

Pollination biology and breeding systems in the terrestrial orchid *Bletilla striata*

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Abstract. The levels of fruit set in different habitats (three inland populations vs. three coastal populations) and the breeding system in the terrestrial orchid *Bletilla striata* were examined in two groups of populations in Haenam-gun, Jollanam-do Province in southern Korea. In total inland populations (mean fruit set = 13.3%) showed about eight-fold higher fruit set per plant than the coastal populations (1.6%), probably due to mild climatic conditions in the inland populations during the flowering period. Honey bee workers *Apis mellifera* were observed in the inland populations, but no visitors were found in the coastal populations. However, a great increase in fruit set was achieved by hand-pollination: the percentage of fruit set through artificial self-pollination and geitonogamous pollination were close to 90%, indicating that *B. striata* is self-compatible. Agamospermy and spontaneous autogamy (automatic self-pollination) were not detected in this study. These indicate that pollinia vectors are essential for achieving fruit set in natural populations of *B. striata*. Except in one inland population examined in 2001, there was no significant correlation between the patch size per population and the average percentage of fruit set, which might reflect deception-pollination of *B. striata* and/or paucity of pollinators. Overall levels of fruit sets within and among patches in each population were homogeneous during a two-year period.

Key words: *Apis mellifera*, breeding system, *Bletilla striata*, fruit set, habitat differences, northeastern Asia, Orchidaceae, pollinators.

Introduction

Low level of fruit set is a common trait in the family Orchidaceae (Neiland and Wilcock 1998). The low level of fruit set found in many nectarless orchids is often attributed to the pollinator limitation due to lack of rewards such as nectar and pollen (Firmage and Cole 1988, Zimmerman and Aide 1989, Johnson and Nilsson 1998, Matsui et al. 2001). Several studies suggest that pollinator limitation would be the most important selection pressure of floral evolution in orchids. Thus pollinator limitation has been suggested being a factor affecting a large number of orchid species for a long period of time (Dafni and Bernhardt 1990, Neiland and Wilcock 1998). Possible causes for the low level of fruit set observed in orchids are often related to the local availability of pollinators (Inoue 1985, 1986a,b; Robertson and Wyatt 1990a,b; Johnson et al. 1998; Matsui et al. 2001), inflorescence size (Waite et al. 1991, Murren and Ellison 1996), density in local populations

(Meléndez–Ackerman and Ackerman 2001), human disturbance (Sugiura et al. 2001), habitat fragmentation (Murren 2002), habitat differences (dry vs. wet locations) (Ehlers et al. 2002), and herbivory by larvae or parasitization by flies (Whigham and O’Neill 1991, Sugiura et al. 1997, Matsui et al. 2001). For these and other reasons, levels of fruit set vary among locations in an orchid species. In addition to these biological aspects of orchid species and environmental factors, climatic conditions during flowering period are also expected to influence the levels of fruit set of orchid species in natural populations.

In Korea, *Bletilla striata* (Thunb.) Reichb. f. is a nectarless terrestrial orchid distributed in southwestern Korea, particularly in Haenam-gun, Jollanam-do Province. In this region, the species grows on humus soils under a low density of *Pinus thunbergii*, several km from the coast (hereafter referred to as ‘inland’ populations) and on sunny grass dominated areas with dwarf *Pinus thunbergii* and *Eurya japonica* (hereafter referred to as ‘coastal’ populations). After several years of field work in the area, we have observed that individuals of inland populations seem to produce more fruits than those in coastal populations. If pollinators are needed for fruit setting, but they are scarce primarily due to environmental factors (e.g. strong wind in coastal areas), then we might predict that fruit production is extraordinarily low at the coast and thus significantly lower than that for inland populations.

To test the prediction, we examined levels of fruit set in natural conditions and documented flower visitors in two groups of populations (inland vs. coastal) of *Bletilla striata* in southern Korea. In addition, we studied the breeding system of *B. striata* as the knowledge of breeding systems of orchid species in northeastern Asia is still very limited.

Materials and methods

Study species. *Bletilla striata* is 30–70 cm tall, including the inflorescence. Leaves are relatively

large (15–30 cm × 1–5 cm), robust, with many longitudinal wrinkles. The blooming period is usually from May to June in southern Korea. Flowers are reddish-purple and large (4.2–5.9 cm × 4.5–6.4 cm), and arranged in a raceme of 2–19 flowers on an erect scape (Sugiura 1995). The whitish-purple labellum is composed of three lobes. The middle one serves as landing platform for insect visitors, and its inner surface has 5-parallel ridges with wavy anterior parts. Two lateral lobes of the labellum embrace the column, and thus form a chamber (‘labellum chamber’, Sugiura 1995) into which insect visitors enter. Fruits (about 3–3.5 cm long) contain large numbers of small seeds.

The species grows in the warmer areas of Japan and China (Kitamura et al. 1986, Sugiura 1995), but on the Korean Peninsula it occurs in a few isolated populations on southwestern Korea (M. Y. Chung and M. G. Chung pers. obs.). *Bletilla striata* grows in grasses covered by pine forests, frequently forming patches connected by flattened corms (2–4 cm in diameter) and rhizomes. Many patches include dozens of ramets, often intermingled with other ones belonging to different genets (M. Y. Chung and M. G. Chung unpubl. data).

Study sites. Six study populations (each 20 × 20 m area) were chosen in Haenam-gun, Jollanam-do Province, southern Korea: the first site (hereafter referred to as HA-1) consisted of seven patches on south-facing hillsides (altitude 100 m asl) in Haenam-eup, Gugyo-ri; the second site (HA-2) consisted of six patches also on south-facing hillsides (90 m asl) in Masan-myeon, Sangdeung-ri; the third site (HA-3) was located 150 m west of HA-2; the fourth site (JU-1) consisted of nine patches on west-facing hillsides (7 m asl) in Hwangsan-myeon, Jingui-ri; the fifth site (JU-2) contained seven patches on south-facing hillsides (8 m asl) in Hwangsan-myeon, Jingui-ri; and finally the sixth site (JU-3) was 100 m eastwards from the JU-2. The population HA-1 was 8.5 km from HA-2 population, JU-1 was 14.5 km from HA-1 and JU-2 was 1 km from JU-1 in a linear distance. The HA-1, HA-2, and HA-3 populations were located inland, several km far from the coast, whereas JU-1, JU-2, and JU-3 were located near the coast. Although dominant trees or shrubs in the inland and coastal populations are similar (*Pinus thunbergii*, *Vaccinium bracteatum*, *Eurya japonica*, and *Rhododendron schlippenbachii*), most trees in the coastal populations are much smaller than those

for inland populations, probably due to strong wind in the coastal areas.

Pollinator observation. Observations for identifying pollinators for *B. striata* were conducted in the largest patches in HA-1 (patch no. 6) and JU-1 (patch no. 1) during a 8-hour period (9:00 to 17:00) for each population on 22 and 23 May 2003, respectively. Since a few visitors were observed during the 8-hour period in 2003, we spent another 8-hour period for each of the same population on 19 and 20 May 2004. During the observation period, we recorded the insect identity and its visiting frequency. Furthermore, several insects were netted and identified later by T. H. Han and J. S. Park (Gyeongsang National University).

Open pollination. Since fruit-set is the most widely used measure of reproductive success for orchids (Proctor and Harder 1994, Neiland and Wilcock 1998), we obtained information on the mating system of *B. striata* from field observations of fruit set, pollinator activities and experimental pollination tests. To quantify percentage of fruit set of *B. striata*, we marked flowering individuals with yellow ribbons and counted the number of flowering individuals and the number of flower scars per scape in HA-1, HA-2, JU-1, and JU-2 in two different years (20 May 2001 and 21 May 2003). In the study area, we recorded the total number of fruits on 12 August 2001 and 15 August 2003.

Hand pollination. On 8 – 11 May and 12 – 15 May 2003, pre-anthesis inflorescences from 165 and 137 flowering individuals of HA-3 and JU-3, respectively, were bagged with a fine mesh plastic net to exclude pollinators. A total of 212 and 153 flowers for HA-3 and JU-3, respectively, were assigned randomly to one of five pollination treatments as described in Dafni (1992): (1) emasculation without pollination for testing presence of agamospermy and to evaluate the rate of nonsexual reproduction, (2) a test for spontaneous self-pollination to measure autogamy and the need for pollinators, (3) artificial self-pollination to test self-compatibility by placing pollinia on the stigmas of the same flowers, (4) artificial geitonogamy to evaluate self-compatibility between different flowers by placing pollinia on stigmas of adjacent flowers of the same inflorescence or different inflorescence belonging to the same genet, and (5) artificial xenogamy or cross-pollination to assess cross-compatibility. After the flowers withered, the bags were removed to minimize any artificial

effects. To calculate percentage of fruit set in open pollination, the number of flower scars per scape and the number of fruits were recorded from nontreated 42 and 45 scapes in HA-3 and JU-3, respectively, on 15 August 2003.

Data analysis. To determine local heterogeneity in fruit set within patches in HA-1, HA-2, JU-1, and JU-2 populations surveyed in 2001 and 2003, we used *G* statistics for the log-likelihood ratio goodness of fit test (e.g. Matsui et al. 2001). To determine whether the average fruit set is different among patches within populations or between groups of populations (inland vs. coastal populations), we used analysis of variances (ANOVAs) because comparisons of fruit per plant is typically done using *t*-tests or ANOVAs. To test significant differences on the flower numbers per plant between inland (HA-1 and HA-2) and coastal populations (JU-1 and JU-2), we conducted unpaired *t*-test. Significance levels were corrected for multiple tests as in Šidák (1967).

Results

Pollinator. In patch HA-1 (no. 6), 26 honey bee workers *Apis mellifera* (Apidae), four *Apis cerana* (Apidae), three *Leptura aethiops* (Cerambycidae), two *Parnara guttata* (Hesperiidae), six *Episyrphus balteatus* (Syrphidae), and two *Melanostoma mellinum* (Syrphidae) visited flowers of *B. striata*. Among the six visitors, only the honey bee workers were observed to receive pollinia on the thorax of the body surface (scutellum). This pollinia attachment observed only when the bees moved backward into the labellum chamber. We observed in the patch number 6 of HA-1 that pollinia attached to the honey bees were transferred to the stigma of another flower. In patch JU-1 (1), however, we failed to observe any visitors during the 16-hour observations, probably due to strong wind in the coastal areas.

Open pollination. In total, *Bletilla striata* set fruits (on a per plant basis) at a very low level [$N=754$, $6.6\% \pm 12.98$ (standard deviation, SD)]. We found a significantly higher fruit set per plant in the inland populations than in the coastal populations in 2001 ($t=8.22$, $P=0.000$) and 2003, including

HA-3 and JU-3 ($t=9.10$, $P=0.000$) (Tables 1 and 2). However, the percentage of fruit set was similar between two inland populations (HA-1 and HA-2) in 2001 and among the three inland populations (HA-1, HA-2, and HA-3) in 2003 and a similar trend was observed in the three coastal populations (JU-1, JU-2, and JU-3) (Tables 1 and 2). Again, the mean number of flowers per scape was similar between HA-1 and HA-2 and between 2001 and 2003 and the same trend was found in the coastal populations. However, the inland populations (HA-1 and HA-2) had a significantly larger mean number of flowers than the coastal population (JU-1 and JU-2) in 2001 ($t=5.68$, $P=0.000$) and in 2003, including HA-3 and JU-3 ($t=6.05$, $P=0.000$).

We found that the number of fruits per flower among individuals or scapes within patches was generally homogeneous (G statistics for the log-likelihood ratio goodness of fit test; data not shown), except for HA-1 (patch no. 6; $G=49.18$, $P=0.0001$). A similar trend was observed among patches in each population. Out of eight tests, only one was significantly different among the patches in HA-2 in 2003 [$F_{(5, 74)}=3.57$, $P=0.0061$; type I error was adjusted for multiple tests by Šidák's (1967) method ($\alpha'=0.0064$ at $P=0.05$)]. No significant correlation of the percentage of fruit set between 2001 and 2003 was found, except for HA-2 (Spearman rank correlation analysis: $r_s=0.985$, $P=0.000$).

Hand pollination. No emasculated flowers produced fruits and no self-pollination (autogamy) was found in *B. striata*. Since agamospermy and spontaneous autogamy were not detected in this study, pollinia vectors are essential for fruit set in natural populations. Although populations of *B. striata* examined in this study showed very low fruit set in natural conditions, a significant increase in fruit set was achieved through hand-pollination compared to open pollination (Table 2). Artificial self-pollination or induced autogamy (91.0% and 87.1%), artificial geitonogamy (88.0% and 87.5%), and cross-pollination or artificial xenogamy (90.8% and 86.5%)

produced fruits in HA-3 and JU-3, respectively (Table 2). There were no significant differences in fruit set between induced autogamy and artificial geitonogamy and artificial xenogamy and between artificial geitonogamy and artificial xenogamy, indicating that *B. striata* is highly self-compatible. Finally, we found that the hand pollination was not significantly different between the two populations.

Discussion

Pollination in natural conditions. After 32 hours of field observations in 2003 and 2004, we found the honey bee *Apis mellifera* as a legitimate pollinator of *Bletilla striata* in the HA-1. This rarity of pollinators in southern Korea contrasts with the pollinators found in a study in Japan. Sugiura (1995) observed floral visitors of *B. striata* within a patch (1.0 × 2.5 m area) at Kobe in Japan and found 26 species of visitors during a total of 9.65 hours in 1992 and 1993. Sugiura reported that seven species received pollinia on their body surface of thorax: *Tetralonia nipponensis*, *Campsomeris prismatica*, *Polistes mandarinus*, *Megachile tsurugensis*, *Osmia taurus*, *Nomada japonica*, and *Apis mellifera*. We suspect that only one pollinator at the present study compared to seven pollinators might be attributed to windy weather conditions in the coastal areas (JU-1, JU-2, and JU-3) and/or probably paucity of insect fauna in the study areas. These factors would reflect approximately four-fold lower levels of fruit set in the study areas than in Japan (6.6% vs. 23.4%, respectively). Furthermore, the percentage of fruit set found in *B. striata* in southern Korea was lower than in most nectarless orchids in northeastern Asia examined (23.7% in *Calanthe sieboldii* in Japan, Sugiura et al. 1998; 10.5% in *Cypripedium macranthos* var. *rebenunse* in Japan, Sugiura et al. 2001, 2002; 15.0% in *Eulophia sinensis* in Hong Kong, Sun 1997; 11.1% in *Liparis kumokiri* in Korea, Oh et al. 2001; 19.2% in *Pogonia japonica* in Japan, Matsui et al. 2001).

Table 1. Flowering and fruit set per plant by open pollination among patches in HA-1, HA-2, JU-1, and JU-2 populations of *Bletilla striata* in 2001 and 2003. Values in no. flowers, no. fruits, and % fruit set are means with standard deviations (SD) in parentheses

Year	Patch	No. plants				No. flowers (SD)				No. fruits (SD)				% fruit set (SD)			
		HA-1	HA-2	JU-1	JU-2	HA-1	HA-2	JU-1	JU-2	HA-1	HA-2	JU-1	JU-2	HA-1	HA-2	JU-1	JU-2
2001	1	4	18	29	24	6.3 (2.22)	5.3 (1.23)	4.6 (1.82)	4.8 (1.75)	0	1.1 (1.02)	0.1 (0.31)	0.1 (0.28)	0	21.1 (19.79)	3.0 (10.21)	2.1 (7.47)
	2	6	13	11	10	4.8 (0.75)	5.2 (1.41)	3.5 (1.97)	4.7 (1.83)	0.3 (0.82)	0.5 (0.78)	0	0.1 (0.32)	6.7 (16.33)	7.3 (12.24)	0 (7.91)	2.5 (3.4)
	3	7	9	3	22	6.6 (0.79)	5.0 (1.58)	5.0 (1.00)	4.7 (1.39)	0.3 (0.49)	0.4 (0.73)	0	0.2 (0.01)	4.1 (6.98)	8.2 (12.46)	0 (10.82)	3.4 (1.8)
	4	13	10	2	25	6.1 (1.71)	5.4 (0.97)	4.5 (2.12)	4.0 (1.40)	1.1 (0.95)	0.7 (0.95)	0	0.1 (0.28)	16.9 (12.05)	12.3 (16.88)	0 (6.27)	1.8 (0)
	5	8	22	6	15	7.3 (2.19)	5.0 (1.29)	4.3 (1.21)	3.9 (2.12)	1.4 (1.69)	0.8 (0.80)	0	0	17.6 (18.17)	15.6 (14.14)	0	0
	6	18	10	7	11	6.1 (2.17)	5.5 (1.43)	4.6 (0.79)	4.4 (1.57)	1.0 (0.91)	0.9 (1.20)	0	0.1 (0.30)	19.5 (18.94)	13.9 (18.19)	0 (15.08)	4.5 (0)
	7	4		6	12	4.8 (1.50)		4.7 (2.16)	4.3 (0.97)	0		0	0	0	0	0	0
	8			6				5.2 (1.72)				0				0	
	9			10				5.2 (1.69)				0				0	
Average (SD)						6.1 (1.87)	5.2 (1.29)	4.5 (1.72)	4.4 (1.59)	0.8 (1.03)	0.8 (0.92)	0.0 (0.19)	0.1 (0.34)	13.0 (15.98)	14.1 (16.23)	1.1 (6.25)	2.2 (8.27)
2003	5	16	32	22		7.6 (2.79)	5.2 (1.17)	4.7 (1.84)	4.4 (1.81)	2.0 (2.12)	1.0 (0.89)	0.1 (0.30)	0.1 (0.21)	24.9 (29.57)	19.9 (16.93)	2.5 (9.47)	0.7 (3.05)
	4	16	8	11		4.5 (1.00)	5.0 (1.32)	3.3 (2.19)	4.6 (1.75)	0.5 (0.58)	0.3 (0.58)	0.1 (0.35)	0	12.5 (14.43)	3.9 (8.43)	6.3 (17.68)	0
	4	7	2	17		6.5 (1.00)	4.9 (1.57)	4.5 (2.12)	4.5 (1.42)	0	0	1.0 (0.00)	0	0	0	25.0 (11.74)	0
	10	10	3	23		7.0 (2.36)	5.2 (1.03)	4.7 (1.53)	4.2 (1.53)	1.4 (0.84)	0.4 (0.70)	0	0	20.2 (11.14)	7.5 (12.69)	0 (10.7)	0
	8	21	5	18		6.5 (2.42)	4.4 (0.80)	4.6 (1.14)	4.6 (2.33)	1.5 (1.60)	0.7 (0.73)	0.4 (0.35)	0	18.8 (18.10)	14.5 (16.25)	10.7 (15.34)	0
	17	10	8	7		5.9 (1.82)	5.6 (1.43)	4.6 (0.74)	4.4 (1.27)	1.4 (1.12)	0.6 (0.97)	0	0.1 (0.38)	24.1 (16.68)	9.1 (14.07)	0 (9.45)	3.6

Table 1. (Continued)

Year	Patch	No. plants				No. flowers (SD)				No. fruits (SD)				% fruit set (SD)			
		HA-1	HA-2	JU-1	JU-2	HA-1	HA-2	JU-1	JU-2	HA-1	HA-2	JU-1	JU-2	HA-1	HA-2	JU-1	JU-2
5		9	9	9	9	4.4 (0.55)	4.3 (1.94)	4.6 (0.88)	0.2 (0.45)	0	0	0	0	5.0 (11.18)	0	0	0
		5					5.4 (1.82)			0					0		
		12					5.1 (1.88)			0					0		
	Average (SD)					6.2 (2.11)	5.0 (1.21)	4.6 (1.77)	4.4 (1.60)	1.2 (1.26)	0.6 (0.78)	0.1 (0.30)	0.0 (0.12)	18.1 (17.37)	10.6 (14.77)	2.8 (9.65)	0.4 (2.76)

Our results support the prediction. In total, the inland populations [HA-1, HA-2, and HA-3; average percentage of fruit set per plant \pm SD (13.3% \pm 15.85)] showed about eight-fold higher fruit set than the coastal populations [JU-1, JU-2, and JU-3, (1.6% \pm 7.07)] ($t=12.27$, $P=0.000$). We failed to encounter honey bees or any visitors in the coastal area during the survey periods, which is attributable to relatively strong winds near the coast. If we examined only inland populations, the percentage of fruit set of *B. striata* is comparable to the average in nectarless orchids in North America (19.5%) and in tropical regions (11.5%) (Neiland and Wilcock 1998). Conversely, if we survey the fruit set in the coastal area, this could be considered as extremely low. Thus, our study demonstrates the importance of examining multiple populations to represent the percentage of fruit set in an orchid species. Fruit set data are generally known to be essential to the understanding of the evolution of floral characteristics in orchids and other flowering plants (Neiland and Wilcock 1998). Heterogeneity in fruit set among populations and over time is just beginning to be recognized as potentially affecting evolutionary processes. If floral characteristics (e.g. size of flower) of *B. striata* are adaptive, a further study on difference of floral morphology between inland and coastal populations would be necessary.

Many studies of orchids reported that a large floral display attracts more pollinators, thus would increase both male and female reproductive success (Waite et al. 1991, Murren and Ellison 1996, Ehlers et al. 2002, Stpiczyńska 2003). However, other studies revealed no significant correlation between the number of flowers and female reproductive success (Hogan 1983, Firmage and Cole 1988, Rodríguez-Robles et al. 1992, Sabat and Ackerman 1996). If flowering of a species is simultaneous on the inflorescence, then a correlation between the number of flowers and female reproductive success would be indicative of the effectiveness of the floral display size. With sequential flowering,

Table 2. Open pollination and hand-pollination scheme on May 2003 and results of the breeding system in two populations (HA-3 and JU-3) of *Bletilla striata*. All hand pollination treatments were bagged. Standard deviations (SD) are in parentheses

Test	Treatment	No.plants		Total no. flowers		Total no. fruits		% fruits set per plant (SD)	
		HA-3	JU-3	HA-3	JU-3	HA-3	JU-3	HA-3	JU-3
Open pollination	None	45	45	277	216	35	4	11.0 (14.07)	1.9 (6.46)
Hand pollination									
Agamospermy	Emasculated	32	28	46	30	0	0	0	0
Spontaneous autogamy	None	31	28	47	32	0	0	0	0
Induced autogamy	Emasculated	39	31	41	32	36	27	91.0 (27.80)	87.1 (34.08)
Artificial geitonogamy	Emasculated	25	24	36	30	32	26	88.0 (29.86)	87.5 (30.40)
Artificial xenogamy	Emasculated	38	26	42	29	37	25	90.8 (25.61)	86.5 (30.19)

however, a correlation is expected if pollinator service is constant throughout the season. The mean number of flowers per scape of *B. striata* is ca. 5 (ranged from 1 to 12 in the study sites) and each flower lasts 5 to 6 days, thus 1 or 2 open flowers were found simultaneously on the same scape. We found no significant differences of the mean number of flowers among patches within populations. Thus a larger patch should have more flowers than a smaller one. If individuals within each patch are a clone, then it is expected that larger patches would set more fruits than smaller patches. However, we found no significant correlation between patch size (number of flowering individuals per patch) and the average percentage of fruit set, except for HA-1 in 2001 (Spearman rank correlation analysis: $r_s = 0.927$, $P = 0.003$). In deception-pollinated species such as *B. striata*, overall no significant correlation might be attributable to the general notion that most of the pollination activity would occur at the beginning of the flowering season as pollinators learn to avoid the non-rewarding flowers (Nilsson 1980, Motten 1982, Ackerman 1989, Fritz 1990).

Similar percentages of fruit set were found within patches of *B. striata*, probably due to a leptokurtic distribution of pollinia dispersal by honey bees. The leptokurtic distribution of flights of honey bees was observed in other herbaceous perennials in Korea (Park and Chung 1997). Although only one test (HA-2 in 2003) found to be significantly varied among patches, several patches set fruits in 2001, but some of them did not set in 2003 and *vice versa* (Table 1). This pattern was strikingly observed in the coastal populations (JU-1 and JU-2), suggesting that a sporadic nature of *B. striata* pollination results from pollinator limitation.

Breeding system. Our artificial pollination experiments revealed a significant increase in fruit set compared to open pollination and that *B. striata* is self-compatible. Given the significant increase in fruit set achieved through hand-pollination and the lack of agamospermy and spontaneous autogamy in this study, pollinia vectors appear to be essential for fruit set in natural populations.

Conservation perspective. It is expected that the number of *B. striata* will rapidly

decrease in southern Korea due to reckless mass collection by plant sellers and enthusiasts as well as habitat destruction and fragmentation caused by construction of new roads in natural habitats containing *B. striata* (M. Y. Chung and M. G. Chung pers. obs.). Information concerning breeding systems and interactions between orchids and their pollinators is essential for long-term conservation strategies focused on maintain habitats with self-sustaining natural populations (Sugiura 1994, 1995). From a conservation perspective, a very low fruit set at the coast could be enough to increase the population, but a much larger fruit production in inland populations may not be sufficient to maintain those populations. Given the heterogeneity in fruit production between the inland and coastal populations, long-term demographic data are clearly needed.

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