Flower Bud Abortion Influences Clonal Growth and Sexual Dimorphism in the Understorey Dioecious Shrub *Aucuba japonica* (Cornaceae)

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Sexual differences were investigated to determine the significance of flower bud abortion in the dioecious shrub *Aucuba japonica* Thunb. The mean number of flowers per inflorescence and the mean number of flowering inflorescences (as opposed to aborted inflorescences) per individual were greater in males than in females in 1997 and 1998. Reproductive investment by males was 0.4-times (1997) and 1.4-times (1998) that by females. In addition, females aborted 30.9 % (1997) and 42.7 % (1998) of their total flower buds without blooming, whereas no male flower buds aborted. One of the architectural traits of this shrub is that in the year that a flower bud is produced at the shoot apex, the shoot will branch into two or more shoots. Thus, there was less sexual difference in the number of current shoots per individual than there was in the number of flowering inflorescences. The relationship between annual growth and reproduction, and the probability of reproduction in the following year, suggested that the higher investment in female reproduction was manifested as a cost for reproductive frequency rather than as a cost for annual growth. The spatial distribution of both males and females was clumped, which may be the result of clonal growth. In addition, overall sex ratios were not skewed and the number of sprouts did not differ significantly between sexes. These results suggested that flower bud abortion by females might reduce sexual dimorphism in terms of clonal growth.

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Key words: *Aucuba japonica*, clonal growth, flower bud abortion, forest understorey, branching, reproductive investment, sexual dimorphism, sprout.

INTRODUCTION

Dioecious plants differ in terms of the sexual dimorphism of their flowers (Eckhart, 1999), in their life histories (Delph, 1999) and in their physiology (Dawson and Geber, 1999) because different selective forces act on male and female reproduction. The fitness gain in males and females is enhanced by having traits that differ between the sexes (Lloyd and Webb, 1977; Willson, 1979). Greater variance in pollination success among males has driven the evolution of their extreme secondary sex characteristics, but female reproductive success is typically limited by resource availability rather than by pollination success (Charnov, 1979; Willson, 1979; Stephenson and Bertin, 1983). The most important factor behind sexual dimorphism is the different selection forces operating on males and females.

When describing life history traits in plants, it is assumed that there are trade-offs between the reproductive and growth processes (Hoffmann and Allende, 1984; Ågren, 1988; Lovett Doust and Lovett Doust, 1988; Snow and Whigham, 1989; Primack and Hall, 1990; Newell, 1991; Cipollini and Whigham, 1994; Obeso, 1997). If such trade-offs exist, the sex with the larger reproductive investment would incur a higher cost in terms of reduced growth rate. However, there is not always a trade-off between reproduction and growth (Willson, 1986; Reekie and Bazzaz, 1987; Bond and Midgley, 1988; Horvitz and Schemske, 1988;

Jennersten, 1991; Ataroff and Schwarzkopf, 1992; Delph and Meagher, 1995). Reproductive investments influence life history traits in various ways (Lloyd and Webb, 1977; Meagher, 1984), such as affecting the mortality rate, the clone ratio (Sakai and Burris, 1985) and chemical defence strategies against herbivores (Jing and Coley, 1990). Some studies have reported a difference between the size of photosynthetic organs in males and females (Wallace and Rundel, 1979; Kohorn, 1994). In clonal dioecious plants in particular, the trade-off between reproduction and growth is likely to have a negative effect on female clonal regeneration. If this is the case, the sexual dimorphism in reproductive investment should be compensated in a way other than through differing growth rates.

The abortion of flowers and ovules has been observed by many authors (e.g. Bawa and Webb, 1984). Explanations for the abortion of surplus flowers and fruit include increased male function, resource limitation, pollen limitation, bet-hedging strategy and selective abortion (Willson and Price, 1977; Wyatt, 1980; Sutherland and Delph, 1984; Holtsford, 1985; Marshall and Ellstrand, 1986; Stephenson and Winsor, 1986; Sutherland, 1987; Ehrlen, 1991; Rocha and Stephenson, 1991). However, there are few studies explaining the significance of flower bud abortion. Flower bud abortion is effected by trigger polysaccharides, such as sucrose, glucose and fructose (Aloni *et al.*, 1997). Stressful environments such as high temperatures and light limitation during bud development can lead to flower bud abortion

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TABLE 1. Sexual dimorphisms of the mean number of inflorescences in *A. japonica*

Traits	Year	Male			Female			<i>t</i>	d.f.	<i>P</i>
		<i>n</i>	Mean	s.d.	<i>n</i>	Mean	s.d.			
Total number of total inflorescences per plant	1997	117	7.9	9.7	126	6.3	6.4	1.98	199.58	0.0487
	1998	135	9.0	10.7	120	6.1	4.9	2.73	217.20	0.0068
Number of flowering inflorescences per plant	1997	117	7.9	9.7	126	4.4	6.4	3.81	201.43	0.0002
	1998	135	9.0	10.7	120	3.5	4.6	5.63	180.74	0.0000
Number of aborted inflorescences per plant	1997	117	0.0	0.0	126	2.0	2.1	10.32	125.00	0.0000
	1998	135	0.0	0.0	120	2.6	2.6	6.65	119.00	0.0000
Number of flowers per inflorescence	1997	973	51.8	26.8	550	8.2	5.0	49.57	1097.20	0.0000
	1998	779	72.2	33.5	318	6.7	4.8	51.57	873.62	0.0000

(Shigeoka and Ohkouchi, 1993). Other studies have shown that the type of resource limitation determines the degree of flower bud abortion (Moe, 1971; de Vries *et al.*, 1981; Pien and Lemeur, 2000).

Aucuba japonica Thunb. is unusual in that branching is caused by flower bud formation, and flower bud abortion sometimes occurs. Sexual dimorphism in reproductive investment and resource allocation patterns were examined in this understorey dioecious shrub, with the aim of determining the significance of flower bud abortion in connection with clonal growth and sexual dimorphism.

MATERIALS AND METHODS

Study species and sites

Aucuba japonica (Cornaceae) is an evergreen dioecious shrub that is common in the understorey of temperate old growth forests and coniferous plantations in Japan. The plant blooms in April and inflorescences are produced at the apex of shoots. Each inflorescence produces between ten and 300 flowers in males, and between one and 30 flowers in females. Each female flower has only one ovule and produces one seed per fruit. In winter, birds disperse the red fruits and the seeds germinate the following autumn. The internode length of shoots can be used as an indicator of growth and can easily be determined from the vestiges of the first and second bud scales (Hara, 1980). The terminal bud develops into two or more current-season shoots when a flower bud is produced at the shoot apex, but develops into only a single shoot when there is no flower bud (Hara, 1980). Large or disturbed plants regenerate clonally by layering of drooping shoots (Isobe and Kikuchi, 1989; Jeník, 1994; Ito *et al.*, 1999).

The study sites were on Mt Tsukuba (36°10'N, 140°10'W, 280 m elevation) and Mt Kaba (36°18'N, 140°08'W, 620 m elevation). A 225 m² quadrat was set up on Mt Tsukuba and a 1600 m² square quadrat on Mt Kaba. The Mt Tsukuba plot was in a cedar plantation; the canopy height was 20 m, and the height of the shrub layer was 3 m. *Aucuba japonica* dominated the shrub layer. *Zanthoxylum piperitum* Seib. et Zucc. and *Helwingia japonica* (Thunb.) F. G. Dietrich were less common components of the shrub layer and flowered at the same time as the study species. The Mt Kaba plot was in a secondary deciduous forest

dominated by *Pinus densiflora* Sieb. et Zucc. and *Carpinus tschonoskii* Maxim. In the forest understorey, *Sikimia japonica* Thunb., *Rhododendron obtusum* (Lindl.) Planchon var. *kaempferi* (Planchon) Wilson, and *Callicarpa japonica* Thunb. were codominant with *A. japonica*. The population density of *A. japonica* on Mt Kaba was less than that on Mt Tsukuba.

Sexual dimorphism

For each plant, the position (*x*- and *y*-coordinates) within the quadrat, the age of the shoots and the size [diameter at ground level (D0) and height] were recorded. The sex ratio was estimated by counting the number of flowering males and females within the plots on Mt Tsukuba and Mt Kaba in 1997 and 1998. The inter-plant distance was calculated from the coordinate data for all adult individuals within the plots. The neighbourhood sex ratio was determined by summing the number of males and females within the distance range of a plant for all adult individuals in each plot. The number and age of sprouts were recorded in November 2000. Sprouts were distinguished from primary stems by the trace of an inflorescence and by the difference in the age of the shoots, which could be determined by counting the number of bud scale vestiges. The number of inflorescences per individual and the number of flowers per inflorescence were counted in the Mt Tsukuba plot during the flowering season (243 adults in 1997 and 255 adults in 1998). The number of aborted flower buds that produced no flowers was recorded during three observations of flowering phenology (Abe, 2001). Size distribution (D0 and height), number of sprouts, flowers and inflorescences per plant, and number of individuals per plot were compared using statistical tests to determine whether there were differences between the sexes.

The relationship between reproduction and growth was analysed. To determine the best indicator of growth, several shoots were sampled in December 1998 when the current-season shoots had stopped growing. These shoots were separated into stem, leaf and bud, dried at 80 °C for 48 h and then weighed. For each shoot sampled, the diameter was measured at the centre point of the internodes. Of the following factors, length ($y = 0.283x$, $r^2 = 0.737$, $n = 193$, $P < 0.001$), diameter ($y = 4.431x$, $r^2 = 0.579$, $n = 193$,

TABLE 2. Mean dry weight of reproductive organs

Sex	Flower			Fruit			
	<i>n</i>	d. wt (mg)	Fl/inf	<i>n</i>	d. wt (mg)	Fruit set	d. wt/inf
Male	230	3.721	51.8 (72.2)	—	—	—	192.7 (268.7)
Female	96	8.709	8.2 (6.7)	40	166.2	0.65 (0.37)	957.3 (470.4)

Values of Fl/inf and fruit set are for 1997 and 1998 (latter within parentheses). Dry weight of flowers includes dry weight of peduncle per flower. Fl, Flower; inf, inflorescence; d. wt, dry weight.

FIG. 1. Size distributions of male and female *A. japonica* plants: upper chart, height; lower chart, diameter at ground level (D0).

$P < 0.001$), diameter $\times$ length ($y = 0.730x$, $r^2 = 0.615$, $n = 193$, $P < 0.001$) and (diameter) $^2 \times$ length ($y = 1.737x$, $r^2 = 0.402$, $n = 193$, $P < 0.001$), the length of the shoot correlated best with dry weight. Dry weight was therefore used as a growth indicator. Reproductive investment was calculated by summing the dry weights of flowers and flower branches (and fruits in females).

Growth and flowering of all shoots were investigated in 12 males and 11 females in the Mt Tsukuba plot in December 1998. The number of flowers per inflorescence was recorded for each shoot to assess the annual fluctuation in flower production. The lengths and diameters of every current-season shoot were measured to calculate growth. Annual growth and flowering frequency were also compared between sexes.

RESULTS

Annual reproductive allocation

On average, males produced 6.3- and 10.9-times as many flowers per inflorescence than did females in 1997 and 1998, respectively (Table 1). The mean number of flowering inflorescences (as opposed to aborted inflorescences) per male was 1.8- (1997) and 2.4-times (1998) greater than that per female (Table 1). In 1997 and 1998, flowers constituted an average of 29.9 % of the total reproductive biomass in males (flowers and flower branches) but only 0.9 % (t -test,

$t = 122.56$, d. f. = 238.23, $P < 0.001$) and 1.5 % ($t = 112.98$, d. f. = 250.68, $P < 0.001$) in females (flowers, flower branches and fruits) (Table 2). Fruits comprised 92.5 and 87.6 % of total female reproductive biomass at the inflorescence level in 1997 and 1998, respectively. Thus, in males, the dry weight per inflorescence was 0.20-times (1997) and 0.57-times (1998) as much as that in females when fruit weight is included. On the other hand, the reproductive investment by males at the plant level was 0.4-times (1997) and 1.4-times (1998) that by females. The reason behind the lower female reproductive investment in 1998 was mainly due to reduced fruit set and a high proportion of flower bud abortion.

Size and spatial distribution

The shrubs in the study population spanned a wide range of sizes. Mean D0 was 1.47 cm in males and 1.57 cm in females (t -test, $t = 1.15$, d. f. = 466.87, $P = 0.2520$) and the mean height was 139.9 cm in males and 153.9 cm in females ($t = 2.00$, d. f. = 462.66, $P < 0.05$). However, the sex ratio did not differ significantly from 1 : 1 either in height (χ^2 test, $\chi^2 = 15.12$, d. f. = 13, $P = 0.3000$) or D0 ($\chi^2 = 7.81$, d. f. = 10, $P = 0.6474$; Fig. 1). The number of sprouts per stem did not differ significantly between sexes either in large or small primary stems (Table 3). Sex ratios in both plots did not differ significantly from 1 : 1 (198 males and 211 females on Mt Tsukuba: χ^2 test, $\chi^2 = 0.41$, d. f. = 1, $P = 0.5203$; and 83 males and 91 females on Mt Kaba: $\chi^2 = 0.37$, d. f. = 1, $P = 0.5442$). The patterns of spatial distribution were very similar in both plots; there was a high proportion of same-sex plants in close proximity to a target plant, with the sex ratio gradually becoming closer to 1 : 1 with distance (Fig. 2). This pattern probably reflects clonal growth.

Female flower bud abortion

Females aborted many flower buds while males aborted no flower buds (Table 1). The proportion of aborted buds was 30.9 % in 1997 and 42.7 % in 1998. There was less difference between the sexes in the total number of inflorescences than in the number of inflorescences that flowered. Flower bud abortion in females occurred in every size class (Table 4).

Annual growth and next season reproduction

The probability of a shoot branching and flowering in the following year is shown in Table 5 for males and females.

TABLE 3. Differences between sexes in the number of sprouts

D0	Male			Female			Mann-Whitney <i>U</i> -test	
	<i>n</i>	Mean	s.d.	<i>n</i>	Mean	s.d.	<i>Z</i>	<i>P</i>
Small	26	1.31	0.55	28	1.25	0.52	0.1483	0.8821
Large	15	1.87	1.30	18	2.39	1.72	0.0000	1.0000

Small, D0 < 1.50 cm; large D0 > 1.50 cm. *n*, Number of primary stems.

FIG. 2. Patterns of same-sex spatial distribution in two plots.

Of the shoots that flowered in 1997, 40.6 % of the shoots in male plants and 17.6 % of those in female plants flowered in 1998 (χ^2 test, $P < 0.001$). The difference between males and females in the amount of branching, which occurs through the production of flower buds, was smaller than the difference in the amount of flowering between sexes. Of the shoots that did not flower in 1997, 34.2 % of the shoots in male plants and 10.6 % of those in female plants flowered in 1998 (χ^2 test, $P < 0.01$).

Current-season growth tended to be greater in females than in males whether the shoot produced an inflorescence or not (Table 6). The expected trade-off between the number of reproductive organs (flowers and fruits) and growth was not observed in 1997 or 1998 (Fig. 3). The number of male reproductive organs in 1997 was positively correlated with annual growth in 1997 and 1998. However, the number of female reproductive organs in 1997 was not correlated with annual growth in 1997 or 1998.

DISCUSSION

Flower bud abortion in females

In *A. japonica*, only female plants abort a considerable proportion of their flower buds. This suggests that flower bud abortion is related to female reproductive function. The abortion rate of flower buds in *Phaseolus vulgaris* depends on the position of the bud within the inflorescence, and flower bud abortion is likely to be selective (Sage and

Webster, 1987). *Viscaria vulgaris* probably aborts flower buds to adjust seed set (Jennersten, 1991). These examples imply that flower bud abortion in females is usually due to limited resources rather than to pollination success. Indeed, hand-pollination experiments have shown that fruit production in *A. japonica* is not restricted by pollen (Abe, 2001). Thus, flower bud abortion which occurs only in females is probably caused by resource limitation. However, *A. japonica* aborted a considerable proportion of flower buds in both years. If flower bud abortion serves only to reduce reproductive allocation or to adjust fruit set, plants should not produce such a vast number of apparently useless flower buds.

One explanation for why flower bud abortion occurs only in females concerns branching. *Aucuba japonica* produces flower buds at the shoot apex and two or more current shoots with some leaves extend into vacant spaces in the flowering season (Hara, 1980). On the other hand, shoots with no flower buds produce only one current shoot. The significance of female flower bud abortion appears to be related to this life history trait.

Reproduction and growth

Aucuba japonica shoots divide into two in a year when a flower bud is produced at the shoot apex. Therefore, the total number of current-season shoots per individual is related to the total number of flower buds produced in previous years. This study has shown that the total number of branches per male is greater than that per female because female plants have considerably lower reproductive frequency and produce slightly fewer flower buds than do male plants. As judged by dry weight per inflorescence, female reproductive investment fluctuated widely with fruit set and was sometimes much higher than that of males at the shoot level. In addition, the probability of reproduction in the following year suggests that females have higher reproductive costs than males. On the other hand, growth was not influenced by reproduction because mean annual growth either did not differ between sexes or else was greater in females, and the relationships between reproductive investment and post-reproductive growth did not exhibit a trade-off, as in some studies (e.g. Obeso, 1997; Hoffmann and Allende, 1984). The expected trade-off between growth and reproduction is sometimes masked by sexual dimorphism in photosynthetic ability and the phenological pattern of resource allocation (Delph and Meagher, 1995; Delph, 1999).

Aucuba japonica sprouts and grows clonally by layering of drooping shoots; this is an important strategy for persistence on the forest floor (Ito *et al.*, 1999). Stem

TABLE 4. Number of flower buds per plant in each height class in 1997 and 1998

Height	Male			Female total						Flowering females				
	<i>n</i>	Mean	s.d.	<i>n</i>	Mean	s.d.	<i>t</i> -test			Mean	s.d.	<i>t</i> -test		
							<i>t</i>	d.f.	<i>P</i>			<i>t</i>	d.f.	<i>P</i>
1997														
50	6	7.00	10.10	4	1.50	0.58	1.33	5.05	0.2402	0.00	0.00	1.70	5.00	0.1503
100	27	1.67	0.92	25	1.84	1.46	0.51	39.86	0.6150	0.28	0.61	6.44	45.59	0.0000
150	72	5.19	6.96	48	3.29	3.10	2.04	105.47	0.0442	1.21	2.58	4.43	97.00	0.0000
200	74	11.31	9.41	74	7.58	5.54	2.94	118.07	0.0040	5.10	5.56	4.89	118.33	0.0000
>200	11	18.55	15.95	29	13.45	9.54	0.99	12.82	0.3383	11.10	9.68	1.45	12.90	0.1710
1998														
50	4	9.25	7.14	0	—	—	—	—	—	—	—	—	—	—
100	10	2.30	1.49	9	1.56	0.73	1.40	13.31	0.1838	0.56	0.88	3.13	14.82	0.0069
150	46	6.54	8.19	25	2.48	2.10	3.18	55.07	0.0024	0.96	1.10	4.55	47.93	0.0000
200	64	10.03	9.61	56	5.80	4.79	2.10	95.02	0.0025	3.34	3.35	5.22	79.96	0.0000
>200	11	18.91	18.67	30	11.13	7.19	1.35	11.11	0.2053	6.83	5.41	2.11	10.62	0.0591

t-Test compares total number of females, or number of flowering females, with males. 'Female total' is the sum of the number of buds that flowered and those that aborted. *n*, Number of plants.

TABLE 5. Sexual differences of the probability of a shoot branching and flowering in the following year (1998)

State in 1997	State in 1998	Frequency		χ^2 test		
		Male	Female	χ^2	d.f.	<i>P</i>
Flower bud	Bud	76 (0.41)	29 (0.24)	9.37	1	0.0022
	No	111 (0.59)	93 (0.76)			
No flower bud	Bud	13 (0.34)	11 (0.37)	0.10	1	0.9920
	No	25 (0.66)	18 (0.62)			
Flower	Flower	76 (0.41)	15 (0.18)	13.88	1	0.0002
	No	111 (0.59)	70 (0.82)			
No flower	Flower	13 (0.34)	7 (0.11)	8.65	1	0.0033
	No	25 (0.66)	59 (0.89)			

TABLE 6. Sexual differences in growth (cm) of shoots that flowered and shoots that did not flower

	1997					1998				
	Male	Female	<i>t</i> -test			Male	Female	<i>t</i> -test		
			<i>t</i>	d.f.	<i>P</i>			<i>t</i>	d.f.	<i>P</i>
Shoots that flowered										
<i>n</i>	107	40				89	22			
Mean	15.9	23.4	3.87	52.24	0.0011	11.7	21.7	3.88	24.67	0.0007
s.d.	20.5	12.4				4.4	9.2			
Shoots that did not flower										
<i>n</i>	38	28				127	109			
Mean	8.1	7.6	0.35	60.61	0.7293	4.2	5.1	2.19	218.33	0.0293
s.d.	5.9	5.5				3.1	3.4			

sprouts sometimes replace the primary stem and the old primary stem begins to creep along the ground. Current shoots of the old primary stem then contribute to spatial expansion as new clones with low mortality. On the forest floor, light and soil conditions are spatially heterogeneous

(Chazdon and Pearcy, 1991; Pearcy *et al.*, 1994; Stark, 1994), and spatial spreading of shoots is adaptive in such environments (Harper, 1977; Svensson *et al.*, 1994; Ackerly and Bazzaz, 1995; Ackerly, 1997; Jódóttir and Watson, 1997; Takenaka, 1997, 2000). Stem sprouts are an important

FIG. 3. Relationship between reproductive investment in 1997 and annual growth in 1997 and 1998. Vertical axis represents the total growth (cm) of all current shoots per individual.

life history strategy for maintaining an individual at a favourable site, and creeping stems are important for spreading in the habitat (van Groenendaal *et al.*, 1997; Bond and Midgley, 2001). In this study, differences between sexes in the number of sprouts per plant and the number of individuals in the plot were relatively small in contrast to the large differences between sexes in reproductive investment. An important effect of female flower bud abortion may be to reduce reproductive investment and facilitate vegetative regeneration. That there is no trade-off between growth and reproduction in *A. japonica* suggests that branching and clonal regeneration, necessary to maintain the present generation in the forest understorey, are more important than investment in the next generation through sexual reproduction.

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