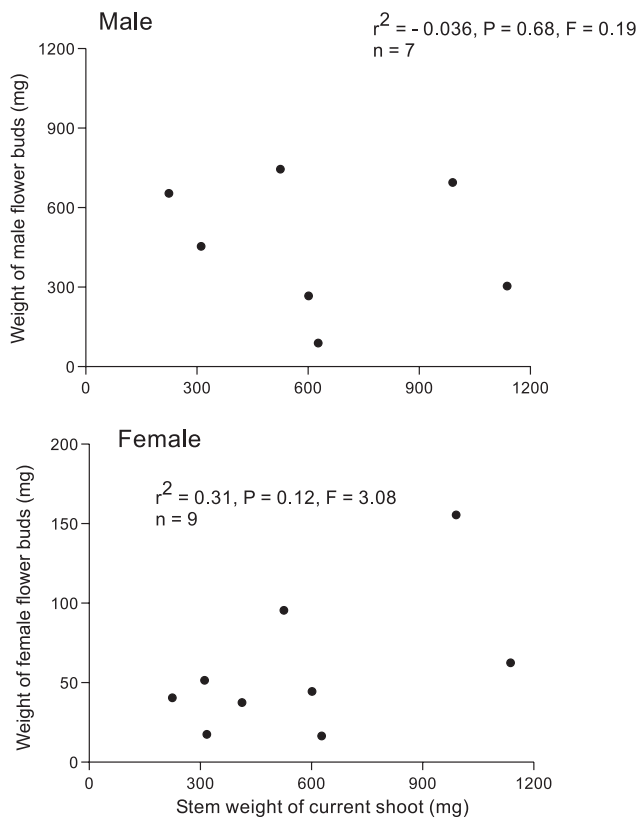
c) 1997

b) 1996

amine the size dependency of reproductive output. The fruit mass per 1-year-old shoot was significantly and positively correlated with stem mass of 1-year-old shoot in 1995 and in 1997 (Fig. 8).
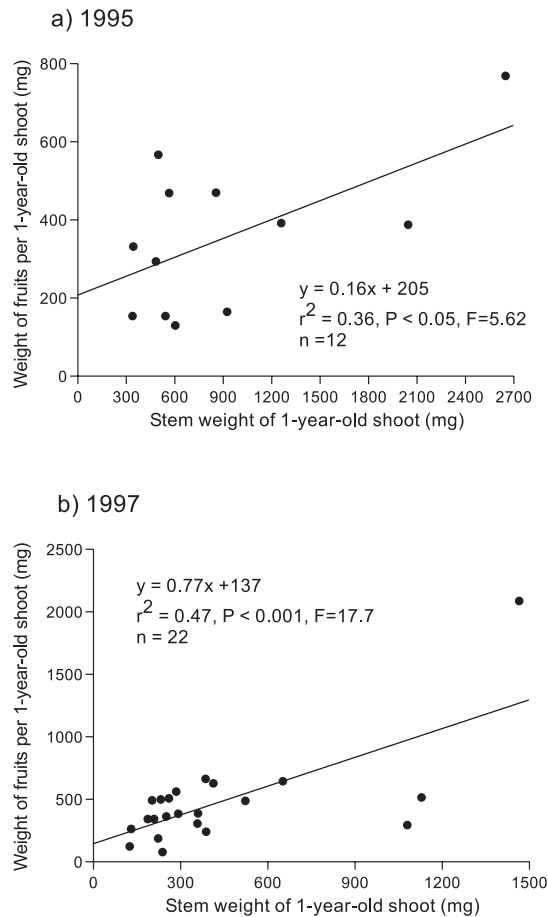
Costs of reproduction in current shoots

Direct cost of reproduction

On average, the male flowers per current shoot weighed 455.3 ± 31.6 mg ($n = 7$) in 1995, 508.1 ± 14.4 mg ($n = 188$) in 1996, and 375.6 ± 34.4 mg ($n = 43$) in 1997. The female flowers weighed 50.1 ± 13.6 mg ($n = 9$) in 1995, 52.4 ± 1.9 mg ($n = 206$) in 1996, and 38.5 ± 2.1 mg ($n = 48$) in 1997. The mass of male flowers per current shoot was more than nine times heavier than that of female flowers per current shoot (9.08, 9.69, and 9.75 in 1995, 1996, and 1997, respectively). On average, the fruit mass per 1-year-old shoot was 299.1 ± 43.4 mg ($n = 11$) in 1995 and 388.9 ± 85.1 mg ($n = 21$) in 1997. Fruits were not obtained in 1996.

Indirect cost of reproduction

Fruiting 1-year-old shoots produced significantly fewer current shoots than non-fruiting 1-year-old shoots in 1997 ($P < 0.05$), but the difference was not significant in 1995 (Table 4). The differences in the average shoot length between current shoots from fruiting and non-fruiting 1-year-old shoots were not significant in 1995 or 1997 (Table 5).

Fig. 8. Relationships between fruit mass per 1-year-old shoot and mass of stem of 1-year-old shoot and the results of regression analysis in (*a*) 1995 and (*b*) 1997.

a) 1995

$y = 0.16x + 205$
$r^2 = 0.36, P < 0.05, F=5.62$
$n =12$

b) 1997

$y = 0.77x +137$
$r^2 = 0.47, P < 0.001, F=17.7$
$n = 22$

Table 4. Effect of reproductive growth in the previous year on the number of current shoots developed on the 1-year-old shoots with 1-year-old shoots as a covariate.

Source	df	MS	*F*	*P*
1995				
Model	2	407.5	177.5	<0.001
Length of 1-year-old shoot	1	814.6	354.8	<0.001
Fruiting vs. non-fruiting	1	2.701	1.176	0.28
Error	172	2.296		
1997				
Model	2	158.2	85.93	<0.001
Length of 1-year-old shoot	1	304.2	165.3	<0.001
Fruiting vs. non-fruiting	1	9.034	4.908	0.028
Error	158	1.841		

Table 5. Effect of reproductive growth in the previous year on the mean length of current shoots developed on the 1-year-old shoots with 1-year-old shoots as a covariate.

	df	MS	*F*	*P*
1995				
Model	2	1044.9	32.32	<0.001
Length of 1-year-old shoot	1	1946.5	60.22	<0.001
Fruiting vs. non-fruiting	1	117.4	3.623	0.058
Error	165	32.33		
1997				
Model	2	425.1	14.43	<0.001
Length of 1-year-old shoot	1	849.9	28.84	<0.001
Fruiting vs. non-fruiting	1	99.89	3.39	0.067
Error	158	29.94		

Current decrement and future increment of reproductive output by abandonment of reproduction

To clarify the demographic patterns of reproduction in the current shoot population, we examined the relationship between 1-year-old shoot length and the proportion of flowering shoots of the current shoots developed on the 1-year-old shoot. We used the samples from November 1996, which had enough flowering shoots. Shoots developing on longer 1-year-old shoots show a higher probability of reproduction, except for size class 60–70 cm, which developed many current shoots longer than 40 cm (Fig. 9).

Because of the indirect costs of reproduction, reproduction by current shoots decreases the number of potential current shoots for the following year, which leads to a decrease in reproductive output by these shoots. When this decrease in reproductive output in the following year surpasses the reproductive output in the current year, the current shoot may cease reproduction in the current year to increase total fecundity of the 1-year-old shoot system in 2 years. To test this hypothesis, we estimated the decrease in reproductive output in the current year and increment of reproductive output in the following year.

In current shoots shorter than 40 cm, the decrease in mass of female flowers in the current year exceeded the increase in mass of female flowers in the following year (Fig. 10).

However, in current shoots longer than 40 cm, the increase in mass of female flowers in the following year surpassed the mass in weight of female flowers in the current year (Fig. 10).
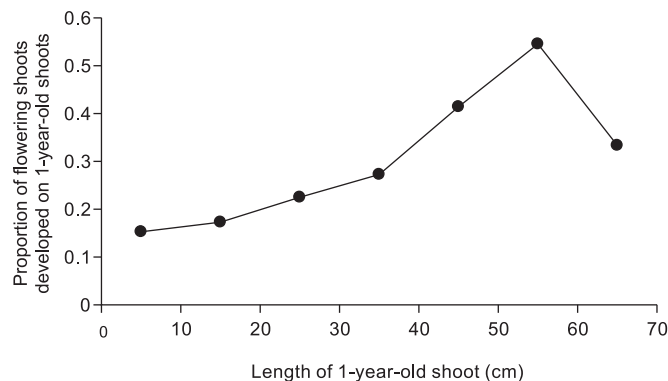
Discussion

The current shoot is a basic unit of shoot architecture and the reproduction of current shoots affects future growth such as shoot architecture and future reproduction. Here, we discuss (*i*) temporal (phenological patterns of reproductive allocation) and (*ii*) spatial (distribution of flowering shoots in the crown) aspects of reproductive ecology, (*iii*) costs of reproduction, and (*iv*) specialization of individual current shoots as a reproductive strategy of *A. hirsuta* var. *sibirica* from the viewpoint of shoot demography.

Phenological patterns of reproductive allocation

Growth patterns of shoot elongation and leaf expansion of deciduous trees are classified into two major types: the predetermined type, which shows a single period of annual shoot elongation, and the heterophyllous type, which shows continuous expansion for a longer period (Kozlowski 1971, Kikuzawa 1978). As shown in Fig. 2, leaves and shoots of *A. hirsuta* var. *sibirica* continue to grow for 4 months, suggesting that this species is classified into the latter type. In the heterophyllous type, the current photosynthate is considered to be allocated to both reproductive and vegetative

Fig. 9. Relationship between the length of 1-year-old shoots and the proportion of flowering current shoots in the shoots developed on the 1-year-old shoots in 1997.


Fig. 10. The estimated relationship between the decrease in mass of female flowers in the current year (open circles) and the increase in mass of female flowers in the following year (solid circles).

growth (Kozlowski and Clausen 1966). Thus, reproductive and vegetative growth may compete for photosynthates. The masses of male flowers, female flowers and fruits began to increase in August when leaf mass was at a maximum and shoot elongation had stopped (Figs. 2 and 3). This suggests that allocation of photosynthates switches from vegetative to reproductive growth in August. Early allocation of resources for reproduction is reported to decrease both vegetative and reproductive growth (Lovett Doust and Eaton 1982). Theoretically, an investment pattern of resources that switches over from 100% vegetative growth to 100% reproductive growth (bang–bang strategy) maximizes allocation to reproduction for annual plants with a given growing period (Cohen 1971, 1976). The investment pattern of *A. hirsuta* var. *sibirica* at the level of current shoot seems to maximize allocation to reproductive activity, although the morphological restriction of flower production at their terminal ends may also influence when to initiate reproduction.

Distribution of flowering shoots within the crown

The number of flowering shoots per year varied drastically (Table 2). This supports previous research that showed that the number of seeds produced by *A. hirsuta* var. *sibirica* varies by year and reaches almost zero every 2 or 3 years (Mizui 1993). Flower numbervariation per year cannot be explained solely from the data obtained in this study. However, as discussed later, the indirect cost of reproduction causes a negative effect on the number of current shoots produced in the following year. This may prevent *A. hirsuta* var. *sibirica* from producing similar numbers of seeds in each year. If there is synchrony of reproduction within the current shoot population, the variability in number of seeds produced by *A. hirsuta* var. *sibirica* may be explained by the indirect cost of reproduction and dynamics of current shoots.

The trend that the proportion of flowering shoots being higher in the upper part of the crown (Table 2) suggests a flowering response to the gradient of light intensity within a crown. *Alnus hirsuta* var. *sibirica* belongs to a heterophyllous type and uses current photosynthate for both vegetative and reproductive growth. Thus, the local resources in the crown are important for the initiation of reproduction (Lovett Doust and Lovett Doust 1988; Seki 1994).
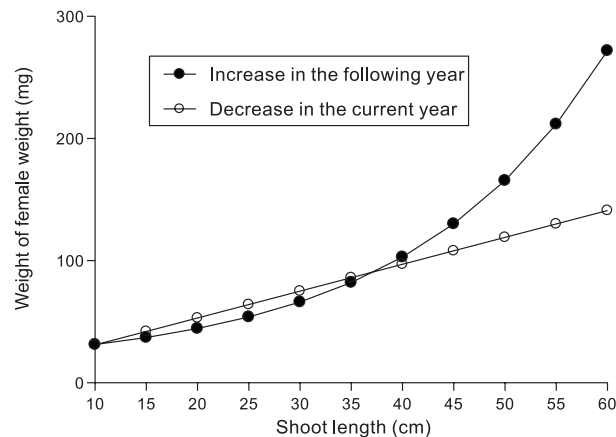
Costs of reproduction in the current shoot

Direct costs of reproduction

Many plant species show size dependency in reproductive output at the individual level (Werner 1975; Samson and Werk 1986; Schmid et al. 1995) and at the shoot module level (Cooper and McGraw 1988; Tuomi et al. 1982). This size dependency of reproductive output is explained by the high energy cost of reproductive events and by the correlation between size and acquired resources. Reproductive output of *A. hirsuta* var. *sibirica* was size dependent at the level of current shoot (Figs. 7 and 8). Since the current shoots of *A. hirsuta* var. *sibirica* grow at the expense of the current photosynthate, the size of the current shoot is a good indicator of photosynthates acquired by the shoot. Thus, we assume that (*i*) the photosynthate acquired by the current shoot is allocated to reproductive organs and (*ii*) the current shoot is a resource unit in reproductive allocation. These results indicate that the reproductive output of *A. hirsuta* var. *sibirica* is determined mainly by resources available at the current shoot.

Mass was more variable in male flowers than in female flowers (Fig. 7). Fruits of *A. hirsuta* var. *sibirica* mature in the year following flower-bud formation. Thus, when current shoots produce female flower buds, it is necessary to determine if they can acquire sufficient resources to mature the flowers into fruits in the subsequent year. On the other hand, male flowers fall off soon after flowering, which means that they do not grow in the subsequent year. This may be one reason why female flowers show stronger size dependency than male flowers.

Male function costs more than female function at the current shoot level for flowering. However, the total cost of making female flowers and maturing them into fruits must be assessed to discuss the differences between total direct cost of male and female function at the level of annual shoot. In *A. hirsuta* var. *sibirica*, female flowers were produced on current shoots and fruits were matured on 1-year-old shoots. Thus, photosynthate allocated to the production of female flowers is different from that allocated to maturing

Fig. 11. Example in which abandonment of reproductive growth in the current year increased the total fecundity of the 1-year-old shoot system. Shaded circles are flowers, and ellipses are leaf buds. Current shoot and 1-year old shoot systems produce two flowers in 2 years when it produced flowers in the current year, whereas they produce three flowers when the current shoot did not produce flowers in the current year.
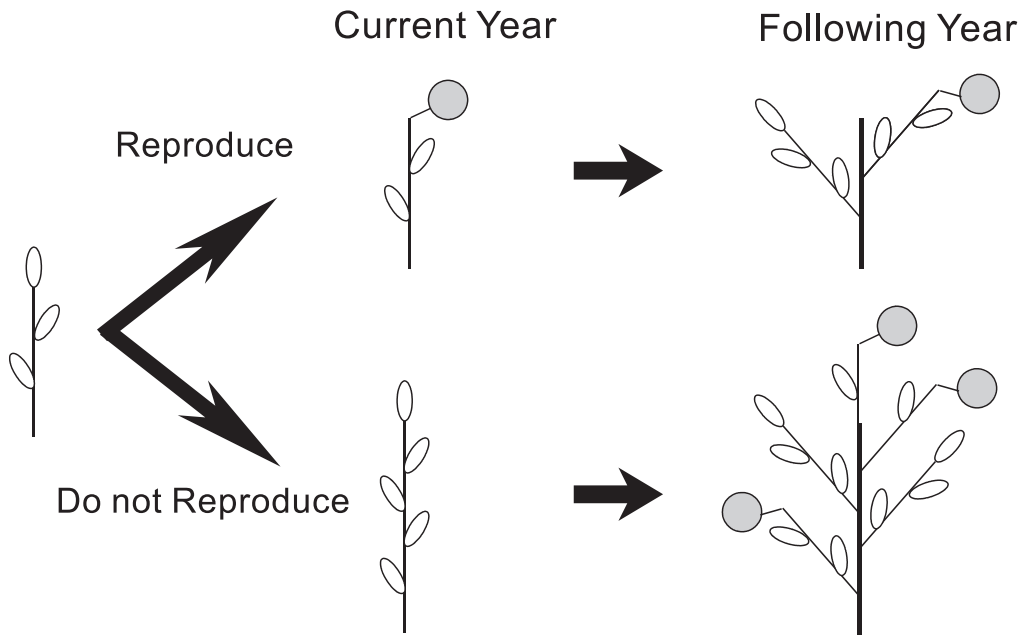
fruits. Here, we assume male and female flower buds get photosynthate from the current shoot and fruits get photosynthate from the current shoots produced on the 1-year-old shoot. Fruiting 1-year-old shoots usually have three to eight current shoots; thus the relative cost of female function may be smaller than that of male function.

The size dependency of fruit mass at the level of a 1-year-old shoot is explained by the results of a census experiment. The experiment demonstrated that the mass of fruits of *A. hirsuta* var. *sibirica* is correlated with the mass of female flowers before maturation, which indicates that the mass of fruit is partially determined when the female flowers developed on current shoots (Hasegawa and Takeda 1998).

Indirect costs of reproduction

Fruiting 1-year-old shoots developed significantly fewer current shoots than non-fruiting 1-year-old shoots in 1997, but the difference was not significant in 1995 (Table 4). Reproductive shoots of *A. hirsuta* var. *sibirica* have terminal end reproductive organs and cannot produce leaf buds (Fig. 1). This morphological restriction causes a reduction in the number of shoots developed from fruiting 1-year-old shoots. However, no significant differences were observed in the mean shoot length between the shoots developed on the fruiting and non-fruiting 1-year-old shoots (Table 5). The size dependency of reproductive organs at the level of current shoots indicates a high resource independency of current shoots in reproduction. This may be a reason that the former reproduction did not affect the growth of current shoots developed from 1-year-old shoots. The indirect cost of reproduction is the decrease in the number of current shoots to be developed in the following year and this affects shoot dynamics.

Functional specialization of the current shoot according to length

The current shoots shorter than 10 cm do not produce reproductive organs because the amount of photosynthate acquired in the current shoot is insufficient to produce reproductive tissues or they are more suitable for photosynthesis than reproduction. The former is supported by our findings that the shoots shorter than 10 cm frequently have no leaf buds (Table 1) whereas the latter is also supported by our findings in that some of the shoots shorter than 10 cm show a high LDI (Fig. 4). There is a minimal threshold size to produce reproductive organs at the individual level (Werner 1975; Schmid et al. 1995) and at the shoot module level (Cooper and McGraw 1988; Obeso 1997) and these phenomena are also explained by shortage of resources needed for reproduction. However, we could not distinguish which factor is dominant in this study.

Current shoots longer than 40 cm did not produce reproductive organs. However, this phenomenon is not explained by morphological traits or scarcity of photosynthate, since LDI of the current shoots longer than 10 cm did not vary as much with shoot length, and the proportion of the current shoots bearing no leaf buds in size classes longer than 10 cm was very small. From the aspect of evolutionary ecology, activities of plants are considered to have been selected so as to increase their lifetime reproductive success (Pianka 1983). Thus, the phenomenon that shoots longer than 40 cm do not produce flowers may contribute to the fecundity of the individual tree. To explain the effect of the indirect cost of reproduction in *A. hirsuta* var. *sibirica*, we examined the demographic cost of reproduction (Tuomi et al. 1982; Horvitz and Schemske 1988). Current shoots may abstain from the production of reproductive organs to increase the total repro-

ductive output in 2 years, if the increase in the reproductive output in the following year exceeded the decrease in the reproductive output in the current year. Figure 11 shows an example in which abandonment of reproductive growth in the current year increases the total fecundity of a 1-year-old shoot system in 2 years. In this example, the increase in the reproductive output in the following year surpasses the decrease in the reproductive output in the current year. The estimated future increase in the reproductive output exceeded the decrease in the reproductive output in the current shoots longer than 40 cm (Fig. 10). This indicates that longer shoots abstain from reproductive growth to increase the total reproductive output in 2 years. Thus, the long shoots may decrease temporal fecundity but may increase lifetime fecundity. In other words, long current shoots may be specialized in shoot extension to increase the lifetime fecundity of the individual tree.

These results suggest that the current shoot population of *A. hirsuta* var. *sibirica* is divided into three functionally different groups: (*i*) flowering shoots; (*ii*) short non-flowering shoots specialized for light capture and photosynthesis; and (*iii*) long non-flowering shoots specialized to grow and explore new space. In other words, we can regard the crown of *A. hirsuta* var. *sibirica* as a metapopulation that consists of three functionally different shoot subpopulations.

These three functional groups in current shoots of *A. hirsuta* var. *sibirica* indicate that the dynamics of current shoots that comprise the crown of a tree may be studied from the perspective of reproductive strategy of the individual tree. The dynamics of the three functional groups with years and the contribution of these functional specialization to the lifetime reproductive success of the tree should be investigated further.

Acknowledgements

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