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journal or publication title	American Journal of Botany
volume	84
page range	1275-1278
year	1997
URL	http://hdl.handle.net/10097/51637

PATTERNS OF WING SIZE VARIATION IN SEEDS OF THE LILY *CARDIOCRINUM CORDATUM* (LILIACEAE)¹

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We examined the patterns of variation in wing-loading and its related characteristics in *Cardiocrinum cordatum* to clarify the factors that determine the variation in seed dispersal ability in this species. The square root of wing-loading of a seed of a plant was not significantly correlated with basal stem diameter of a plant, indicating that large plants did not necessarily produce seeds with high dispersal ability. This result was inconsistent with the hypothesis that large plants produce seeds with high dispersal ability to avoid high mortality of seeds and seedlings in the vicinity of the parents. On the other hand, the square root of wing-loading of a seed of a fruit was negatively dependent on seed number of a fruit. Thus, many-seeded fruits produced seeds with high dispersal ability. This was because the projected surface area per seed was large in large fruits and large fruits contained large numbers of seeds. The cost per seed of producing fruit structures was small for many-seeded fruits. Thus, high dispersal ability of seeds in many-seeded fruits may be a result of an effective resource allocation pattern in which a high proportion of resources are allocated to those many-seeded fruits, enabling seeds to develop large wings and thus reducing the structural cost of fruits per seed.

Key words: *Cardiocrinum cordatum*; Liliaceae; seed dispersal; seed size variation; wind-dispersed seed; wing-loading; wing size variation.

Many plant species show variations in dispersal ability of seeds or fruits within and among plants in single species (e.g., Janzen, 1978; Augspurger and Hogan, 1983; McGinley et al., 1990; Ganeshiah and Uma Shaanker, 1991). Several hypotheses can explain these variations in seed dispersal ability within single species. (1) Venable (1992) proposed that sib-interaction in the vicinity of the parent selects for seed size variation depending on the resource status of the parent. Thus, large parents, which produce many seeds, disperse their seeds to a wide area by producing large dispersal structures to reduce the seed and seedling density in the vicinity of the parents. (2) Variations in the size of dispersal structures and seeds are the result of developmental, morphological, physiological, and space constraints, and do not have adaptive significances (e.g., McGinley, Temme, and Geber, 1987; McGinley et al., 1990; Winn, 1991). For example, wing and seed size are constrained by cone scale size and decrease from the base to the tip of the cone in *Pinus contorta* (McGinley et al., 1990). (3) Variations in dispersal ability result in uniform seed dispersal within the seed shadow area (e.g., Janzen, 1978; Augspurger and Hogan, 1983; Michaels et al., 1988). However, within-plant variation is unlikely to reduce density-dependent mortality or sib-competition by uniform seed dispersal (Greene and Johnson, 1992). Thus, this last hypothesis may be unlikely for most cases.

Which factors are significant for the evolution of the variations in seed dispersal ability within single species? Are there any other factors that produce variations in seed dispersal ability? In the present paper, we examine the patterns of variation in wing-loading and its related characteristics in *Cardiocrinum cordatum* (Thunb.) Makino

to clarify the factors that determine the variation in seed dispersal ability in this species. Here, wing-loading is the force of gravity on the seed divided by its projected surface area, and wind speed and release height being equal, the dispersal distance of a seed is inversely proportional to its square root of wing-loading (e.g., Green 1980; Augspurger and Franson, 1987; Greene and Johnson, 1993). Variation in wing-loading hence results in variation in seed dispersal ability. Thus, as well as experimental (e.g., Augspurger and Franson, 1987) and theoretical approaches (e.g., Okubo and Levin, 1989), which examine the relationships between seed (fruit) characteristics and dispersal distance, it is also useful to measure variation in wing-loading for the present purpose. We show that variation in seed dispersal ability may have an adaptive significance other than that stated above, or that this variation may be the result of effective resource allocation by plants.

MATERIALS AND METHODS

Cardiocrinum cordatum is a self-compatible perennial lily that grows under the closed canopy of deciduous forests in Honshu, Shikoku, and Kyushu, Japan. Each plant has a single stem and produces ~1–10 greenish white flowers on the terminal apex and in the upper leaf axils. Stem heights of fertile plants are ~0.6–1.5 m. Flowers are ~7–10 cm in length and ~2–4 cm in diameter and they bloom in July and August and fruits mature in the period from October to November. Seeds are undulators (see Augspurger, 1986), and each seed has a very thin wing around the albumen. Each fruit contains several hundred seeds; there is little pollen limitation, probably because of self-compatibility.

During July 1995, we measured the basal stem diameter of each of 74 plants growing naturally in deciduous-coniferous mixed forests of Mt. Aoba, Miyagi Prefecture, northern Honshu, Japan. We also marked 188 flowers randomly sampled (about two-thirds of all flowers on the 74 plants) and measured the length and width of the largest petal of each flower. At the same time, we collected one newly opened flower of 38 other plants. The length and width of the largest petal were measured for each collected sample and the flower dry mass (the sum of the flower stem, the corolla, the androecium, and the gynoecium) was

¹ Manuscript received 7 August 1996; revision accepted 18 February 1997.

The authors thank E. Kasuya and T. Yahara for their helpful advice during data analyses.

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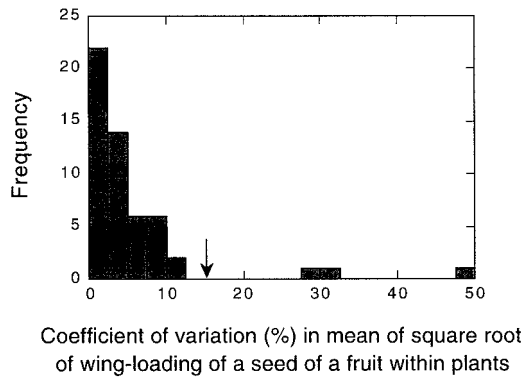


Fig. 1. Frequency distribution of the coefficients of variation (%) in the square root of wing-loading of a seed of a fruit (WLF) within plants for plants that have more than three fruits. The vertical arrow shows the coefficient of variation in the square root of wing-loading of a seed of a plant (WLP) among plants.

recorded for each sample after drying in an oven for 3 d at 85°C. We determined the length \times width of the largest petal – flower dry mass regression equation from these data [$y = -4.8686 + 0.0047493x - 1.3466 \times 10^{-6}x^2 + 1.2942 \times 10^{-10}x^3$ with $R = 0.707$] to estimate the dry masses of the marked flowers.

During November 1995, we collected all matured fruits of the marked samples (183 fruits in total since five flowers failed to mature; however, not all the 183 fruits were used for all measurements) and recorded the total mass of developed seeds and the number of developed seeds for each fruit. We then calculated the mean seed mass for each fruit by dividing the total seed mass by the total number of seeds. We also weighed each fruit (including fruit stem) other than seeds after drying in an oven for 3 d at 85°C to estimate the total cost of fruit.

To calculate wing-loading, we randomly subsampled 20 seeds from each sampled fruit and measured their projected surface areas to calculate the projected surface area per seed. Here, the projected surface area of a seed includes both the area of the wing and that of the embryo and the albumen because the latter area may also contribute to reducing wing-loading. We also weighed the total mass of the 20 subsampled seeds of each fruit to calculate the mean seed mass of a fruit. We then estimated the wing-loading of a seed of each fruit (WLF) by dividing the mean seed mass by the mean area of horizontal projection. Similarly, we recorded the mean area of horizontal projection and the mean seed mass for all subsampled seeds for each plant to estimate the wing-loading of a seed of each plant (WLP).

We computed a Spearman's rank correlation coefficient between the basal stem diameters of plants and WLP. We also conducted multiple

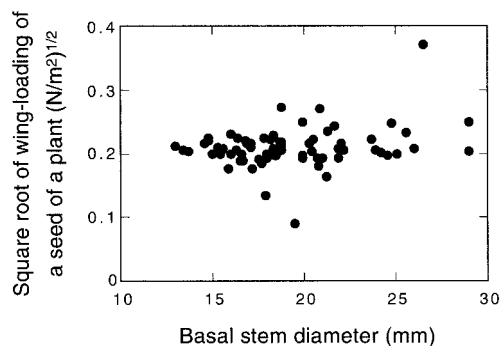


Fig. 2. Relationship between the basal stem diameter of a plant and the square root of wing-loading of a seed of a plant with a Spearman's rank correlation coefficient ($r_s = -0.129$, $P < 0.272$, $N = 74$).

TABLE 1. Multiple regression of the square root of wing-loading of a seed of a fruit. $R^2 = 0.559$, $N = 150$.

Source	Coefficient	<i>P</i>
Constant	0.276	<0.0001
Estimated dry mass of the flower from which a fruit developed	-0.039	0.5307
Fruit position	0.001	0.9794
Number of seeds of a fruit	-1.330	<0.0001
Total mass of a fruit	0.655	0.0001

regression analyses for characteristics related to seed dispersal ability, where WLF, the projected surface area per seed of a fruit (PSA), and the mean seed mass of a fruit (SM) are functions of the estimated dry mass of the flower from which a fruit developed, the fruit position in order from the terminal axis on a stem, the number of seeds of a fruit, and the total mass of a fruit.

RESULTS

The square root of wing-loading of a seed of a plant (WLP) varied among plants and the mean \pm standard deviation were 0.209 ± 0.0318 (Newton per square metre)^{1/2} (the coefficient of variation was 15.20). The square root of wing-loading of a seed of a fruit (WLF) also varied within single plants, though the coefficients of variation were smaller within plants than among plants (Fig. 1).

However, at the plant level, we found no significant correlation between the basal stem diameter of a plant and WLP (Fig. 2). Thus, large plants did not necessarily produce seeds with high dispersal ability.

At the fruit/flower level, we found that WLF was significantly negatively dependent on the number of seeds of a fruit (Table 1). This indicates that fruits that contained large numbers of seeds produced seeds with high dispersal ability. On the other hand, WLF was significantly positively dependent on the total mass of a fruit, indicating that large fruits produced seeds with low dispersal ability. However, WLF was not significantly dependent on the estimated dry mass of the flower from which a fruit developed, nor on the fruit position along a stem.

Further multiple regression analyses were conducted to examine the effects of each parameter on each of the two components of wing-loading, the projected surface area per seed of a fruit (PSA) and the mean seed mass of a fruit (SM). We found that PSA was significantly positively dependent on the total mass of a fruit (Table 2). However, PSA was not significantly dependent on the other parameters, including the number of seeds of a fruit. SM was significantly negatively dependent on the num-

TABLE 2. Multiple regression of the projected surface area per seed of a fruit. $R^2 = 0.783$, $N = 150$.

Source	Coefficient	<i>P</i>
Constant	0.341	0.0004
Estimated dry mass of the flower from which a fruit developed	0.031	0.4771
Fruit position	-0.046	0.2520
Number of seeds of a fruit	-0.067	0.5550
Total mass of a fruit	0.939	<0.0001

TABLE 3. Multiple regression of the mean seed mass of a fruit. $R^2 = 0.851$, $N = 150$.

Source	Coefficient	P
Constant	2.896	<0.0001
Estimated dry mass of the flower from which a fruit developed	0.043	0.2288
Fruit position	-0.070	0.0351
Number of seeds of a fruit	-1.988	<0.0001
Total mass of a fruit	2.406	<0.0001

ber of seeds of a fruit, indicating the presence of a trade-off between the number of seeds and the mass at the fruit level (Table 3). SM was also slightly negatively dependent on the fruit position and was significantly positively dependent on the total mass of a fruit (Table 3). These results indicate that the number of seeds of a fruit contributed to reduction of wing-loading through its negative relationship with SM. In addition, a large mass of a fruit contributed to a wide PSA, though at the same time being related to a large SM, which has negative effects on dispersal ability. Lower fruits produced slightly lighter seeds, but the fruit position had no effect on PSA.

Figure 3A, B shows the relationships of the number of seeds of a fruit to the total mass of a fruit, and to PSA, respectively. Fruits that contained large seeds were large in size, and many-seeded fruits produced a large PSA. However, as shown in Table 2, the latter relationship was due to the positive dependence of PSA on the fruit size.

DISCUSSION

In *C. cordatum*, the square root of wing-loading of a seed of a plant (WLP) was not correlated with the basal stem diameter (Fig. 2) and plants with a large resource status did not produce seeds with high dispersal ability. This suggests that avoiding high mortality in the vicinity of the parent is not an important factor in the evolution of seed dispersal in this species. On the other hand, the square root of wing-loading of a seed of a fruit (WLF) was negatively dependent on the number of seeds of a fruit (Table 1) and fruits that contained large numbers of seeds produced seeds with high dispersal ability. Thus, the difference in the number of seeds successfully developed in a fruit had a significant effect on the variation in seed dispersal ability in this species. In addition, large fruits produced seeds with low dispersal ability, which also contributes to this variation.

The projected surface area per seed (PSA), which reduces wing-loading, was large in large fruits (Table 2), and as a result, PSA was also large in many-seeded fruits (Fig. 3B). This result can be understood in the context of effective resource allocation to seed production. Namely, it is better to produce large fruits because wings can develop well in those fruits. On the other hand, the cost per seed of producing fruit may be small for many-seeded fruits due to the structural cost of the fruits. In fact, the dry mass of fruit structures of a fruit divided by the number of seeds of a fruit (y) decreased with the number of seeds of a fruit (x) ($y = 0.196/x + 0.769$), which supports this view. Hence, many seeds can develop large wings with the same resource allocation to the fruit by allocating these resources to many-seeded fruits. On the other

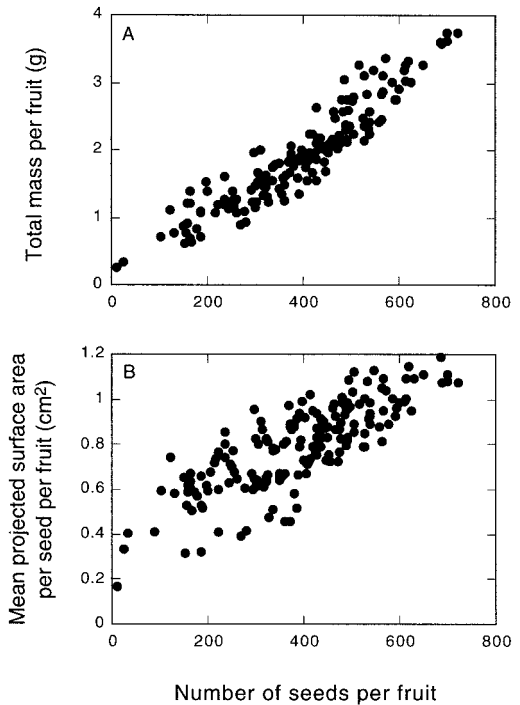


Fig. 3. Relationships between (A) the number of seeds of a fruit and the total mass of a fruit ($r_s = 0.945$, $P < 0.0001$, $N = 160$), and (B) the number of seeds of a fruit and the projected surface area per seed of a fruit ($r_s = 0.808$, $P < 0.0001$, $N = 183$) with Spearman's rank correlation coefficients.

hand, large flowers did not produce large winged seeds (Table 2). This suggests that the constraint that large meristems inevitably produce large organs (McGinley et al., 1990) has little effect and that plants can regulate wing size of their seeds depending on events after flower production. Thus, the wing size variation we found seems to be the adaptive strategy for effective resource allocation in response to the number of seeds successfully developed in each fruit within the plants. Here, wing-loading of a seed was large in large fruits because the mean seed mass was large in such fruits (Table 3), which increases wing-loading.

These arguments can be summarized as follows. The cost per seed of producing fruit is small for many-seeded fruits. Hence, it is effective to allocate more resources to many-seeded fruits, and seeds in these fruits can develop large wings. Thus, dispersal ability is high in many-seeded fruits.

Aside from the variability in seed dispersal ability within plants, seed dispersal itself can have two other advantages in addition to avoiding high mortality in the vicinity of the parents: exploiting safe sites that are suitable for germination and establishment, and directional seed dispersal to special sites (Howe and Smallwood, 1982; Willson, 1992). Here, directional seed dispersal is unlikely in the case of wind-dispersed seeds, though it is possible for animal-dispersed seeds. Thus, exploiting safe sites may be the most feasible selective advantage for seed dispersal in *C. cordatum* since avoiding high mortality in the vicinity of the parents is also unlikely. Recently, Sakai, Kikuzawa, and Umeki (1997) re-analyzed

the exploitation of safe sites hypothesis and pointed out that the probability of one seed falling at a safe site is independent of its dispersal distance and, if the same number of seeds are dispersed, the number of seeds expected to fall at safe sites is the same whether seeds are dispersed over a wide area or in a narrow area. They then showed that sib-competition within safe sites selects for seed dispersal in terms of exploiting safe sites because dispersing seeds over a wide area results in finding a large number of safe sites while reducing sib-competition within each safe site. However, a plant disperses its seeds within a narrow area if there is strong non-sib-competition relative to sib-competition. It is thus necessary to analyze the degree of sib- and non-sib-competition to clarify the adaptive significance of seed dispersal itself in this species.

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