Effects of flower production and predispersal seed predation on reproduction in *Cirsium purpuratum*

Kazuharu Ohashi and Tetsukazu Yahara

Abstract: Researchers have often assumed that the reproductive success of a plant increases with flower production. However, if predispersal seed predation also increases with flower production, this may counteract the increase in reproductive success expected with such increased flower production. To investigate this, we examined the effect of flower number and predispersal seed predation on seed production in two field populations of *Cirsium purpuratum* (Maxim.) Matsum. At both sites, the proportion of seeds or heads preyed upon per plant increased with the number of flowers (florets or heads) on each plant, while the proportion of mature seeds per plant was independent of flower number per plant. Based on these results, we predicted that an increased level of seed predation at the population level would reduce the annual flower production of each plant. The observed pattern of flower production supported this prediction. Our results suggest that increased flower production may not always improve plant reproductive success under the influence of predispersal seed predation.

Key words: plant reprodutive success, predispersal seed predation, *Cirsium purpuratum*, flower production, plant–animal interaction.

Résumé : Les chercheurs ont souvent pris pour acquis que les succès de reproduction d'une plante augmentent avec la production de fleurs. Cependant, si la prédation des graines avant dispersion augmente également avec la production de fleurs, ceci pourrait contrer l'augmentation du succès de reproduction attendu d'une telle augmentation de fleurs. Pour étudier cette question, les auteurs ont examiné l'effet du nombre de fleurs et de la prédation des graines avant dispersion sur la production de graines, dans deux populations de *Cirsium purpuratum* (Maxim.) Matsum, sur le terrain. Sur les deux sites, la proportion de graines ou d'inflorescences subissant la prédation par plante augmente avec le nombre de fleurs (fleurons ou inflorescences) sur chaque plante, alors que la proportion de graines matures par plante est indépendante du nombre de fleurs par plante. Sur la base de ces résultats, les auteurs prédisent qu'un augmentation de l'intensité de la prédation des graines au niveau de la population réduira la production annuelle de fleur par plant. Le patron de production des fleurs observé supporte cette prédiction. Les résultats suggèrent qu'une augmentation de la production des fleurs n'améliore pas toujours le succès de reproduction, sous l'influence d'une prédation des graines avant la dispersion.

Mots clés : succès reproductif des plantes, prédation des graines avant dispersion, *Cirsium purpuratum*, production de fleurs, interaction plantes–animaux.

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Introduction

Interactions between plants and their pollinators are thought to be a driving force in the evolution of angiosperm flowers. Plant ecologists, therefore, have been inclined to focus on pollination in evolutionary studies of seed production and floral traits (Willson and Price 1977; Waser 1983; Bell 1985). However, in natural populations, pollinators are not the only animals that may visit flowers. Since flowers yield nutritious fruits and seeds, predispersal seed predators whose larvae consume developing fruits and (or) seeds also visit flowers for oviposition. They often impose heavy damage on plant reproduction at the population level (for a review see Crawley 1992). Furthermore, several studies have reported that seed predation rates varied between individual plants within a population (Moore 1978; Heithaus et al. 1982; Gómez and Zamora 1994). Therefore, predispersal seed predation as well as pollination is likely to be an important selective force in the evolution of plant reproductive traits.

Among various floral traits that have been studied so far, flower production per plant often has a strong positive effect on the annual reproductive success of the plant (Devlin 1989; Broyles and Wyatt 1990). This is mainly because additional flower production directly increases potential seed production (i.e., ovule number). In addition, sometimes it

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further improves male and (or) female success per flower through enhanced pollinator attraction (Willson and Rathcke 1974; Schemske 1980; Dudash 1991; Travis 1992). Based on these empirical data, many authors have assumed that plants could produce more seeds by increasing flower production (de Jong and Klinkhamer 1994 and references therein).

However, if predispersal seed predators also respond positively to flower production per plant, they may counteract the potential increase in annual reproductive success. A few previous studies have reported that seed-predation rate is positively correlated with flower production (Chater 1931; De Steven 1983; Hainsworth et al. 1984; Bullock et al. 1994). Based on these observations, some authors have pointed out the possibility that seed predators exert a counteracting selection pressure on annual flower production (Brody 1992; Travis 1992). Despite these suggestions, few attempts have been made to examine seed predation along with pollination and seed set (but see Heithaus et al. 1982; Louda 1982; Campbell 1991), and little is known about the evolutionary effects of predispersal seed predation on annual flower production per plant.

The aim of this study was to elucidate how flower production and predispersal seed predation affect annual seed production per plant, and to determine if there is a possible counteracting selection pressure due to predispersal seed predation on annual flower production, in the thistle *Cirsium purpuratum* (Maxim.) Matsum. (Asteraceae) in Japan. First, we propose a simple model to predict how selection pressure acts on annual flower production through annual reproductive success if seed-predation rate is positively correlated with flower number. Next, we examine how annual flower production per plant and other traits affect seed set and predispersal seed predation in two native populations of *C. purpuratum*. We then substitute the observed data into the above model and demonstrate how annual reproductive success changes with increasing flower production. Finally, we calculate the "optimal" upper limit of annual flower production for each plant population and compare it with the observed flower production.

Materials and methods

Expectation

Flower production will translate into a suitable index for reproductive success if the two variables have a rank-order correlation over the entire range of flower production values. However, if the seed predation rate is an increasing function of flower production per plant, then this will result in a number of flowers beyond which a further increase leads to decreased reproductive success. We propose a simple model to visualize this expectation. Let flower production (the number of flowers produced by a plant over one season) be F and the probability of setting fruit be S. To simplify the model, we assume that all flowers are perfect and resource allocation between male and female functions within a flower is constant, that fruit set is independent of the number of flowers, that male success is positively correlated with female success, and that all seeds within a damaged fruit are eaten. The proportion of damaged fruits per plant, Pr, can be expressed as a saturating function of the number of flowers on the plant:

$$[1] \quad \mathrm{Pr} = 1 - e^{-FA}$$

where Pr increases asymptotically from zero to one, and A is a rate constant ($A \geq 0$). As a plant produces additional flowers, the probability of a flower (fruit) escaping predation increases by a constant rate, e^{-A}. Then, we can write annual reproductive success, W, of a plant type that produces F flowers as:

$$[2] \quad W = (1 - \mathrm{Pr})SFtu$$

where t and u represent the number of seeds sired by a flower and the number of mature seeds per fruit (constant), respectively. We can calculate the optimal number of flowers by solving $dW/dF = 0$ and $dW^2/dF^2 < 0$. The solution is expressed as $1/A$. Thus, a plant type that produces more flowers than $1/A$ in any one year is expected to yield fewer seeds, owing to increased seed predation, and be selected against. That is, optimally, plants should not produce more than $1/A$ flowers per year even when they have more resources available for reproduction. In iteroparous plants, reproductive investment in the current year may be determined not only by annual reproductive success but also by a trade-off between current reproduction and survivorship and (or) growth in subsequent years (Iwasa and Cohen 1989; Snow and Whigham 1989; Galen 1993). This may further emphasize the selective advantage of restraining reproduction below $1/A$. We examined the patterns of seed set and seed predation in *C. purpuratum* in this light.

Organisms and study sites

Cirsium purpuratum is a polycarpic perennial that occurs on flood plains or volcanic barrens in the Kanto and Central Districts of mainland Japan. It forms a large basal rosette that sometimes approaches 200 cm in diameter. The flowering season extends from late August to early November. A flower head is composed of 400–700 florets and has a maximum diameter of 10 cm. All florets are monomorphic, perfect, and protandrous. The primary pollinator of *C. purpuratum* is a bumblebee, *Bombus diversus* Smith. Other minor pollinators have been described elsewhere (Ohashi and Yahara 1998). *Cirsium purpuratum is* not autogamous, although it is self-compatible, and self and outcross pollen have equivalent siring ability (K. Ohashi, unpublished data). As the functional seed of *C. purpuratum* is the achene (i.e., one achene contains one seed), for the remainder of this paper, we will refer to an achene as a "seed." Flower heads of *C. purpuratum* are used by two predispersal seed predators, *Larinus meleagris* Petri (Coleoptera, Curculionidae) and *Delia platula* (Meigen) (Diptera, Anthomyiidae). Larvae of both insects crawl among the florets, excavating the developing seeds one after another, until they pupate within a flower head. They come out of the heads at the end of the season and overwinter as adults.

This study was conducted in two native populations of *C. purpuratum* in Tochigi Prefecture, Japan. One population is located on a flood plain along the River Daiya in Nikko City (elevation ca. 750 m). The other is located near Lake Kawamata (elevation ca. 1000 m), which is about 50 km north of the former population. We refer to the two populations as the Nikko population and the Kawamata population, respectively. Both populations grow in open dry habitats. The density of *C. purpuratum* plants was intermediate (average distance to nearest neighbor = 3.06 m, n = 13, SD = 2.41 m) in the Nikko population, while it varied greatly among local patches in the Kawamata population (see below).

Field observations

Nikko population

In mid-August of 1993, we established a 30 × 70 m quadrat in the Nikko population that contained all the adult plants in the population. We consecutively numbered all the plants with plastic tape and recorded their locations on a map. We then selected 13 individuals at random and examined them at 5- to 7-day intervals during the season. At the time of each census, we marked any head (on its peduncle with a dot of acrylic paint) that had just initiated blooming. Paints of different colors were used to distinguish census days. When the seeds complete development, the color of involucral bracts turns from purple to brown. We collected such brown heads as they matured. We recorded the identity of the maternal plant of each head. Each sampled head was stored in a polyethylene bag, which was left open to avoid any rise in temperature or relative humidity. Sampled heads burst within 1–3 days and developing larvae within them were dried. Therefore, the degree of seed predation in these stored heads reflects what actually would have occurred in nature before seed dispersal. At the end of the season, we measured the maximum length of the radical leaves (radius of rosette) of each plant as an index of plant size. For other individuals in the population, we recorded flower (head) production and radius of rosettes. After the season, we measured the diameter of involucres of each sampled flower head in the laboratory. All heads were then dissected to score seed number, floret number, and the number of seed-feeding insects present.

Kawamata population

The following season, we conducted field work in the Kawamata population, in which local plant density varied between patches, to obtain information about the effect of flower production and plant density on seed predation. In the late summer of 1994, we classified patches of *C. purpuratum* in three categories, depending on their density. The distance to the nearest three neighbors was <0.5, 2–5, and >7 m in high-density, middle-density, and low-density patches, respectively. In each patch, we selected from 8 to11 individuals for examination. To minimize the bias in flowering phenology and size of flower head among the three categories, we selected plants that had initiated blooming at the same date and had similarly sized flower heads. We visited this site every 2 weeks and collected mature flower heads at the time of each census. Each head collected was stored in an open polyethylene bag. At the end of the season, we measured the maximum length of the radical leaves (radius of rosette) of each plant as an index of plant size. For other individuals in the population, we recorded flower (head) production and radius of rosettes. After the season, all flower heads sampled were dissected and examined in the laboratory.

Data analysis

For data obtained from the Nikko population, the spatial distribution pattern of the seed predators among plants was analyzed by I_δ (Morisita 1959) defined as:

$$[3] \quad I_\delta = \frac{\sum_{i=1}^{q} x_i(x_i - 1)}{N(N-1)}$$

in which q is the number of samples (plants), N is the total number of insects, and x_i is the number of insects in the ith sample. I_δ equals one when the insects are distributed randomly, is greater than one when the insects aggregate, and is less than one when the insects are evenly distributed among samples. To test the significance of the difference between I_δ and one, we performed a randomization test (Manly 1991).

Since larvae of seed predators do not consume petals and pappus hairs, we counted florets for each head to determine the "potential seed production" (T). We subsequently counted seeds that had escaped predation. The undamaged seeds (U) were divided into two categories, "normal seed" (x) and "aborted seed" (y). Normal seed refers to a seed that was successfully fertilized and provisioned. Aborted seed refers to a seed that failed to be fertilized or provisioned and can be distinguished by its shriveled appearance and (or) lack of firmness. Thus, we could obtain T, x, and y for each head and plant. Since the larvae often consume a seed entirely, we determined the number of seeds lost due to predation as the potential seed production (T) minus the number of undamaged seeds ($U = x + y$) for each head and plant. To assess a possible association between plant traits and seed set and (or) seed predation, multiple regressions were performed at the individual level considering the following as dependent variables: the proportion of mature seeds, $1 - U/T$ (estimated from absolute counts in the entire plant); and the proportion of damaged seeds, x/U (estimated from absolute counts in the entire plant). The independent variables considered in the model were total number of florets per plant, average diameter of flower heads produced (calculated from all heads on a plant), average distance to the two nearest plants, and first flowering date within the season. To correct for lack of normality, we arcsine transformed the dependent variables and logarithmically transformed the independent variables (Zar 1984).

For data obtained in the Kawamata population, we performed a multiple regression at the individual level considering the proportion of heads infested per plant as the dependent variable and total number of flower heads per plant and plant density level as independent variables. Here again, we transformed both variables prior to analysis to correct for lack of normality.

Finally, we fitted a saturating function ($\Pr = x/U = 1 - e^{-AF}$) to the observed data to estimate the "optimal" upper limit of annual flower production, $1/A$ (see Materials and methods, Expectation). We then compared the prediction with the actual relationship between plant size (rosette area) and annual flower (head) production per plant for both populations.

Results

Seed set

In the Nikko population, the proportion of mature seeds ($1 - U/T$) was 78.8±0.40% (mean ± 95% confidence interval; estimated from absolute counts in the entire population) at the population level and varied from 42.5 to 92.6% at the individual level. We did not find any significant relationship between the proportion of mature seeds per plant and plant traits (Table 1A). In particular, we did not detect any significant effect of flower production on the proportion of mature seeds (Fig. 1B).

Seed predation

Nikko population

We found that 44% of the seed-eating insects were *L. meleagris* and 56% were *D. platula*. The proportion of infested heads per plant and the probability of a seed being preyed upon were 90.8±5.42% (mean ± 95% confidence interval; $n = 109$) and 25.3±3.67% ($n = 54315$; estimated from absolute counts in the entire population), respectively. The average number of insects per head was 5.4 ($n = 76$, SD = 5.6). At the plant level, the distribution of insect larvae was significantly clumped (Nikko population: mean number of insects per plant = 26.5, $I_\delta = 2.71$, $P = 0.0001$). Furthermore, we found a significant correlation between the number of seed predators and the proportion of seeds damaged per plant ($n = 13$, $r^2 = 0.48$, $P = 0.001$). The number of insects per plant, therefore, directly affects the degree of seed predation that each plant suffers. These tendencies did not qualitatively differ when each species of seed predator was analyzed separately and their effect was additive.

Table 1. Multiple regression analyses.

(A) Parameters of multiple regression analyses relating the proportion of mature seeds to plant traits of *C. purpuratum*.

Independent variable	*b* ± SE	SC	*t*	*P*	*r*
No. of florets per plant	8.73±13.6	0.26	0.64	0.54	0.33
Average diameter of flower heads	7.63±40.7	0.072	0.19	0.86	0.21
Mean distance to nearest two neighbors	3.02±4.84	0.23	0.62	0.55	0.061
First flowering date	–26.1±39.3	–0.25	–0.66	0.53	–0.22

Complete model: $F_{4.8} = 0.404$, $P = 0.801$, $R^2 = 0.168$

(B) Parameters of multiple regression analyses relating the proportion of damaged seeds to plant traits of *C. purpuratum*.

Independent variable	*b* ± SE	SC	*t*	*P*	*r*
No. of florets per plant	19.2±6.98	0.86	2.34	0.048	0.61
Average diameter of flower heads	–26.8±21.0	–0.38	–0.88	0.41	0.072
Mean distance to nearest two neighbors	–0.043±2.49	–0.05	0.73	0.48	–0.086
First flowering date	11.6±20.2	0.17	–1.43	0.19	0.063

Complete model: $F_{4.8} = 1.95$, $P = 0.200$, $R^2 = 0.494$

(C) Parameters of multiple regression analysis relating the proportion of flower heads infested per plant to plant density and flower head number in *C. purpuratum*; data from the Kawamata population (1994).

Independent variable	*b* ± SE	SC	*t*	*P*	*r*
No. of flower heads per plant	28.6±9.63	0.52	2.97	0.0067	0.54
Plant density	3.91±7.77	0.088	0.50	0.62	0.19

Complete model: $F_{2.24} = 5.001$, $P = 0.0153$, $R^2 = 0.235$

Note: *b*, regression coefficient; SC, standard partial regression coefficient; *r* = simple correlation coeffecient.

The proportion of seeds damaged per plant (x/U) varied from 7.9 to 51.5%. We found a marginally significant positive relationship between the proportion of seeds damaged per plant and the total number of florets produced by the plant (Table 1B). No other plant traits could significantly explain the variance in the degree of seed predation per plant. A saturating function was fitted to the observed relationship between the proportion of seeds damaged per plant, Pr ($=x/U$) and the total number of florets on the plant, F: $\mathrm{Pr} = 1 - e^{-0.000063F}$ ($n = 13$, $r^2 = 0.44$, $P = 0.013$; Fig. 1A).

Kawamata population

We found that 84% of the insects were *L. meleagris* and 16% were *D. platula*. The proportion of heads infested per plant was 31.3±5.62% ($n = 262$). At both sites, we found no predators or parasitoids emerging from the pupae of seed predators.

We found that the number of flower heads per plant explained the variance in the proportion of heads infested (ranging from 0 to 85.7%) per plant (Table 1C). The average number of insects per head was 0.26 ($n = 262$, SD = 0.66) and most of the infested heads contained only one insect. For a comparison with the Nikko population, therefore, we estimated the proportion of seeds damaged per plant and the number of florets per plant, assuming that any one head did not contain more than one insect. We used the average number of florets per head (451) and the average number of seeds predated by an insect (52), based on the data from the Nikko population. The estimated proportion of seeds damaged per plant varied from 0 to 9.9%. A saturating function was fitted to the estimated relationship between the proportion of seeds suffering predation per plant, Pr ($= x/U$), and the total number of florets on the plant, F: $\mathrm{Pr} = 1 - e^{-0.0000075F}$ ($n = 27$, $r^2 = 0.26$, $P = 0.007$; Fig. 1A).

Testing predictions of the model

Substituting the estimated regression equations (saturating functions) for both populations into [2], we can illustrate how annual seed production ($W' = W/t$) changes with the number of florets (F) when the probability of setting seeds is one ($S = 1$), as shown in Fig. 2. Assuming that t is a constant (male reproductive success per flower correlates with female success per flower), the upper limits of annual flower production, $1/A$, are estimated to be 15 783 and 133 280 florets, which corresponds, approximately, to 35 and 296 heads, respectively. Figure 3 shows the actual relationships between plant size (rosette area) and annual flower (head) production per plant in the two populations. In the Nikko population, the maximum number of flowers produced by a given size of plant was smaller than that of a similarly sized plant in the Kawamata population. The observed maximum number of flower heads per plant in the Nikko and Kawamata populations was 33 and 65, respectively.

Discussion

At both sites, we found that the degree of seed predation varied greatly among individual plants and significantly correlated with the number of flowers (florets or heads) produced by the plant. This result agrees with observations in a few previous studies (Chater 1931; De Steven 1983; Hainsworth et al. 1984; Bullock et al. 1994; but see Heithaus et al. 1982; Gómez and Zamora 1994). There are two possible reasons for such a positive relationship between flower number and seed predation rate. One is that larval mortality may be higher on plants with fewer flowers. This could occur if plants with fewer flowers have a lower probability of setting seed, i.e., provide seed-eating insects lower-quality sites (Brody and Waser 1995). However, our observation that

Fig. 1. (A) The relationship between seed predation rate per plant, Pr, and the number of florets produced by a plant over the season, *F*. The regression lines are $Pr = 1 - e^{-0.000063F}$ for the Nikko population (n = 13, r^2 = 0.44, P = 0.013) and $Pr = 1 - e^{-0.0000075F}$ for the Kawamata population (n = 27, r^2 = 0.26, P = 0.007). (B) The relationship between the probability of setting seed, *S*, and the number of flowers per plant, *F*, for the Nikko population. No significant correlation was found (n = 13, r = 0.29, P = 0.34).

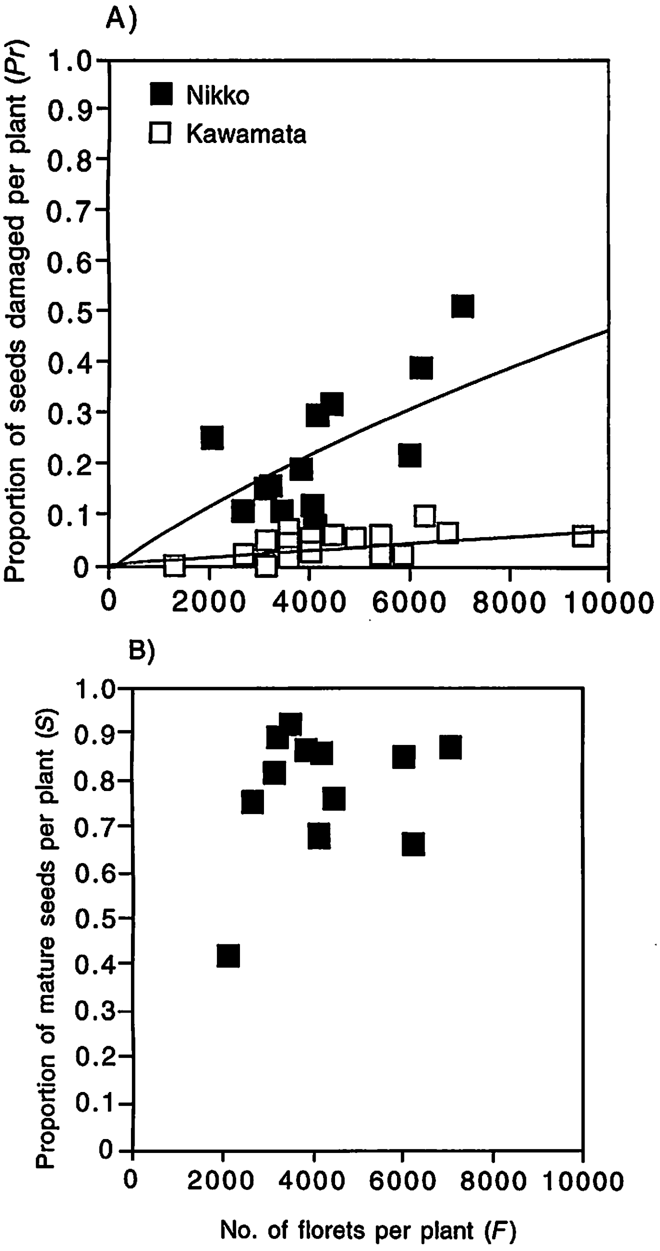


Fig. 2. The expected relationship between the number of florets (*F*) and annual seed production per *C. purpuratum* plant ($W' = W/t$). The probability of setting seed (*S*) is one. Solid lines represent the predictions of the model $W' = (1 - Pr)SF$ for the two populations. The broken line represents the case in which there is no predation (Pr = 0).

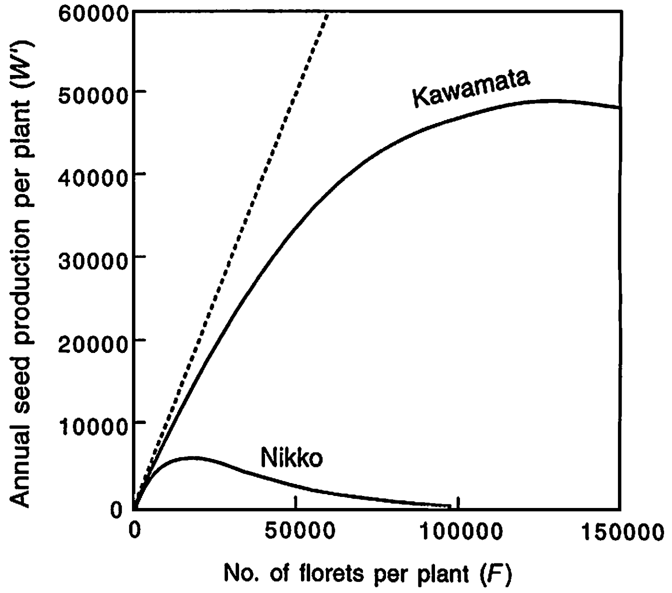
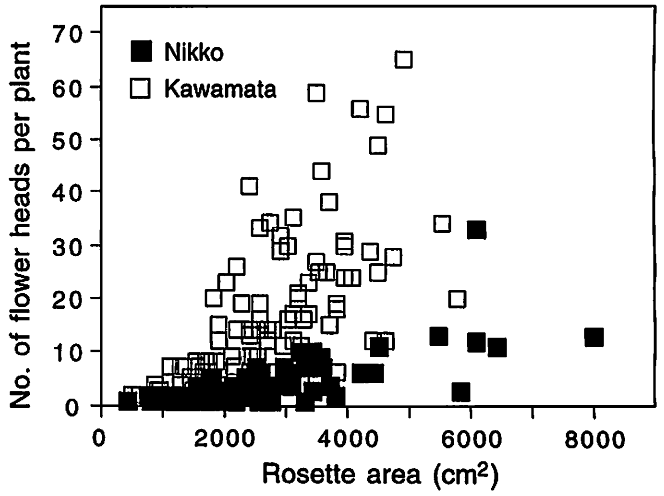


Fig. 3. The observed number of flower heads produced by *C. purpuratum* plants in relation to their plant size (rosette area); *n* is 72 in the Nikko population (1993) and 104 in the Kawamata population (1994).



the probability of setting seed at the plant level was independent of the number of flowers per plant argues against this. The other possibility is that ovipositing females respond to flower number per plant by aggregation. Some authors have suggested that oviposition of females is concentrated on plants with more flowers or with flowers that have larger petals (Brody and Mitchell 1997; Kudo and Whigham 1998). Such preferences for large floral displays may reflect some sensory limitations (i.e., visual and olfactory acuity) or a habit of favoring intense stimuli. Otherwise, it may represent a strategy for adult females to spread the risk of predator attack and to find food or mates. However, to determine which factor is most important, a detailed examination of behavioral patterns of ovipositing insects needs to be performed in the future. In contrast with this, there was no association between the proportion of mature seeds and flower number (and other plant traits). In *C. purpuratum*, Ohashi and Yahara (1998) found that the pollinator visitation rate per head was independent of the number of flowers per plant. Since *C. purpuratum* is self-compatible and self and outcross pollen have equivalent siring ability (K. Ohashi, unpublished data), this result agrees well with the observed pattern of pollinator visitation. That is, we suggest that each plant received a similar amount of pollen per head irrespective of the number of flowers per plant. Although the proportion of mature seeds varied from plant to plant, this variation was mainly due to one plant that yielded an exceptionally low seed set (42.5%). Some authors have also reported the lack of a significant relationship between the number of flowers and the probability of setting fruit and (or) seed (Geber 1985; Thomson 1988; Schmid-Hempel and Speiser 1988; Robertson and Macnair 1995; Pettersson 1997), although others have found a positive (Willson and Rathcke 1974; Schemske 1980; Dudash 1991) or negative (Andersson 1988) relationship.

Thus, data obtained here agree with our initial assumptions that the predispersal seed predation rate may increase with the number of flowers produced by the plant, while the probability of setting fruit (seed) may be independent of flower production. The estimated optimal upper limit of annual flower production, $1/A$, in the Kawamata population was 8.5 times that in the Nikko population, in which the level of seed predation was much higher. This implies that a higher level of predispersal seed predation potentially reduces annual flower production per plant. Our observation that the maximum annual flower production produced by a given size of plant in the Nikko population was lower than that of a similarly sized plant in the Kawamata population well supports this prediction, although data are limited to 1 year of observation.

Previous workers have suggested that plants could produce more seeds by increasing flower production, even if there is a decelerating relationship between the number of flowers and fitness (de Jong and Klinkhamer 1994 and references therein). However, we suggest that this belief may sometimes be misleading, owing to the influence of predispersal seed predators. Note that such an effect may be overlooked in plant populations in which plants have adapted to seed predation and restrain their flower production below the upper limit. At present, the model has many potential complications, which may require a more formal analysis than our simple approach. For example, male reproductive success may not always be correlated with female success (e.g., Stanton et al. 1986). Also, female reproductive success may correlate with flower number in terms of seed quality. In addition, it is still unknown how widespread the observed pattern is in plant–animal systems. Thus, further empirical studies are needed.

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References

Andersson, S. 1988. Size-dependent pollination efficiency in *Anchusa officinalis* (Boraginaceae): causes and consequences. Oecologia, **76**: 125–130.

Bell, G. 1985. On the function of flowers. Proc. R. Soc. Lond. B Biol. Sci. **224**: 223–265.

Brody, A.K. 1992. Oviposition choices by a pre-dispersal seed predator (*Hylemya* sp.) II. A positive association between female choice and fruit set. Oecologia, **91**: 63–67.

Brody, A.K., and Mitchell, R.J. 1997. Effects of experimental manipulation of inflorescence size on pollination and pre-dispersal seed predation in the hummingbird-pollinated plant *Ipomopsis aggregata*. Oecologia, **110**: 86–93.

Brody, A.K., and Waser, N.M. 1995. Oviposition patterns and larval success of a predispersal seed predator attacking two confamilial host plants. Oikos, **74**: 447–452.

Broyles, S.B., and Wyatt, R. 1990. Plant parenthood in milkweeds: a direct test of the pollen donation hypothesis. Plant Species Biol. **5**: 131–142.

Bullock, J.M., Hill, B.C., and Silvertown, J. 1994. Demography of *Cirsium vulgare* in a grazing experiment. J. Ecol. **82**: 101–111.

Campbell, D.R. 1991. Effects of floral traits on sequential components of fitness in *Ipomopsis aggregata*. Am. Nat. **137**: 713–737.

Chater, E.H. 1931. A contribution to the study of the natural control of gorse. Bull. Entomol. Res. **22**: 225–235.

Crawley, M.J. 1992. Seed predators and plant population dynamics. *In* Seeds. *Edited by* M. Fenner. Commonwealth Agricultural Bureaux International, Wallingford, U.K. pp. 157–191.

de Jong, T.J., and Klinkhamer, P.G. 1994. Plant size and reproductive success through female and male function. J. Ecol. **82**: 399–402.

De Steven, D. 1983. Reproductive consequences of insect seed predation in *Hamamelis virginiana*. Ecology, **64**: 89–98.

Devlin, B. 1989. Components of seed and pollen yield of *Lobelia cardinalis* variation and correlations. Am. J. Bot. **76**: 204–214.

Dudash, M.R. 1991. Plant size effects on female and male function in hermaphroditic *Sabatia angularis* (Gentianaceae). Ecology, **72**: 1004–1012.

Galen, C. 1993. Cost of reproduction in *Polemonium viscosum*: phenotypic and genetic approaches. Evolution, **47**: 1073–1079.

Geber, M.A. 1985. The relationship of plant size to self-pollination in *Mertensia cliata*. Ecology, **66**: 762–772.

Gómez, J.M., and Zamora, R. 1994. Top-down effects in a tritrophic system: parasitoids enhance plant fitness. Ecology, **75**: 1023–1030.

Hainsworth, F.R., Wolf, L.L., and Mercier, T. 1984. Pollination and pre-dispersal seed predation: net effects on reproduction and inflorescence characteristics in *Ipomopsis aggregata*. Oecologia, **63**: 405–409.

Heithaus, E.R., Stashko, E., and Anderson, P.K. 1982. Cumulative effects of plant–animal interactions on seed production by *Bauhinia ungulata*, a neotropical legume. Ecology, **63**: 1294–1302.

Iwasa, Y., and Cohen, D. 1989. Optimal growth schedule of a perennial plant. Am. Nat. **133**: 480–505.

Kudo, H., and Whigham, D.F. 1998. The effect of petal size manipulation on pollinator/seed-predator mediated female reproductive success of *Hibiscus moscheutos*. Oecologia, **117**: 70–79.

Louda, S.M. 1982. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. J. Ecol. **70**: 43–53.

Manly, B.F.J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, Tokyo.

Moore, L.R. 1978. Seed predation in the legume *Crotalaria*. II. Correlates of interplant variability in predation intensity. Oecologia, **34**: 203–223.

Morisita, M. 1959. Measuring of dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ. Ser. E Biol. **2**: 215–235.

Ohashi, K., and Yahara, T. 1998. Effects of variation in flower number on pollinator visits in *Cirsium purpuratum* (Asteraceae). Am. J. Bot. **85**: 219–224.

Pettersson, M.W. 1997. Solitary plants do as well as clumped ones in *Silene uniflora* (Caryophyllaceae). Ecography, **20**: 375–382.

Robertson, A.W., and Macnair, M.R. 1995. The effects of floral display size on pollinator service to individual flowers of *Mysotis* and *Mimulus*. Oikos, **72**: 106–114.

Schemske, D.W. 1980. Evolution of floral display in the orchid *Brassavola nodosa*. Evolution, **34**: 489–493.

Schmid-Hempel, P., and Speiser, B. 1988. Effects of inflorescence size on pollination in *Epilobium angustifolium*. Oikos, **53**: 98–104.

Snow, A.A., and Whigham, D.F. 1989. Costs of flower and fruit production in *Tiularia discolor* (Orchidaceae). Ecology, **70**: 1286–1293.

Stanton, M.L., Snow, A.A., and Handel, S.N. 1986. Floral evolution: attractiveness to pollinators increases male fitness. Science (Washington, D.C.), **232**: 1625–1627.

Thomson, J.D. 1988. Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of *Aralia hispida*. Evol. Ecol. **2**: 65–76.

Travis, J. 1992. Components of reproductive success in the herbaceous perennial *Amianthium muscaetoxicum*. *In* Ecology and evolution of plant reproduction. *Edited by* R. Wyatt. Chapman and Hall, New York. pp. 255–280.

Waser, N.M. 1983. The adaptive nature of floral traits: ideas and evidence. *In* Pollination biology. *Edited by* L. Real. Academic Press, London. pp. 242–285.

Willson, M.F., and Price, P.W. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). Evolution, **31**: 495–511.

Willson, M.F., and Rathcke, B.J. 1974. Adaptive design of the floral display in *Asclepias syriaca* L. Am. Midl. Nat. **92**: 47–57.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J.