Chapter 1.

Patterns of seed set and related biological interactions for *Primula sieboldii* populations in a fragmented landscape

Introduction

In recent years, instances of 'fruitless falls', i.e., seed set failure in flowering plants, have been appreciated for both cultivated and wild plants (Buchmann & Nabhan 1996). According to Buchmann & Nabhan (1996), among 258 species in which limiting factors for fruit set under natural conditions were investigated in detail, 62 percent of the species were shown to suffer from limited fruit set because of insufficient pollinator services.

Pollinator service is essential for 'reproduction by seed' in outcrossing plants and a loss or reduction in pollinator service may cause reproductive failure (reviewed by Bawa 1990; Rathcke & Jules 1993; Ågren 1996; Kearns & Inouye 1997; Allen-Wardell et al. 1998; Groom 1998; Kearns et al. 1998), a decrease in effective population size through reduced gene flow (Sork et al. 1999), or in case of self compatible plants, an inclination to selfing (Jennersten 1988; reviewed by Bawa 1990; Menges 1991a; Aizen & Feinsinger 1994), which may cause loss of genetic diversity and/or reduced progeny fitness due to inbreeding depression (Charlesworth & Charlesworth 1987; Karron et al. 1988; Karron 1989; Barrett & Kohn 1991; Menges 1991a; Husband & Schemske 1996; Markus & Diethart 1998).

Species with a sophisticated entomophilous breeding system such as heterostyly are

likely to be most vulnerable to the detrimental effects of pollinator loss or isolation, resulting in fruitless falls through compatible pollen limitation. *Primula sieboldii* E. Morren (Primulaceae) provides a typical example of a plant species threatened by reduced pollinator service, i.e., seed set failure and strong fertility selection for self-fertile morphs (Washitani et al. 1991, 1994b). Heterostylous species require specific pollinators for legitimate pollination between mutually compatible morphs (Washitani et al 1994b).

Although *P. sieboldii* was once very common, in recent years it has declined and is now listed as VU (vulnerable) in the Japanese plant red list (Environment Agency 1997). Most remaining populations of the species are more or less isolated because of habitat fragmentation (Endangered Plant Survey Group 1989) and are suspected to be subjected to pollinator limitations or other detrimental impacts on fertility. Serious effects of pollinator loss have been suggested for a *P. sieboldii* population in a small, isolated nature reserve (Washitani et al. 1991, 1994b).

However, flower-visitor assemblages for any one plant species vary through time and space (e.g., Horvitz & Schemske 1990; Herrera 1995; Waser et al. 1996), so that seed set failure in a certain year could be merely in the range of natural fluctuation because of yearly variation in pollinator availability. In addition, pollinator loss is not the sole reason for the seed set failure of plant populations in fragmented landscapes. A reduced opportunity for mating because of isolation, i.e., a typical form of the Allee effects (Allee 1951), may be another major cause of fruitless falls for small populations or isolated genets of declining populations (Washitani 1999). The relative importance and/or concerted influences of pollinator limitation on plant reproductive success versus within-plant resource or genetic limitations must be analyzed to clarify the precise status of the circumstances of the reproduction of an isolated plant population.

Moreover, there are many other biological factors, such as herbivores and pathogens,

that affect the reproduction success of a plant population (Washitani et al. 1996). Therefore, in order to determine the contribution of pollinator limitations or population size or structure to plant reproductive failure, various factors potentially affecting fertility must be evaluated simultaneously, as well as comparing a large number of populations in a landscape for a number of seasons.

In the present study, such an approach was attempted and spatial and temporal variations in fruit and seed sets and biological factors limiting them were studied for 24 *P. sieboldii* populations. The studied populations were growing in southern Hokkaido, where many populations of the species remain, although intensively fragmented and isolated.

The species has following features that are useful in such a comparative study. 1) Individual genets can be easily identified because of a large variation in floral morphology (i.e., size, color, and shape; Washitani et al. 1991). 2) Possible mating counterparts for each genet can be specified to some degree, because self- and intra- morph pollination are largely incompatible (Washitani et al. 1994b). 3) Through previous studies, biological factors affecting the reproductive success of the species, pollinators, herbivores, and pathogens are relatively well understood (Washitani et al. 1994a, 1996). 4) Pollinator availability for individual populations can be assessed quantitatively using the claw marks left by effective pollinators, i.e., queen bumblebees (Washitani et al. 1994a).

Materials and Methods

PLANT SPECIES AND STUDY AREA

Primula sieboldii E. Morren (Primulaceae) is a clonally growing geophyte that once was common in a range of moist habitats throughout Japan. Each genet of the species is composed of various numbers of physiologically independent ramets, which are clonally propagated by short rhizomes.

In the Hidaka region of the southern Hokkaido, *P. sieboldii* is closely associated with the maritime, deciduous, broad-leaved forests dominated by *Quercus dentata* Thunb. ex Murray.

The present study was carried out with 24 *P. sieboldii* populations (Fig. 1) located within an area of 17 km × 20 km in the municipality of Monbetsu (42° 30' N, 142° 0' E, at an altitude of 20-150 m a.s.l.) in the Hidaka region. Annual mean air temperature and annual precipitation as recorded at the standard meteorological station at Monbetsu (9-year averages for 1987-1995) are 7.2℃ and 976.9 mm, respectively. The daily mean, maximum, and minimum air temperatures for early June, the peak flowering season of *P. sieboldii* (3-year averages for 1995-1997), are 11.3, 14.5, and 8.4℃, respectively.

In this region, the landscape has already been heavily fragmented, mainly because of the clearance of *Q. dentata* forests for pasture development. Total area occupied by *Q. dentata* forests in 1983 was as small as 14.1% of that in 1953 (Fig. 2).

Almost all the populations of *P. sieboldii* were surveyed in this study. Among the 24 populations investigated in the present study, 18 populations contained more than six genets (these populations will be labeled using uppercase letters) and six populations with less than four genets (these will be labeled using lowercase letters). Most of the populations

grow in the fragmented forests of *Q. dentata* that have been preserved as windbreaks, but populations J and Q grow in the newly planted forest of *Robinia pseudoacacia* L.

MEASUREMENTS OF BASIC POPULATION TRAITS

In each population, the number of all genets having any flowering ramets and the number of flowering ramets per individual genet were counted. Individual genets were mapped and measured for their occupied area by paces and a scale. For the largest population, P (Fig 1), these measurements were carried out in the middle part (2500 m^2) of the whole population, which extended for more than 3 ha. In populations C, D, G, H, O, and Q (Fig. 1), I surveyed only a part of each population in 1995, but the entire population in 1996 and 1997. Area-based densities for the genets and ramets were calculated from the ramet map for individual populations.

MEASUREMENTS OF BIOLOGICAL FACTORS AND SEED PRODUCTION

In the flowering season of 1995, 1996, and 1997, fruit and seed sets, pollinator availability, and antagonistic biological factors were measured. In the small populations containing less than 10 genets, the measurements were carried out using all the genets, while in larger populations, 10 flowering genets from each of the long-styled and the short-styled morph in 1995 and 1997, but 20 genets from each of the morphs in 1996 were arbitrarily chosen for the measurements in each population.

POLLINATOR AVAILABILITY

The most important pollinator for *P. sieboldii* is thought to be the queens of *Bombus diversus tersatus* Smith (Washitani et al. 1994a). On visiting the flowers of *P. sieboldii,* the queen bumblebees cling to the flower petals, leaving clear claw marks on the petals.

They are therefore useful indicators of the pollinator services provided by the bumblebees (Washitani et al. 1994a).

In the late flowering season of *P. sieboldii,* when almost all the flowers of all populations had bloomed, inflorescences with or without claw marks were counted for individual genets. The pollinator availability for each population was evaluated by the proportion of inflorescences with flowers on which I recognized claw marks.

For populations P, J, and Q (Fig. 1) in 1993 the data collected by Matsumura & Washitani (2000) were used.

FRUIT AND SEED SETS AND ANTAGONISTIC BIOLOGICAL FACTORS

In mid July, 10-20 infructescences with matured capsules and/or flower vestiges were collected from the flowering ramets investigated. The numbers of capsules, vestigial flowers, and matured seeds in individual capsules were counted. The presence or absence of any damages to flowers, capsules, or seeds by herbivores or fungi, including *Urocystis tranzshelina* (Lavrov) Zundel (Ustilaginales), a specialist pathogen of *P. sieboldii* (Kakishima et al. 1995), was also recorded. Population means for fruit and seed set per flower and the proportions of the flowers consumed by herbivores or infected by fungi were calculated from these data.

For populations P, J, and Q (Fig. 1) in 1993 and 1994 the data collected by Matsumura & Washitani (2000) were used.

ARTIFICIAL POLLINATION

During peak flowering of *P. sieboldii* in 1996, hand pollination was performed for seven genets (three long-styled and four short-styled) in population J, in which pollinator availability was relatively low.

In the late May, immediately before flowering of *P. sieboldii*, 20 randomly chosen ramets from the individual genets were marked at the stalk with small strips of vinyl chloride tape and the inflorescences were individually wrapped with fine nylon mesh with 160 μm square openings. Four arbitrarily chosen ramets from each genet were subjected to each of the following 3 treatments: (1) anther removal and self- (within flower) pollination (10-28 flowers), (2) anther removal and inter-morph pollination (legitimate pollination) (6-34 flowers), and (3) open pollination control, without wrapping the inflorescences (5-24 flowers). Anther removal treatment was carried out before anthesis. The pollen application was performed by rubbing the recipient stigma with the dehisced anthers from a donor flower picked with fine forceps. Whenever new flowers bloomed in the inflorescence, these treatments were repeated. Immediately after hand pollination, inflorescences were covered with the fine nylon mesh to exclude any insects.

After the fruits had matured in July, the infructescences of the experimental plants were harvested and the seeds from individual capsules were counted.

STATISTICAL ANALYSES

Significant differences in numbers of genets and ramets between the morphs in each population with more than six genets were tested by a Chi-square test for independence or Fisher's exact probability test. The latter was used when data had cells of which the expected frequency was five or less.

Differences in the proportions of flowers infected by fungi or consumed by herbivores between the years were tested by using ANOVA (Sokal & Rohlf 1995). Paired comparisons between the years were tested by using Sheffé's *post hoc* test (Sheffé 1959). The data for the proportion of flowers infected by fungi, the proportion of flowers consumed by herbivores, and fruit set were arcsine transformed before parametric statistical analyses were carried

out (Sokal & Rohlf 1995). Significant differences in the values between the populations were tested by Chi-squared test for independence. Data from population u were excluded from data set for the Chi-squared test because the sample number was too small to test.

Effects of morph, population, and their interaction on seed set per flower were analyzed by two-way ANOVA (Sokal & Rohlf 1995).

The significance of the relationship between pollinator availability and population means of fruit and seed sets per undamaged flower was examined by product moment correlation coefficients. The data for pollinator availability and fruit set per undamaged flower were arcsine transformed before parametric statistical analyses (Sokal & Rohlf 1995).

All the significance levels for the ANOVA were based on type III sums of squares. All statistical tests were performed by using statistical packages Super ANOVA (Abacus-Concepts, Calabasas, CA; Abacus-Concepts 1989) and Stat View 4.11 (Abacus-Concepts, Calabasas, CA; Abacus-Concepts 1992).

Results

POPULATION TRAITS

The total number of flowering genets varied greatly among the populations, ranging from 1 to 183 in 1995, from 1 to 306 in 1996, and 1 to 396 in 1997, respectively (Table 1). Several populations in pasture and roadside habitats tended to have smaller numbers of genets (populations s, t, u, v, w, and x). All of these populations were isolated from the closest *P. sieboldii* population by 60 m to 250 m. The number of total flowering ramets also varied greatly among the populations, ranging from three to 2833 in 1996 and from one to 2843 in 1997 (Table 1).

Occurrences of the long- and short-styled morph genets were roughly equal within almost all populations containing more than six genets, while morph bias was marked in smaller populations (populations s, t, u, v, w, and x) because of the stochasticity caused by a small sample size (Table 1). The number of flowering ramets of the short-styled morph was significantly higher than that of the long-styled morph in most of the larger populations (Chi-squared test for independence, $P < 0.0001$ for the populations A, E, F, G, J, M, N, P, and R; $P < 0.05$ for population D in 1996; $P < 0.0001$ for the populations A, E, F, J, M, P, Q, and R; $P<0.001$ for the population G, $P < 0.05$ for the population N in 1997). In most of the populations, there were no marked differences in the genet and ramet densities between the years (Table 1).

BIOLOGICAL FACTORS AFFECTING SEED PRODUCTION

Pollinator availability, which was assessed by the proportion of flowering inflorescences with claw marks, varied beween the populations, ranging from 0.04 to 0.98 in 1995 (mean

± s.d., 0.67 ± 0.22), while it was generally high in most populations in 1996 (mean ± s.d., 0.79 ± 0.22) and 1997 (mean ± s.d., 0.82 ± 0.22; Table 2).

Several kinds of lepidopteran larva, including *Platyptilia jezoensis* Matsumura (Pterophoridae) were observed to consume the flowers or fruits of *P. sieboldii* in some populations (Table 3). The proportion of the flowers consumed by herbivores varied significantly among the populations in each year (Chi-squared test for independence: $P < 0.0001$), but there was no significant difference between the years (Table 3; ANOVA: d.f. = 2, $F = 0.119$, $P = 0.89$).

Infection by the smut fungus *Urocystis tranzshelina* was observed only in populations P, Q, L, and M. The proportion of flowers infected by any fungi, including *U. tranzshelina,* varied significantly among the populations within each year (Chi-squared test for independence: $P < 0.0001$) and also over the years (ANOVA: d.f. = 2, $F = 7.192$, $P < 0.01$; Table 4). The mean was significantly higher in 1996 than in 1995 (Sheffé's *post hoc* test, $P = 0.002$) and 1997 (Sheffé's *post hoc* test: $P < 0.05$).

FRUIT AND SEED SETS

The quantity of fruit and seed set varied significantly among populations and between morphs within each year. Fruit set per flower varied significantly among the populations (Chi-squared test for independence: $P < 0.0001$ for each year) and between the morphs (Chi-squared test for independence: $P < 0.0001$ for each year; Fig. 3). Two-way ANOVA for seed set per flower revealed that both the effects of population (d.f. = 19, $F = 42.24$, $P < 0.0001$ in 1995; d.f. = 15, $F = 83.15$, $P < 0.0001$ in 1996; d.f. = 19, $F = 36.05$, $P < 0.0001$ in 1997) and morph (d.f. = 1, $F = 84.24$, $P < 0.0001$ in 1995; d.f. = 1, $F = 259.77$, $P < 0.0001$ in 1996; d.f. = 1, $F = 92.20$, $P < 0.0001$ in 1997) were significant and that the interaction of these factors was also significant (d.f. = 16, $F = 9.15$, $P < 0.0001$ in 1995,

d.f. = 13, F = 12.70, $P < 0.0001$ in 1996, d.f. = 15, F = 6.25, $P < 0.0001$; Fig. 4).

In smaller populations with less than four genets, no or negligible numbers of fruit and seeds were set during the study period (Figs. 3 and 4). The fruit and seed sets varied within each year among the populations with more than six genets (Fig. 3; ANOVA for seed set: d.f. = 16, F = 46.86, $P < 0.0001$ in 1995; d.f. = 13, F = 94.66, $P < 0.0001$ in 1996; d.f. = 14, F = 45.53, $P < 0.0001$ in 1997). Variation in the amount of fruit set among the populations (Fig. 3; Chi-squared test for fruit set: $P < 0.0001$ for every year) was largely responsible for the variation in the amount of seed set among the populations (Fig. 4; ANOVA for seed set: d.f. = 16, F = 46.86, $P < 0.0001$ in 1995; d.f. = 13, F = 94.66, $P < 0.0001$, in 1996; d.f. = 14, F = 45.53, $P < 0.0001$ in 1997). In some populations in which fruit and seed sets were relatively low (especially populations J and Q in 1995) the mean values of fruit and seed set per flower were higher in the long-styled than in the short-styled morph (Figs. 3 and 4).

INTERPOPULATION PATTERNS OF SEED SET AND EFFECTS OF BIOLOGICAL FACTORS

In the populations with more than six genets, the predominant causes for fruit set failure varied year by year (Fig. 5).

In 1995, proportions of failed flowers without any damage by fungi or herbivores were relatively high (Fig. 5), but fruit set per flower varied greatly among the populations (Fig. 3). Correlations of fruit (r = 0.589, P = 0.011) and seed set (r = 0.688, $P < 0.01$) with pollinator availability in the populations were highly significant in 1995 (Figs. 6 and 7). In contrast, the relationships were not significant in 1996 and 1997 (Figs. 6 and 7) and fungal infection accounted for more than one-half of fruit set failure in populations D, E, F, J, M, O, Q, and R in 1996 and in population F in 1997 (Fig. 5).

Mean seed set per undamaged flower in population P, in which pollinator availability was relatively high throughout the 5 years from 1993 to 1997, was constantly high except in 1997 (Fig. 8). In contrast, in populations J and Q, seed set was constantly low during 1993-1995 when pollinator availability was limited and relatively high in 1996 and 1997 when pollinator availability increased (Fig. 8).

ARTIFICIAL POLLINATION

Artificial legitimate pollination resulted in a high genet mean of seed set per flower in both morphs, ranging from 45.82 to 90.67 for the long-styled, and from 28.33 to 74.64 for the short-styled morph (Fig. 9). These seed set values are comparable to the naturally recorded mean seed set per undamaged flower in population P with constantly high pollinator availability (Fig. 7). Self pollination increased seed sets in only three long-styled morph genets (Fig. 9). Spontaneous seed sets were found in only two among the three long-styled morph genets (Fig. 9).

Discussion

In today's world, habitat fragmentation ranks among the most serious causes of biodiversity degradation (Wilcox & Murphy 1985; McNeely et al. 1990). Habitat fragmentation as well as other threats to biodiversity, such as over-exploitation and biological invasion, results in small population sizes and isolated populations or genets with elevated probabilities of extinction (Lande 1987; Holsinger & Gottlieb 1991; Menges 1991b). The impairment of species interaction essential to reproduction may have a detrimental impact on an isolated plant population (Janzen 1974; Howe 1984). Especially, reduced pollinator services due to fauna degradation occur ubiquitously in present day landscapes throughout the world (Buchmann & Nabhan 1996). The absence of pollinators and the solitude of isolated plants may impose several types of drawbacks on a plant population depending on the species' reproductive biology and population history (Washitani 1999).

Analysis of the relative importance or combined effects of pollinator limitation and within-plant factors on plant reproductive success is needed before any generalizations or discernible patterns that affect remedial techniques can be recognized.

The present study demonstrated that not only fertility but also limiting factors were significantly variable depending on the year and site among the *P. siboldii* populations within a regional landscape.

In the isolated small populations (genets $\leqq$ 3), which were left in pastures after deforestation, fertility was constantly negligible for all the plants, probably because of a lack of compatible mating partners due to stochasticity caused by small sample size, i.e., one typical form of the Allee effect. Seed production is thought to be more sensitive to habitat fragmentation and isolation in heterostylous or dioecious plants than in plants with

other breeding systems because the potential mating partners are more limited (Levin 1975; Wyatt & Hellwig 1979; DeMauro 1993; Ågren 1996). However, solitude is suggested to be a more common reason for pollination failure and thus infertility of wild plants irrespective of whether the plant is a pollinator specialist or generalist (Washitani 1999).

In the larger populations (genets $\geqq$ 7), the seed set in the individual populations was strongly limited by pollinator availability in certain years. Pollinator availability has been thought to be the main factor responsible for the fertility variation of *P. sieboldii* between landscapes (Washitani et al. 1991; 1994a, b). Within this highly fragmented landscape, it is an important factor creating among-population variation in the years when pollinator activity is generally limited. Plant species depending on specific pollinators, i.e., pollinator specialists, would be exposed to a higher risk of pollination limitation because of pollinator loss when compared with a pollinator generalist (Allen-Wardell et al. 1998; Washitani 1999).

However, antagonistic interactions with herbivores and pathogens were suggested to be the major factors causing variation among the populations in the years without pollinator limitation. A previous study revealed that the negative impacts were largely local and mainly restricted to the subpopulations constituting a metapopulation of a forest habitat with high levels of pollinator availability (Washitani et al. 1996).

In 1997, seed production of *P. sieboldii* invariably low in most of the populations, irrespective to relatively high pollinator availability. Flower damage caused by severe spring storm in the height of flowering of *P. sieboldii* would be among the reasons for generally low seed set of this year.

Population P, with a constantly high pollinator availability and seed set, was located in an extensive network of windbreak *Q. dentata* forests. The forest floor of this habitat contained many plant species having flowers that can be foraged by bumblebee queens and

workers throughout the growing seasons of their colonies. Intermittent summer grazing by cows, which prevent domination by the perennial dwarf bamboo grass *Sasa nipponica* (Makino) Makino et Shibata (Gramineae) and other summer competitive plants, would be an essential condition for maintaining such a rich forest floor flora.

In 1995, when the correlations of fruit and seed sets with pollinator availability were highly significant, pollinator availability and seed set were low in populations J and Q. In the newly forested habitats of these populations with highly fluctuating pollinator availability over the study years, the herbaceous layer was overdominated by *S. nipponica,* and summer to autumn flowering plant species were scarce.

These spatial fluctuation patterns accorded with the finding of Jennersten (1988), who found that the diversity and abundance of flower-visiting insects in fragmented habitats were typically low, but with high local and temporal variation, while in undisturbed habitats, insect diversity and abundance were more constant. In ecological systems, the network of biological interactions fluctuate within a certain range because of ecosystem stability and the evolution of cooperation (Perry 1995). However, in fragmented landscapes, the amplitude of fluctuation of biological agents is larger than that in undisturbed landscapes and is linked to an irreversible decrease in the biological agents (Shaffer 1981; Gilpin & Soulè 1986). I cannot clearly conclude yet whether the fluctuation of pollinator availability recognized in populations J and Q over the study period are in the direction of an irreversible decrease. For any conclusions to be drawn, further monitoring is needed.

In populations J and Q, in which the mean fruit and seed set in a given year were low because of limited pollinator availability, the fruit and seed sets of the year differed significantly between the heterostylous morphs, and those were higher in the long- than in the short-styled morph. Previous studies have suggested that the stigmas of the long-styled morph capture a large amount of self- or non-self intramorph pollen grains with low

pollinator availability (Washitani et al. 1994b). In the populations with low pollinator availability, flowers deficient in compatible pollen deposition might increase selfing rate because of the partial self-compatibility of the long-styled morph, which was also ascertained in the hand pollination experiment. Strong inbreeding depression is suggested to manifest itself in the early life stages of the progeny (Kawakami, Nishihiro & Washitani, in preparation) and partially selfed mother plants can leave much fewer fit progeny than expected from the quantity of seeds produced. Simulation with a genetic population model predicts an overall recruitment failure under conditions of constant severe pollinator limitation in the case of the presence of very strong inbreeding depression (Washitani 1996).

Before I can draw any firm conclusions on the conditions for population persistence through 'reproduction by seeds', the probability of successful seed germination and seedling establishment in a habitat should be properly evaluated. However, successful seed production is a prerequisite for reproductive success. It is suggested from the present study that population size influencing both morph balance and within-morph compatibility (Darwin 1877; Johnston 1993) and pollination services by queen bumblebees are among the essential requirements for the reproductive success of this species. In order to fulfil the above requirements, a large population size and maintenance of extensive networks of habitats of *Q. dentata* forests and appropriate management to intervene in the development of *S. nipponica* stands would be needed.

Table 1 Traits of the *Primula sieboldii* populations investigated in 1995, 1996, and 1997

		Occupied area (m^2)			No. of flowering genets									Flowering genet density m^{-2}								
		1995	1996	1997	1995			1996			1997			1995			1996			1997		
Population	Habitat				Total	Long	Short	Total	Long	Short	Total	Long	Short	Total	Long	Short	Total	Long	Short	Total	Long	Short
(No. of genets ≧7)																						
A	forest	8400	8400	8400	68	27	41	42	16	26	95	38	57	0.01	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.01
B	forest	525	480	480	14	6	8	17	8	9	21	10	11	0.03	0.01	0.02	0.04	0.02	0.02	0.04	0.02	0.02
C	forest	60	–	219	13	8	5	–	–	–	43	21	22	0.22	0.13	0.08	–	–	–	0.20	0.10	0.10
D	pasture	123	249	249	23	12	11	46	16	30	43	17	26	0.19	0.10	0.09	0.19	0.06	0.12	0.17	0.07	0.10
E	forest	340	255	255	16	6	10	21	6	15	29	11	18	0.05	0.02	0.03	0.08	0.02	0.06	0.11	0.04	0.07
F	forest	700	816	816	23	8	15	27	7	20	58	19	39	0.03	0.01	0.02	0.03	0.01	0.03	0.07	0.02	0.05
G	forest	36	132	132	12	4	8	22	5	17	20	6	14	0.33	0.11	0.22	0.17	0.04	0.13	0.15	0.05	0.11
H	forest	48	255	255	21	10	11	21	5	16	46	16	30	0.44	0.21	0.23	0.08	0.02	0.06	0.18	0.06	0.12
I	forest	300	–	–	18	9	9	–	–	–	–	–	–	0.06	0.03	0.03	–	–	–	–	–	–
J	forest	1375	1182	1182	183	87	96	107	43	64	253	104	149	0.13	0.06	0.07	0.09	0.04	0.05	0.21	0.09	0.13
K	forest	110	–	–	7	3	4	–	–	–	–	–	–	0.06	0.03	0.04	–	–	–	–	–	–
L	forest	160	–	–	12	6	6	–	–	–	–	–	–	0.08	0.04	0.04	–	–	–	–	–	–
M	forest	2000	2760	2760	51	29	22	48	28	20	84	51	33	0.03	0.01	0.01	0.02	0.01	0.01	0.03	0.02	0.01
N	forest	1500	1980	1980	43	20	23	32	19	13	71	33	38	0.03	0.01	0.02	0.02	0.01	0.01	0.04	0.02	0.02
O	forest	117	928	928	81	43	38	49	23	26	73	33	40	0.69	0.37	0.32	0.05	0.03	0.03	0.08	0.04	0.04
P (a part)	forest	2500	2500	2500	177	87	90	306	161	145	396	185	211	0.07	0.03	0.04	0.12	0.06	0.06	0.16	0.07	0.08
Q	forest	600	1700	1700	22	11	11	220	115	105	259	126	133	0.04	0.02	0.02	0.13	0.07	0.06	0.15	0.07	0.08
R	forest	–	1680	1680	–	–	–	35	15	20	60	28	32	–	–	–	0.02	0.01	0.01	0.04	0.02	0.02
(No. of genets ≦3)																						
s	pasture	16	–	–	2		2	–	–	–	–	–	–	–		–	–	–	–	–	–	–
t	pasture	0.06	0.06	0.06	1		1	1		1	1		1	–		–	–		–	–		–
u	pasture	0.06	0.04	0.04	1		1	–	–	–	1		1	–		–	–	–	–	–		–
v	pasture	–	0.36	0.36	–	–	–	1	1		1	1		–	–	–	–	–		–	–	
w	roadside	–	–	0.75	–	–	–	–	–	–	2		2	–	–	–	–	–	–	–		–
x	roadside	–	–	6	–	–	–	–	–	–	3	1	2	–	–	–	–	–	–	–	–	–

'–' indicates 'lack of data' or 'not calculated'. Blank indicates absence of genet. 'Long' or 'Short' indicates the long-styled or short-styled morph.

Table 1 Continued.

	No. of flowering ramets						Flowering ramet density m^{-2}					
	1996			1997			1996			1997		
Population	Total	Long	Short	Total	Long	Short	Total	Long	Short	Total	Long	Short
(No. of genets ≧7)												
A	415	94	321	790	231	559	0.05	0.01	0.04	0.09	0.03	0.07
B	373	212	161	305	170	135	0.78	0.44	0.34	0.64	0.35	0.28
C	–	–	–	210	118	92	–	–	–	0.96	0.54	0.42
D	988	443	545	214	94	120	3.97	1.78	2.19	0.86	0.38	0.48
E	736	174	562	861	247	614	2.89	0.68	2.20	3.38	0.97	2.41
F	1053	152	901	1040	295	745	1.29	0.19	1.10	1.27	0.36	0.91
G	264	72	192	126	34	92	2.00	0.55	1.46	0.95	0.26	0.70
H	119	46	73	347	192	155	0.47	0.18	0.29	1.36	0.75	0.61
I	–	–	–	–	–	–	–	–	–	–	–	–
J	1730	545	1185	1697	643	1054	1.46	0.46	1.00	1.44	0.54	0.89
K	–	–	–	–	–	–	–	–	–	–	–	–
L	–	–	–	–	–	–	–	–	–	–	–	–
M	1835	1205	630	2843	2005	838	0.67	0.44	0.23	1.03	0.73	0.30
N	147	108	39	291	172	119	0.07	0.06	0.02	0.15	0.09	0.06
O	341	162	179	314	135	179	0.37	0.18	0.19	0.34	0.15	0.19
P (a part)	2833	1192	1641	2055	723	1332	1.13	0.48	0.66	0.82	0.29	0.53
Q	2441	1261	1180	2707	1183	1524	1.44	0.74	0.69	1.59	0.70	0.90
R	1089	341	748	1178	453	725	0.65	0.20	0.45	0.70	0.27	0.43
(No. of genets ≦3)												
s	–	–	–	–	–	–	–	–	–	–	–	–
t	3		3	3		3	–		–	–		–
u	–	–	–	1		1	–	–	–	–		–
v	5	5		14	14		–	–		–	–	
w	–	–	–	23		23	–	–	–	–		–
x	–	–	–	27	1	26	–	–	–	–	–	–

Table 2 Mean ± S.D. of proportion of inflorescences with claw marks of bumblebees in 1995, 1996, and 1997 for the populations of *Primula sieboldii* studied

	1995						1996						1997					
Population	Total	n	Long	n	Short	n	Total	n	Long	n	Short	n	Total	n	Long	n	Short	n
(No. of genets ≧7)																		
A	0.68±0.44	46	0.60±0.47	20	0.54±0.48	26	0.91±0.14	26	0.97±0.05	11	0.86±0.17	15	0.83±0.19	20	0.82±0.21	10	0.83±0.19	10
B	0.67±0.27	13	0.68±0.28	6	0.67±0.27	7	0.84±0.14	12	0.84±0.11	5	0.84±0.17	7	0.94±0.09	15	0.97±0.05	7	0.91±0.12	8
C	0.98±0.09	12	0.99±0.04	8	0.90±0.13	4	–	–	–	–	–	–	0.82±0.22	16	0.76±0.25	8	0.88±0.19	8
D	0.58±0.28	13	0.66±0.22	7	0.48±0.33	6	0.92±0.16	17	0.98±0.06	7	0.89±0.20	10	0.73±0.34	16	0.72±0.42	7	0.74±0.30	9
E	0.63±0.22	9	0.57±0.28	3	0.67±0.21	6	0.85±0.14	13	0.83±0.11	5	0.87±0.17	8	0.96±0.07	17	0.97±0.05	8	0.94±0.08	9
F	0.68±0.29	14	0.67±0.31	6	0.70±0.30	8	0.92±0.16	16	0.88±0.25	6	0.95±0.08	10	0.94±0.08	21	0.93±0.10	10	0.96±0.06	11
G	0.57±0.26	8	0.40±0.00	2	0.62±0.29	6	0.77±0.23	15	0.80±0.27	5	0.76±0.22	10	0.83±0.24	12	0.74±0.38	4	0.88±0.14	8
H	0.98±0.06	16	0.98±0.05	8	0.98±0.07	8	1.00±0.01	15	1.00±0.00	5	0.99±0.02	10	0.75±0.33	19	0.70±0.36	11	0.84±0.28	8
I	0.65±0.36	5	0.53±0.45	3	0.82±0.10	2	–	–	–	–	–	–	–	–	–	–	–	–
J	0.04±0.14	20	0.08±0.20	10	0.00±0.00	10	0.25±0.26	21	0.12±0.14	10	0.37±0.30	11	0.67±0.24	20	0.54±0.23	10	0.80±0.16	10
K	0.93±0.10	7	0.88±0.13	3	0.97±0.06	4	–	–	–	–	–	–	–	–	–	–	–	–
L	0.91±0.24	9	0.99±0.03	5	0.82±0.36	4	–	–	–	–	–	–	–	–	–	–	–	–
M	0.81±0.21	19	0.85±0.18	9	0.77±0.24	10	0.85±0.18	19	0.78±0.21	10	0.93±0.10	9	0.74±0.31	20	0.66±0.32	10	0.81±0.30	10
N	0.61±0.26	17	0.63±0.29	8	0.60±0.26	9	0.83±0.29	18	0.80±0.25	9	0.86±0.33	9	0.87±0.28	21	0.83±0.26	10	0.91±0.30	11
O	0.66±0.30	22	0.67±0.36	11	0.66±0.25	11	0.93±0.17	19	0.94±0.18	10	0.92±0.16	9	0.91±0.15	18	0.91±0.17	9	0.91±0.13	9
P (a part)	0.83±0.15	20	0.85±0.17	10	0.81±0.14	10	1.00±0.03	40	1.00±0.00	20	0.99±0.04	20	1.00±0.00	20	1.00±0.00	10	1.00±0.00	10
Q	0.45±0.44	21	0.18±0.34	11	0.75±0.34	10	0.27±0.23	43	0.19±0.17	16	0.31±0.25	27	0.76±0.24	21	0.85±0.19	11	0.66±0.26	10
R	–	–	–	–	–	–	0.87±0.12	19	0.90±0.11	8	0.85±0.13	11	0.88±0.15	20	0.85±0.17	10	0.90±0.13	10
(No. of genets ≦3)																		
s	0.70±0.28	2			0.70±0.28	2	–	–	–	–	–	–	–	–	–	–	–	–
t	0.33	1			0.33	1	0.67	1			0.67	1	1.00	1			1.00	1
u	0.63	1			0.63	1	–	–	–	–	–	–	0.00	1			0.00	1
v	–	–	–	–	–	–	0.80	1	0.80	1			0.93	1	0.93	1		
w	–	–	–	–	–	–	–	–		–	–	–	0.93±0.10	2			0.93±0.10	2
x	–	–	–	–	–	–	–	–	–	–	–	–	1.00±0.00	3	1.00	1	1.00±0.00	2

'–' indicates 'lack of data' or 'not calculated'. Blank indicates absence of genet. 'Long' or 'Short' indicates the long-styled or short-styled morph.

Table 3 Mean ± S.D. of proportion of flowers consumed by herbivores in 1995, 1996, and 1997 for the populations of *Primula sieboldii* studied

	1995						1996						1997					
Population	Total	n	Long	n	Short	n	Total	n	Long	n	Short	n	Total	n	Long	n	Short	n
(No. of genets ≧7)																		
A	0.08 ± 0.27	1052	0.08 ± 0.27	410	0.08 ± 0.27	642	0.04 ± 0.19	994	0.03 ± 0.18	286	0.04 ± 0.19	708	0.06 ± 0.24	942	0.08 ± 0.27	436	0.05 ± 0.21	506
B	0.09 ± 0.29	564	0.09 ± 0.29	305	0.10 ± 0.30	259	0.48 ± 0.50	432	0.51 ± 0.50	224	0.45 ± 0.50	208	0.05 ± 0.21	491	0.01 ± 0.11	268	0.09 ± 0.29	223
C	0.35 ± 0.48	383	0.34 ± 0.47	284	0.38 ± 0.49	99	–	–	–	–	–	–	0.08 ± 0.28	578	0.11 ± 0.31	312	0.05 ± 0.22	266
D	0.18 ± 0.39	566	0.25 ± 0.43	350	0.08 ± 0.27	216	0.10 ± 0.30	800	0.10 ± 0.31	316	0.10 ± 0.29	484	0.03 ± 0.18	349	0.02 ± 0.15	218	0.05 ± 0.21	131
E	0.06 ± 0.23	887	0.09 ± 0.29	296	0.04 ± 0.19	591	0.07 ± 0.26	1090	0.06 ± 0.23	362	0.08 ± 0.27	728	0.14 ± 0.35	863	0.26 ± 0.44	370	0.05 ± 0.21	493
F	0.12 ± 0.33	678	0.17 ± 0.38	271	0.09 ± 0.29	407	0.17 ± 0.37	1154	0.28 ± 0.45	223	0.14 ± 0.35	931	0.07 ± 0.26	1217	0.13 ± 0.33	574	0.02 ± 0.15	643
G	0.10 ± 0.30	347	0.13 ± 0.34	76	0.09 ± 0.29	271	0.06 ± 0.24	746	0.10 ± 0.30	239	0.05 ± 0.21	507	0.08 ± 0.28	292	0.17 ± 0.38	64	0.06 ± 0.23	228
H	0.20 ± 0.40	266	0.35 ± 0.48	105	0.11 ± 0.31	161	0.02 ± 0.14	419	0.02 ± 0.13	177	0.02 ± 0.14	242	0.10 ± 0.30	738	0.07 ± 0.26	378	0.13 ± 0.34	360
I	0.11 ± 0.31	261	0.19 ± 0.40	144	0.00 ± 0.00	117	–	–	–	–	–	–	–	–	–	–	–	–
J	0.09 ± 0.28	1087	0.17 ± 0.37	501	0.02 ± 0.14	586	0.07 ± 0.25	1123	0.07 ± 0.25	536	0.06 ± 0.24	587	0.06 ± 0.24	861	0.09 ± 0.29	448	0.03 ± 0.17	413
K	0.12 ± 0.32	221	0.08 ± 0.28	49	0.13 ± 0.34	172	–	–	–	–	–	–	–	–	–	–	–	–
L	0.27 ± 0.44	316	0.36 ± 0.48	131	0.20 ± 0.40	185	–	–	–	–	–	–	–	–	–	–	–	–
M	0.13 ± 0.34	981	0.14 ± 0.35	451	0.12 ± 0.33	530	0.19 ± 0.39	910	0.25 ± 0.43	458	0.13 ± 0.34	452	0.12 ± 0.32	933	0.14 ± 0.34	453	0.10 ± 0.30	480
N	0.06 ± 0.23	650	0.06 ± 0.23	366	0.06 ± 0.24	284	0.19 ± 0.40	270	0.22 ± 0.41	183	0.14 ± 0.35	87	0.16 ± 0.37	362	0.17 ± 0.37	303	0.15 ± 0.36	59
O	0.08 ± 0.27	695	0.10 ± 0.30	304	0.07 ± 0.25	391	0.22 ± 0.41	618	0.33 ± 0.47	244	0.14 ± 0.35	374	0.13 ± 0.34	650	0.21 ± 0.41	323	0.05 ± 0.22	327
P (a part)	0.13 ± 0.33	973	0.09 ± 0.29	454	0.15 ± 0.36	519	0.13 ± 0.34	1666	0.13 ± 0.34	694	0.13 ± 0.34	972	0.25 ± 0.43	1103	0.24 ± 0.43	481	0.25 ± 0.44	622
Q	0.18 ± 0.38	413	0.08 ± 0.27	289	0.40 ± 0.49	124	0.05 ± 0.22	2515	0.06 ± 0.24	1122	0.05 ± 0.21	1393	0.02 ± 0.15	1101	0.03 ± 0.17	603	0.02 ± 0.13	498
R	–	–	–	–	–	–	0.15 ± 0.36	825	0.24 ± 0.43	275	0.11 ± 0.31	550	0.13 ± 0.33	949	0.14 ± 0.35	457	0.11 ± 0.31	492
(No. of genets ≦3)																		
s	0.00 ± 0.00	135			0.00 ± 0.00	135	–	–	–	–	–	–	–	–	–	–	–	–
t	0.00 ± 0.00	36			0.00 ± 0.00	36	0.00 ± 0.00	19			0.00 ± 0.00	19	0.00 ± 0.00	21			0.00 ± 0.00	21
u	0.12 ± 0.32	43			0.12 ± 0.32	43	–	–	–	–	–	–	1.00 ± 0.00	3			1.00 ± 0.00	3
v	–	–	–	–	–	–	0.52 ± 0.51	29	0.52 ± 0.51	29			0.04 ± 0.21	68	0.04 ± 0.21	68		
w	–	–	–	–	–	–	–	–	–	–	–	–	0.00 ± 0.00	121			0.00 ± 0.00	121
x	–	–	–	–	–	–	–	–	–	–	–	–	0.01 ± 0.10	101	0.00 ± 0.00	6	0.01 ± 0.10	95

'–' indicates 'lack of data' or 'not calculated'. Blank indicates absence of genet. 'Long' or 'Short' indicates the long-styled or short-styled morph.

Table 4 Mean ± S.D. of proportion of flowers infected by fungi including *Urocystis tranzshelina* in 1995, 1996, and 1997 for the populations of *Primula sieboldii* studied

	1995						1996						1997					
Population	Total	n	Long	n	Short	n	Total	n	Long	n	Short	n	Total	n	Long	n	Short	n
(No. of genets ≧7)																		
A	0.01 ± 0.10	1052	0.01 ± 0.09	410	0.01 ± 0.11	642	0.06 ± 0.24	994	0.01 ± 0.12	286	0.08 ± 0.27	708	0.17 ± 0.37	942	0.11 ± 0.32	436	0.22 ± 0.41	506
B	0.02 ± 0.15	564	0.00 ± 0.00	305	0.05 ± 0.22	259	0.31 ± 0.46	432	0.31 ± 0.46	224	0.30 ± 0.46	208	0.02 ± 0.13	491	0.01 ± 0.12	268	0.02 ± 0.15	223
C	0.02 ± 0.13	383	0.01 ± 0.08	284	0.05 ± 0.22	99	-	-	-	-	-	-	0.04 ± 0.19	578	0.02 ± 0.13	312	0.06 ± 0.24	266
D	0.00 ± 0.04	566	0.00 ± 0.05	350	0.00 ± 0.00	216	0.53 ± 0.50	800	0.42 ± 0.49	316	0.60 ± 0.49	484	0.08 ± 0.27	349	0.10 ± 0.30	218	0.04 ± 0.19	131
E	0.24 ± 0.42	887	0.21 ± 0.40	296	0.25 ± 0.43	591	0.44 ± 0.50	1090	0.39 ± 0.49	362	0.46 ± 0.50	728	0.30 ± 0.46	863	0.17 ± 0.38	370	0.40 ± 0.49	493
F	0.11 ± 0.32	678	0.07 ± 0.25	271	0.14 ± 0.35	407	0.47 ± 0.50	1154	0.31 ± 0.46	223	0.50 ± 0.50	931	0.31 ± 0.46	1217	0.20 ± 0.40	574	0.40 ± 0.49	643
G	0.04 ± 0.20	347	0.00 ± 0.00	76	0.06 ± 0.23	271	0.01 ± 0.12	746	0.03 ± 0.16	239	0.01 ± 0.09	507	0.23 ± 0.42	292	0.22 ± 0.41	64	0.24 ± 0.43	228
H	0.01 ± 0.11	266	0.01 ± 0.10	105	0.01 ± 0.11	161	0.24 ± 0.43	419	0.44 ± 0.50	177	0.10 ± 0.29	242	0.25 ± 0.44	738	0.26 ± 0.44	378	0.25 ± 0.43	360
I	0.08 ± 0.27	261	0.07 ± 0.25	144	0.09 ± 0.28	117	-	-	-	-	-	-	-	-	-	-	-	-
J	0.25 ± 0.43	1087	0.25 ± 0.43	501	0.25 ± 0.43	586	0.47 ± 0.50	1123	0.35 ± 0.48	536	0.58 ± 0.49	587	0.31 ± 0.46	861	0.29 ± 0.45	448	0.33 ± 0.47	413
K	0.01 ± 0.12	221	0.00 ± 0.00	49	0.02 ± 0.13	172	-	-	-	-	-	-	-	-	-	-	-	-
L	0.06 ± 0.24	316	0.15 ± 0.36	131	0.00 ± 0.00	185	-	-	-	-	-	-	-	-	-	-	-	-
M	0.19 ± 0.39	981	0.34 ± 0.47	451	0.06 ± 0.23	530	0.47 ± 0.50	910	0.36 ± 0.48	458	0.57 ± 0.50	452	0.33 ± 0.47	933	0.28 ± 0.45	453	0.38 ± 0.48	480
N	0.08 ± 0.28	650	0.06 ± 0.24	366	0.12 ± 0.32	284	0.20 ± 0.40	270	0.26 ± 0.44	183	0.09 ± 0.29	87	0.05 ± 0.22	362	0.05 ± 0.22	303	0.05 ± 0.22	59
O	0.06 ± 0.23	695	0.07 ± 0.26	304	0.04 ± 0.20	391	0.55 ± 0.50	618	0.38 ± 0.49	244	0.67 ± 0.47	374	0.19 ± 0.39	650	0.11 ± 0.32	323	0.26 ± 0.44	327
P (a part)	0.08 ± 0.28	973	0.07 ± 0.26	454	0.09 ± 0.29	519	0.10 ± 0.30	1666	0.07 ± 0.26	694	0.13 ± 0.33	972	0.14 ± 0.35	1103	0.13 ± 0.34	481	0.14 ± 0.35	622
Q	0.31 ± 0.46	413	0.29 ± 0.45	289	0.37 ± 0.48	124	0.60 ± 0.49	2515	0.48 ± 0.50	1122	0.70 ± 0.46	1393	0.39 ± 0.49	1101	0.37 ± 0.48	603	0.41 ± 0.49	498
R	-	-	-	-	-	-	0.42 ± 0.49	825	0.40 ± 0.49	275	0.42 ± 0.49	550	0.02 ± 0.15	949	0.02 ± 0.15	457	0.03 ± 0.16	492
(No. of genets ≦3)																		
s	0.00 ± 0.00	135			0.00 ± 0.00	135	-	-	-	-	-	-	-	-	-	-	-	-
t	0.00 ± 0.00	36			0.00 ± 0.00	36	0.00 ± 0.00	19			0.00 ± 0.00	19	0.00 ± 0.00	21			0.00 ± 0.00	21
u	0.00 ± 0.00	43			0.00 ± 0.00	43	-	-	-	-	-	-	0.00 ± 0.00	3			0.00 ± 0.00	3
v	-	-	-	-	-	-	0.00 ± 0.00	29	0.00 ± 0.00	29			0.00 ± 0.00	68	0.00 ± 0.00	68		
w	-	-	-	-	-	-	-	-	-	-	-	-	0.02 ± 0.13	121			0.02 ± 0.13	121
x	-	-	-	-	-	-	-	-	-	-	-	-	0.01 ± 0.10	101	0.00 ± 0.00	6	0.01 ± 0.10	95

'-' indicates 'lack of data' or 'not calculated'. Blank indicates absence of genet. 'Long' or 'Short' indicates the long-styled or short-styled morph.

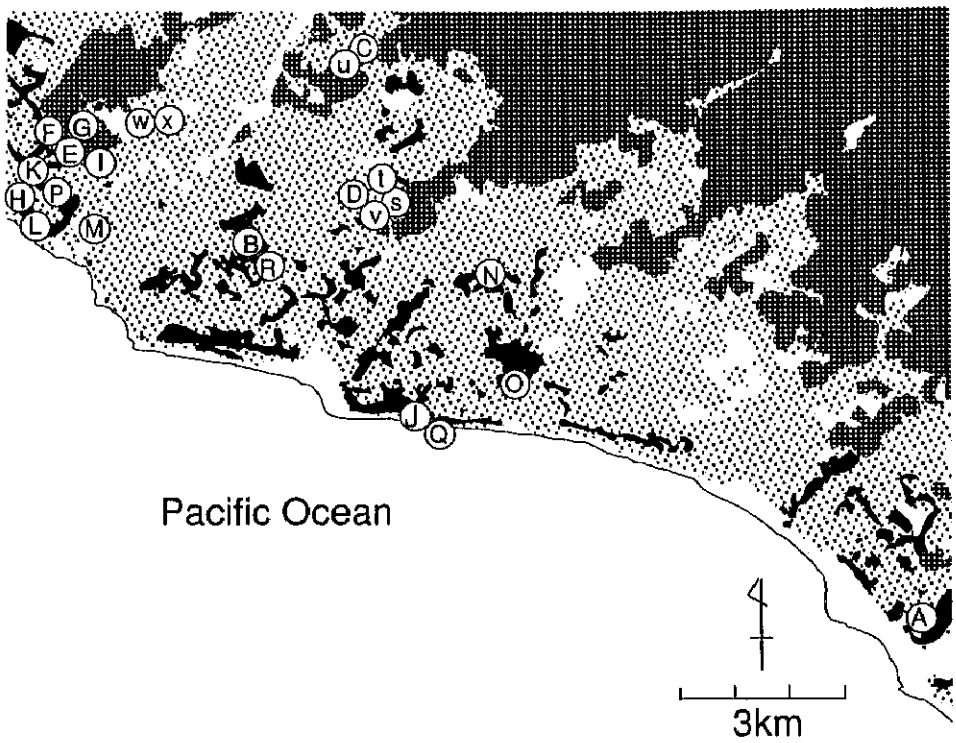

Fig. 1 Vegetation map of the study area in southern Hokkaido, showing the location of the populations of *Primula sieboldii* chosen for the present study. Uppercase letters indicate populations with more than six genets and lowercase letters indicate populations with less than four genets. (■) *Quercus dentata* forest; (▨) farming land and pasture; (▩) forests other than *Q. dentata.*

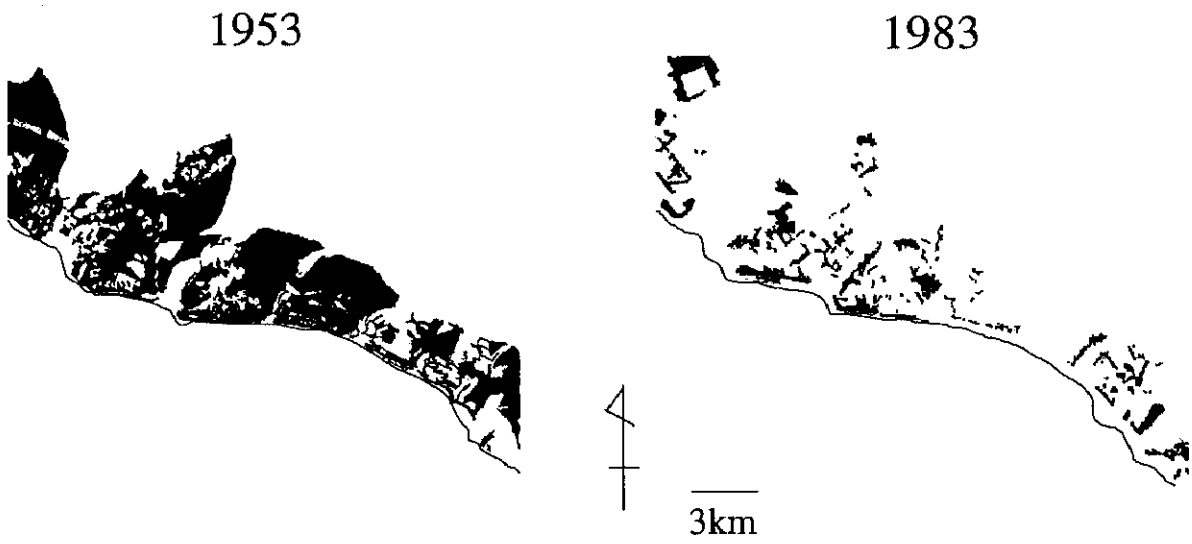

Fig. 2. Distribution of *Quercus dentata* forests (■) over the study area in the year 1953, which was reconstructed from aerial photos, and the modern distribution redrawn from the vegetation map made in 1983 (Environment Agency 1984).

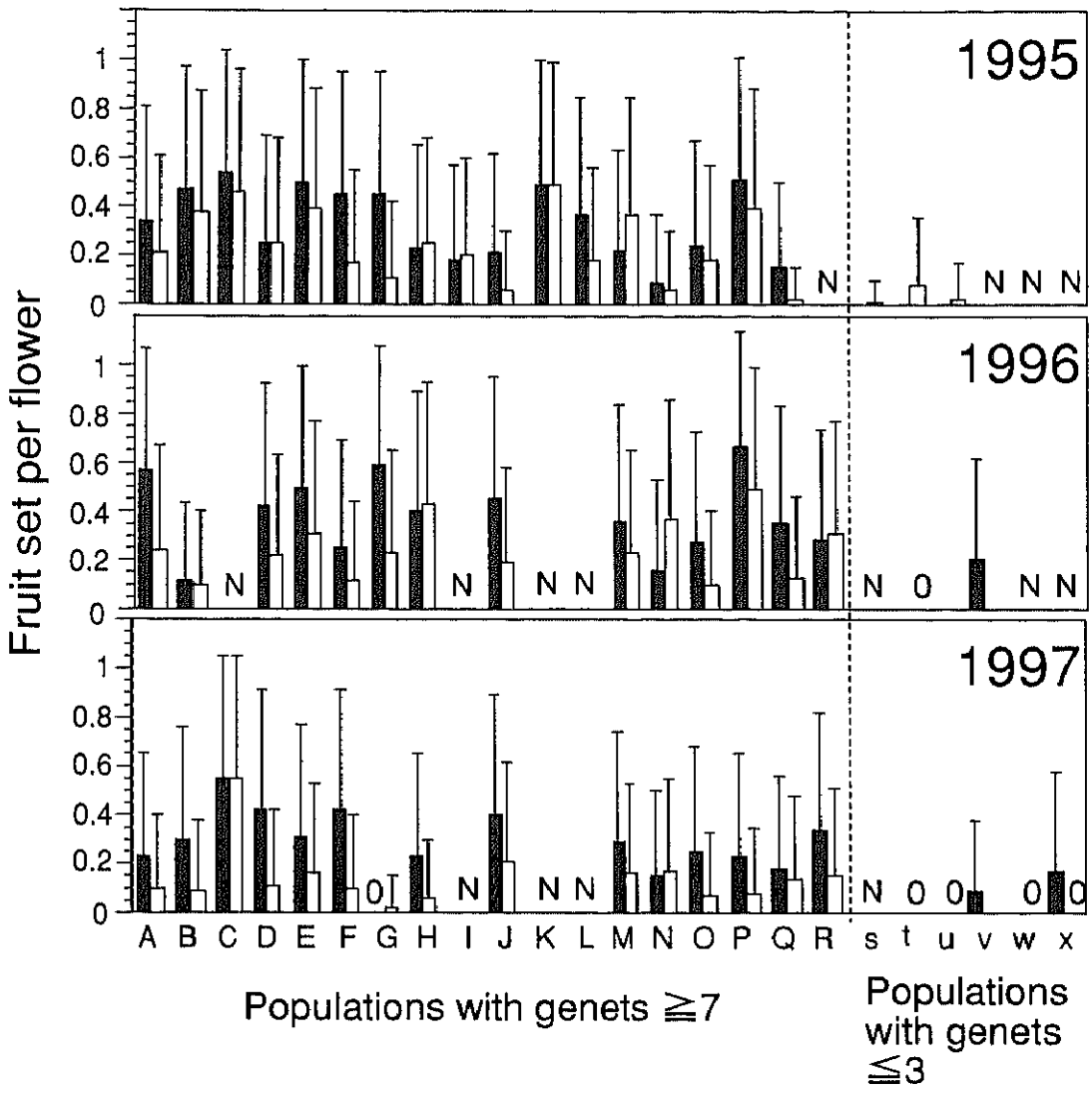

Fig. 3. Population mean (column) and S.D. (bar) of fruit set per flower for the long-styled (■) and short-styled (□) morphs of the populations of *Primula sieboldii* in 1995, 1996, and 1997. '0' indicates zero value. 'N' indicates 'lack of data' and blank indicates no genet.

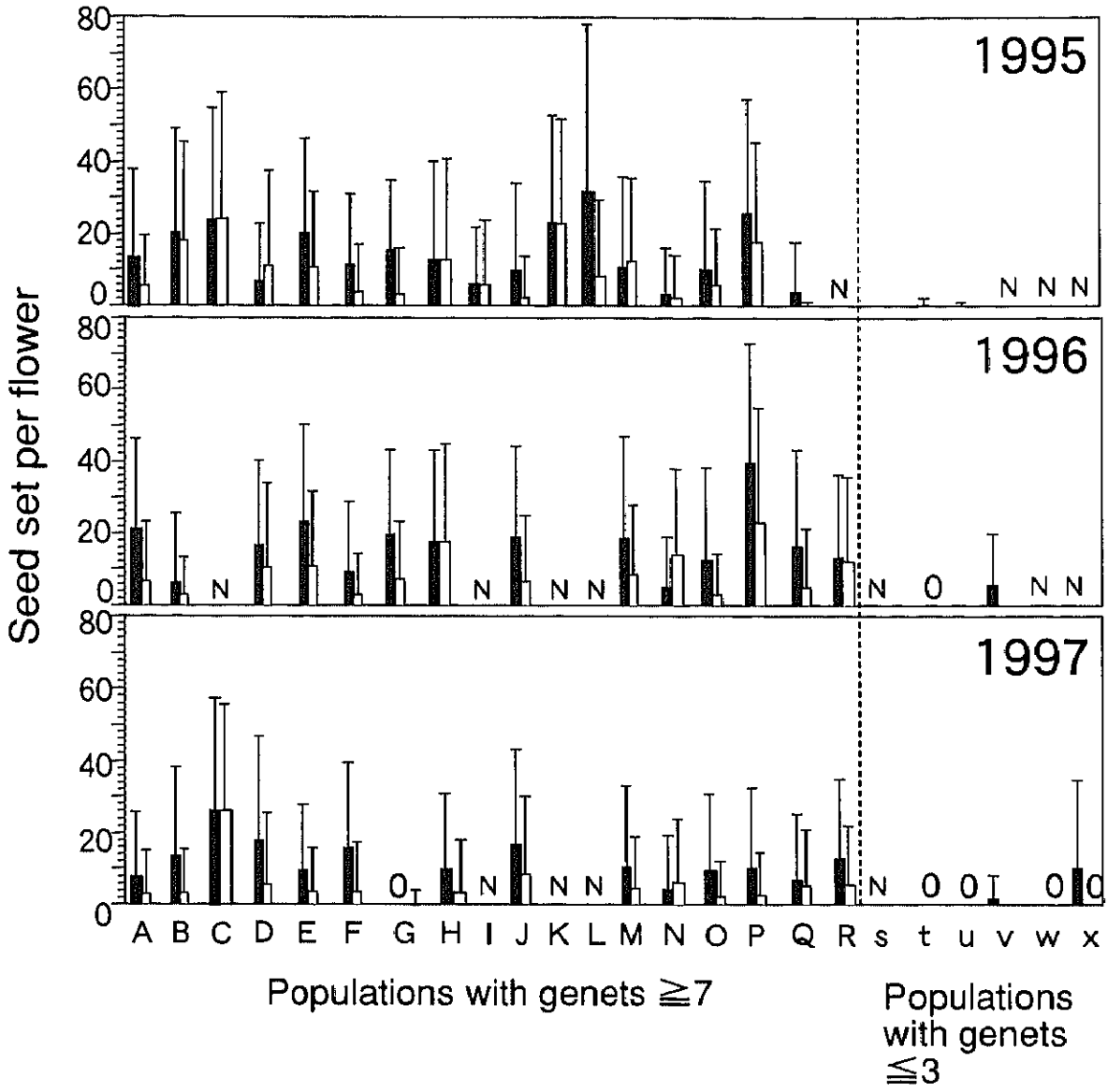

Fig. 4. Population mean (column) and S.D. (bar) of seed set per flower for the long-styled (■) and short-styled (□) morphs of the populations of *Primula sieboldii* in 1995, 1996, and 1997. '0' indicates zero value. 'N' indicates 'lack of data' and blank indicates no genet.

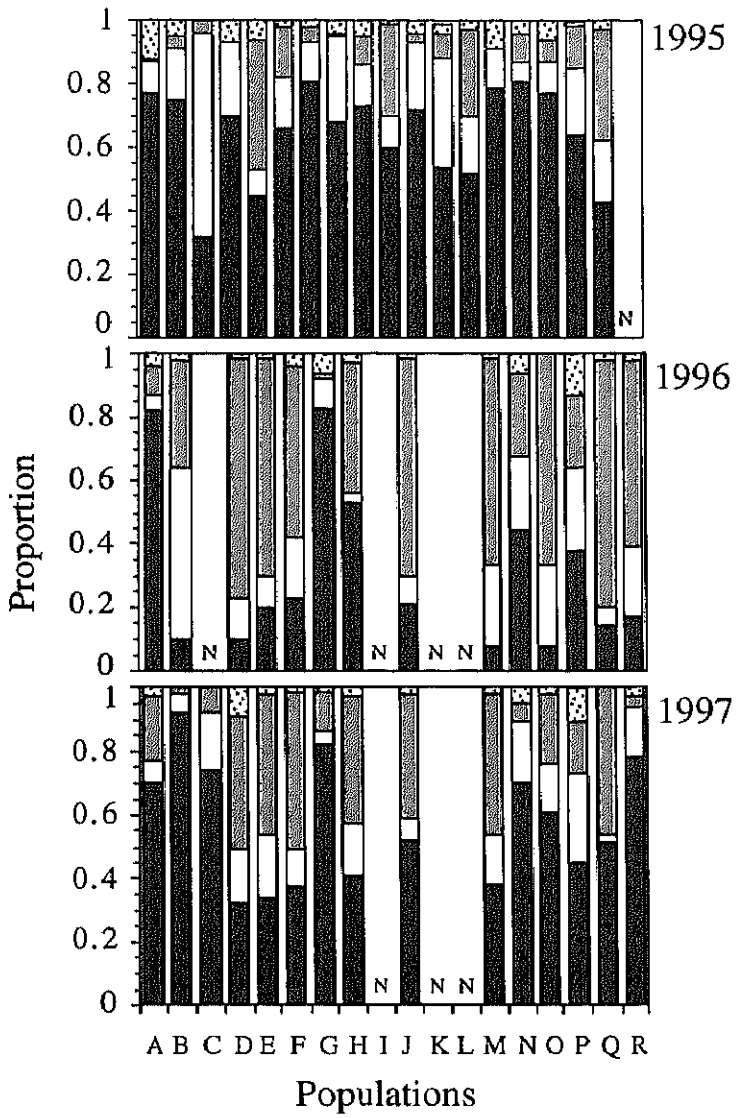

Fig. 5. Proportion of flowers infected by fungi (▣), consumed by herbivores (□), without any damage (■), or lost (⊡) to the total number of flowers failing to set fruit for populations of *Primula sieboldii* in 1995, 1996, and 1997. 'N' indicates 'lack of data'.

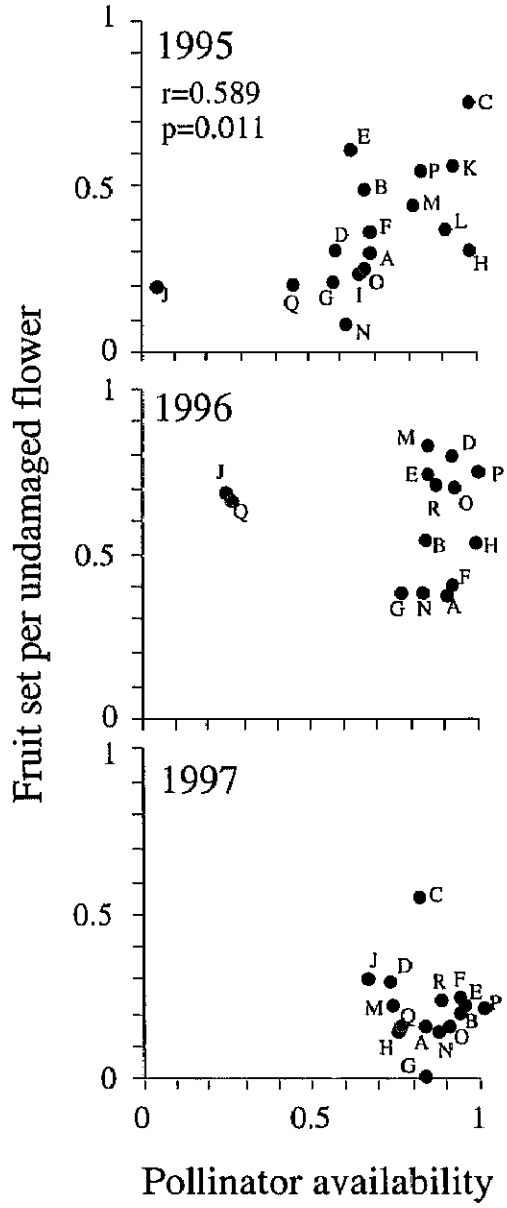

Fig. 6. Relationships between pollinator availability, i.e., proportion of inflorescences with claw marks, and mean fruit set per undamaged flower for the populations with genet number more than 6 in the years 1995, 1996, and 1997. Correlation coefficient and its significance level are shown in 1995. Uppercase letters indicate the populations.

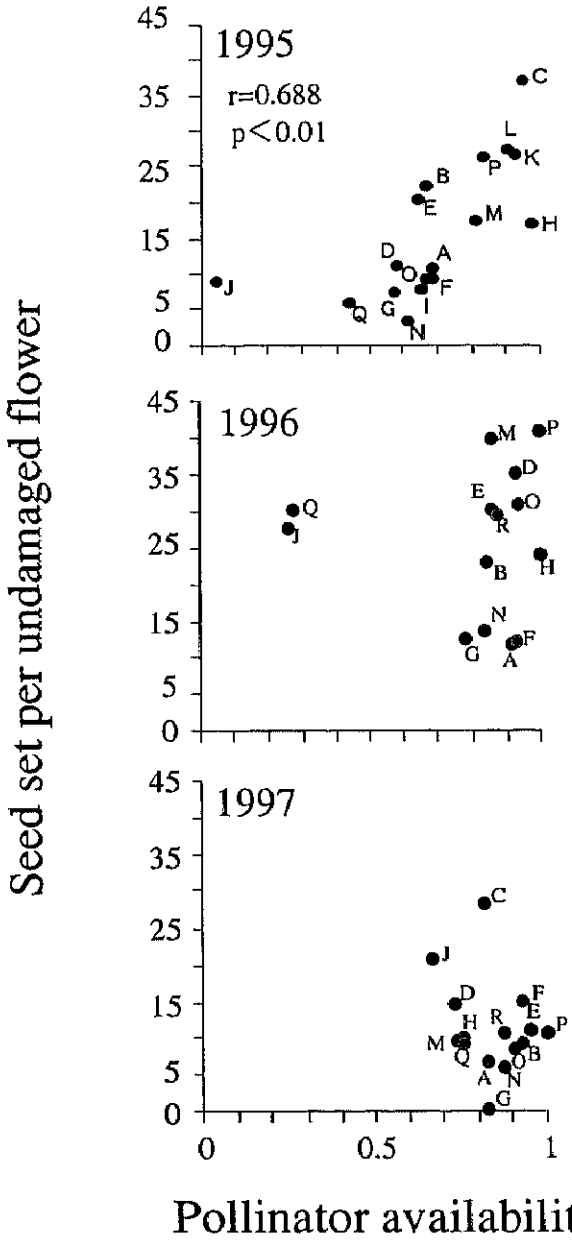

Fig. 7. Relationships between pollinator availability, i.e. proportion of inflorescences with claw marks, and mean seed set per undamaged flower for the populations with genet number more than 6 in the years 1995, 1996, and 1997. Correlation coefficient and its significance level are shown in 1995 Uppercase letters indicate the populations.

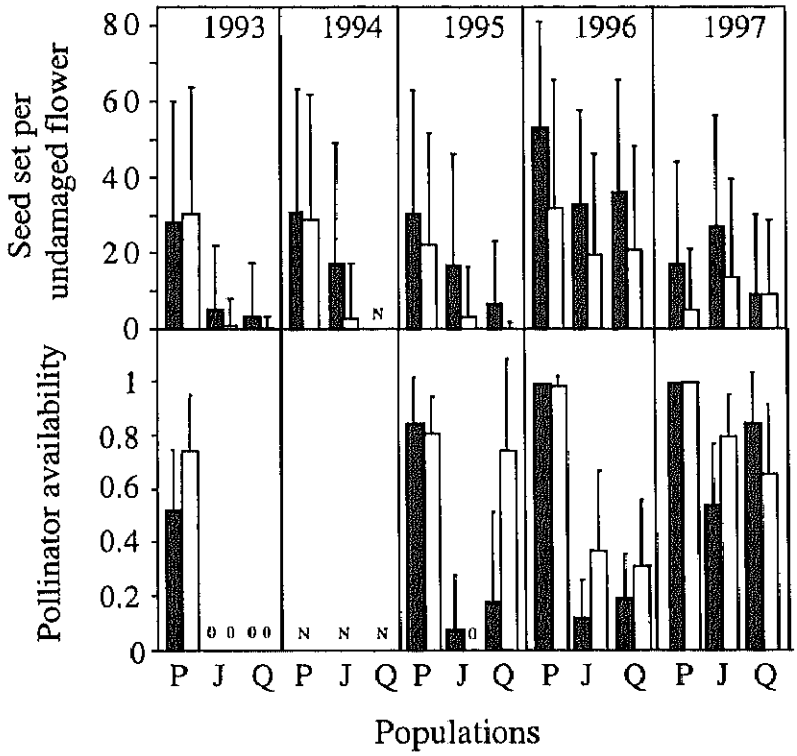

Fig. 8 Yearly trend of mean (column) and S.D. (bar) of the seed set per undamaged flower for the long-styled (■) and short-styled (□) morphs and pollinator availability for population P, in which pollinator availability was constantly high throughout the 5 years, and populations J and Q, in which pollinator availability fluctuated highly year by year. '0' indicates zero value. 'N' indicates 'lack of data'.

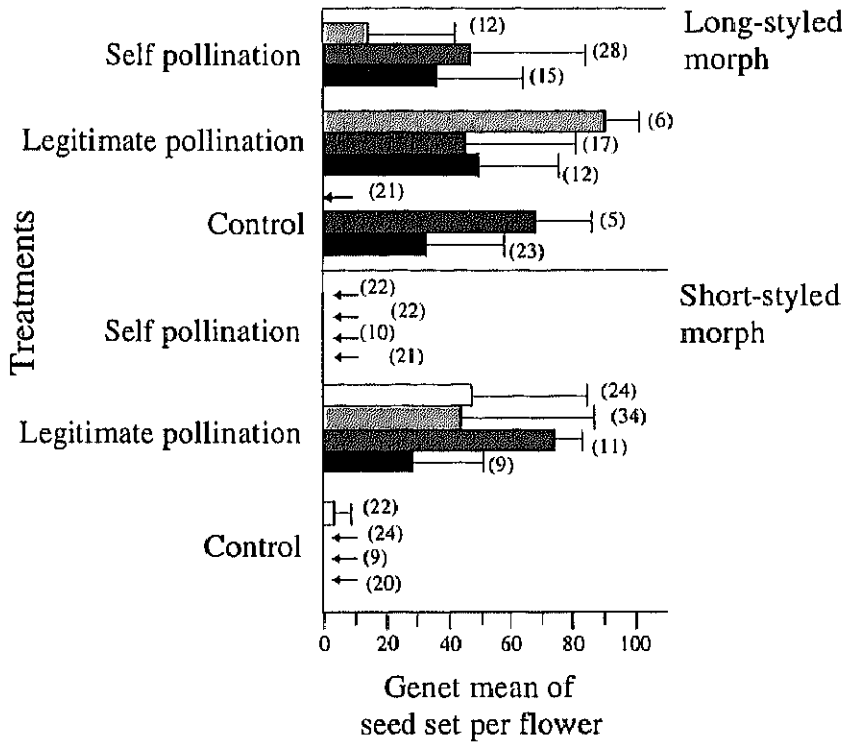

Fig. 9. Genet mean (column) and S.D. (bar) of seed set per flower obtained from the hand pollination experiments, in which the flowers were subjected to three types of treatments: (1) anther removal and self- (within flower) pollination on the stigmas (10 - 28 flowers), (2) anther removal and inter-morph pollination (legitimate pollination) on the stigma (6 - 34 flowers), and (3) open pollination control, without wrapping the inflorescences (5 - 24 flowers). Different shadings correspond to different genets subjected to the same treatment and an arrow indicates a genet with no seeds. The number of the flowers subjected to each treatment in individual genets is given in parentheses.