POLLINATOR VISITATION AND POLLEN LIMITATION IN CONTRASTING HABITATS IN A POPULATION OF *CAMPANULA PERSICIFOLIA*

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FORORD

Det har vært en lang prosess å skrive denne hovedoppgaven, men nå er jeg i mål. Faglig har det vært svært interessant, og jeg har hatt og vil i framtiden få stort utbytte av kunnskapen jeg har tilegnet meg i løpet av prosessen. Jeg har også oppdaget mange nye sider ved meg selv, både gode og mindre gode. Jeg ser det som en stor fordel at jeg nå er blitt mer bevisst på mine sterke og svake sider.

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SAMMENDRAG

Planters hunlige reproduktive suksess påvirkes av abiotiske og biotiske miljøforhold. Høy grad av romlig variasjon i miljøforholdene innen området til en populasjon er vanlig, og det er derfor sannsynlig at pollinering og reproduktiv suksess varierer mellom ulike voksesteder innen samme populasjon. Jeg undersøkte en populasjon av *Campanula persicifolia* (Campanulaceae) på Jeløya i Moss kommune i Østfold. Populasjonens voksested var heterogent, og individene var fordelt over et område med skog og eng.

Frøproduksjonen i begge habitater var pollenbegrenset. Det var ingen forskjell i frøproduksjon eller pollenbegrensning mellom habitatene. Antall aborterte frø var høyere i skogen enn på engen, og antall aborterte frø økte i begge habitater når ekstra pollen ble gitt. Frøvekten var den samme i begge habitater, og den var upåvirket av ekstra pollen.

Billen *Miarus camapnulae* sto for ca 75 % av insektbesøkene på engen, og når billebesøkene var inkludert i analysene var den totale besøksraten høyere på engen enn i skogen. Besøksraten var den samme i begge habitater når besøkene fra billen var ekskludert, sannsynligvis fordi *C. persicifolia*-populasjonen var relativt liten, og tilgangen på føde i området var derfor begrenset. Det er usikkert hvor viktig *M. campanulae* er for pollineringen av *C. persicifolia.*

Jeg målte en rekke morfologiske karaktertrekk og brukte dem som et mål på plantenes tilgjengelighet av ressurser. Frøproduksjonen i skogen hadde en positiv sammenheng med antall blomster pr. individ, bladlengde og blomsterstørrelse, mens på enga fant jeg en svak signifikant positiv sammenheng kun mellom frøproduksjon og blomsterstørrelse. Verken abortering av frø eller frøvekt så ut til å ha noen sammenheng med karaktertrekkene. Plantehøyde var det eneste karaktertrekket som var forskjellig mellom de to habitatene. Økt lengdevekst kan være en kompenserende respons på skygge, men kan også skyldes ulik tilgang på næring eller vann.

Selv om det er sannsynlig at de miljømessige forholdene i habitatene er forskjellige, var det ingen forskjell i pollenbegrensning eller frøproduksjon. Dette kan forklares av at det ikke var noen signifikant forskjell i besøksrate mellom habitatene, samt at optimal ressurs allokering kan motvirke de sannsynlige romlige forskjellene i miljøforhold.

SUMMARY

The female reproductive success of plants is affected by abiotic and biotic environmental conditions. Large spatial variation in these factors inside the area of a population is common. It is therefor highly conceivable that pollination and reproductive success vary spatially between different patches within the same population. I studied a population of *Campanula persicifolia* (Campanulaceae) on Jeløya in Moss district in Østfold county. The growing area of the population was heterogeneous, with individuals growing in a forested habitat and on an open meadow habitat.

Seed production in both habitats was pollen limited. There was no difference in seed production or pollen limitation between the habitats. Number of aborted seeds was higher in the forest than on the meadow, and increased in both habitats under supplemental pollination. Seed weight did not differ between habitats, and it was unaffected by supplemental pollination.

The beetle *Miarus campanulae* made about 75 % of the visits on the meadow, and visitation rate was higher on the meadow than in the forest when beetles were included. Visitation rate was the same in both habitats when the beetles were excluded. The insects in the area likely have a restricted access to food, and therefore visit individuals both in the forest and on the meadow. It is uncertain how important *M. campanulae* is for the pollination of *C. persicifolia*.

I measured several morphological traits and used them as parameters for the plants access to resources. The number of flowers, leaf length and flower size was positively related to seed number in the forest, while flower size was marginally significantly related to seed number on the meadow. Neither the number of aborted seeds nor seed weight was affected by any of the morphological traits. Plant height was the only trait that differed between the habitats. Enhanced length growth may be a compensatory response to shade or nutrient and water availability may be different in the habitats.

The lack of difference in pollen limitation and seed production between habitats may be explained by no significant difference in visitation rate. It is also possible that optimal resource allocation may counteract the environmental differences.

INTRODUCTION

The female reproductive success of plants is affected by abiotic and biotic environmental conditions. The abiotic factor includes environmental conditions such as light, climate, soil, nutrient availability, water availability and soil structure, while the biotic factor includes interactions with herbivores, pollinators, parasites and competitors.

Large spatial variation in environmental conditions within the habitat of a population is common (e.g. Robertson et al. 1988, Lechowicz and Bell 1991, Herrera 1997, Nicotra et al. 1999, Anthony and Hoegh-Guldberg 2003, He and Dong 2003). Bell and Lechowicz (1991) found that many characters related to plant fitness, such as time to maturity, dry weight of above-ground parts, germination time, height, root mass and shoot mass, all can vary because of small-scale environmental variation.

Light conditions are highly spatially variable, and strongly affect the photosynthetic environment of plants, but also pollinator behaviour. For example, Herrera (1997) found a large spatially heterogeneity in the composition of pollinating insects in *Lavandula latifolia*. This plant grows in the understorey of forests, and experiences a spatio-temporal mosaic of sunlight and shaded patches. 59 % of the pollinating species selected situations of either higher or lower than average irradiance. The difference in light preference of the pollinating insects is partly caused by differences in their thermal biology. Large insects have higher body temperature than small insects, and the need for regulation of body temperature affect their choice of irradiance level. Such spatial variation in pollinator composition and activity may have consequences for the quantity and quality of pollination of plants situated in contrasting light patches. Flowers on individuals highly exposed to sunlight may experience proportionally more visits of small-sized bees, while flowers on extensively shaded individuals may be visited more frequently by dipterans and large bees. Lundberg (1980) found that male bumblebees need more light while foraging than queens and workers. Temperature or light may be a limiting factor in the evening, while temperature alone seemed to be the limiting factor in the morning. The workers were observed at high wind velocities, and they tended to fly close to the ground and to forage in shelter.

Both abiotic and biotic habitat conditions affect plant growth, and plant size can affect both male and female reproductive success (Mitchell 1994). For example, plant size affected both female and male reproductive function in *Sabatia angularis* (Dudash 1991). Large plants had approximately 1.5-fold greater pollen grain deposition on their stigmas, and produced on average twice the number of seeds per fruit compared to small plants. A greater proportion of flowers on large individuals than on small individuals developed into fruits. Flowers of large plants produced more pollen per flower than small plants, and more pollinator visits occurred within large plants than within small plants. Mitchell (1994) showed that plant size strongly affect total flower production, and total number of flowers in turn strongly influence the number of open flowers at any given time. Plant height had positive influence on proportion fruit set.

Many experiments have demonstrated pollen limitation on seed or fruit production at the whole population level (e.g. Hainsworth et al. 1985, Fox 1992, Campbell and Halama 1993, Mitchell 1994, Parker 1997, Totland et al. 1998, Larson and Barret 2000). In a literature survey, Burd (1994) showed that 159 out of 258 species (62 %) suffered from pollen limitation on seed set or fruit production at least some years or at some sites. None of these examples of pollen limitation consider if pollen limitation varies among contrasting habitats occupied by the same population. Nevertheless, given the large small-scale variation in pollination activity and abiotic environmental conditions, it is highly conceivable that pollination and reproductive success vary spatially between different patches within the same population. Still, most studies ignore a possible habitat effect on pollen limitation.

In this thesis I examine whether seed set of *Campanula persicifolia* L. (Campanulaceae) is limited by pollen availability, and if possible differences in pollen limitation exist between individuals of the same population that grow in different habitats; on a forest floor and on an open meadow. *Campanula persicifolia* has few flowers, and is thereby well suited for pollination experiments.

I ask the following questions:

1. Is seed production in *Campanula persicifolia* limited by pollen supply, and are there differences in pollen limitation between the forested and meadow habitat?
2. Are there differences in visitation rates of potential pollinators between plants growing on the forest floor and on the open meadow?
3. Are there differences in number of seeds produced, number of aborted seeds and seed weight between plants growing on the forest floor and on the open meadow?

4. Are there any relations between the morphological traits and seed production, abortion rate and seed weight?
5. Are there differences in morphological traits between individuals growing on the forest floor and on the open meadow?

MATERIAL AND METHOD

Study site

The study site was on Jeløya in Moss district in Østfold county. The site was at Reier, about 20 meters towards west from the bottom of Jomfrubakken, at ca 5 meters elevation. The total area of the site was about 400 m^2.

The site bordered to forest in the north, south and east, and a cultivated field in the west. The site was heterogeneous with forested and open patches. The forested patches consisted of deciduous species, with *Fraxinus excelsior* as the dominating canopy species, while *Juniperus communis* and *Rosa* sp. dominated the shrub-layer. The site fitted well for my experiment because the population of *C. persicifolia* grew both in the open and in the forested patches, so habitat effects on individuals from the same population could be compared.

Study species

Campanula persicifolia is a perennial herb that flowers in June-August. It occurs in most of Europe and in Siberia, although not in the northern areas. The species is fairly common in Norway, and common in Europe and Asia. *Campanula persicifolia* occurs on meadows and in open forest, often in somewhat dry habitats. Height of the individuals varies from ca 25 – 80 cm, and the stalk is unbranched. The individuals have a rosette of lanceolate leaves near the ground, while the stalk-leaves are linear. The hermaphroditic flowers are bell-shaped and actinomorphic, with short pedicles. Blue flowers are most common, but they can also be white. The corolla length is 20 – 50 mm. Many different insects can easily visit and perhaps pollinate the large and open flower. Each individual can have 1 – 10 flowers that bloom more or less sequentially. Individual flowers are open for about 4 – 6 days. The upright mature capsule is hairy, and contains from 0 – 700 seeds. Three openings towards the capsule top form when the seeds are mature. Wind or animals cause movement in the stalk, and the seeds are spread through the openings of the seed capsule (Lagerberg et al. 1958).

Campanulaceae has secondary pollen presentation. The flowers of *C. persicifolia* are protandrous, and the anthers mature when the flower is in the bud-stage. The anthers are not united, but initially stand together forming a tube. The anthers release their pollen while the style is growing through the tube, and the pollen stick to the hairy style. At this stage the stigma lobes are closed up against one another, so the pollen do not come in contact with the stigma. The stamens wither as the corolla opens, and insects collect pollen from the style.

When the pollen has been removed from the style, the stigma lobes unfold and are receptive for pollen. In some Campanulaceae-species the stigma lobes coil up like a spiral to touch the style towards the end of the anthesis, and if there is pollen left on the style self-pollination can occur (Heywood 1978). This is not the case for *C. persicifolia*. Even though the stigma lobes coil up, it depends entirely on pollinator service for seed production (Nyman 1992).

Fieldwork

I conducted the fieldwork during the period July-August 2002. Based on observations, I defined one part of the area as forest and one part as meadow. Exposure to sunlight was the main factor for deciding the border between the two habitats. The edge zone towards the cultivated fields was about one meter wide, and it was defined as meadow along the whole study site. I avoided using individuals growing in the border zone between the forest and meadow habitat.

Pollen limitation on seed production

To examine if female reproductive success was constrained by pollen availability and whether pollen limitation differed between habitats, I selected 15 pairs of *C. persicifolia* plants in the forest and 16 pairs on the meadow. The two plants in each pair grew up to 1.5 m from each other and were in the same flowering stage. To be included in this part of the study, the total number of buds and open flowers had to exceed the number of wilted flowers on each plant. One randomly selected plant in each pair was given additional pollen by hand-pollination, while the other plant functioned as a control, and was not given additional pollen.

All the plants were labelled with light grey pieces of plastic attached to the plants with rubber bands. Individual flowers were marked with small pieces of drinking straws in different colours cut lengthwise and placed around the peduncle.

Pollen limitation on seed set can be demonstrated by giving additional outcrossed pollen to the majority of the flowers on an individual by hand-pollination, and then compare seed production with naturally pollinated individuals (Zimmerman and Pyke 1988, Dudash 1993).

I performed the hand-pollination when the stigmas were receptive for pollen, by collecting the style from a donor flower, and then gently rubbing the area with pollen against the stigma in the experimental flower. I checked that the donor style was covered with pollen before I used it in the experiment. I always chose a donor that grew at least 5 meters away from the pollen recipient plant. I hand-pollinated each flower in the experiment once. I pollinated 77.1 % of the flowers on experimental plants on the meadow, and 81.3 % of the flowers on experimental plants in the forest. The other flowers had wilted when I started the experiment.

I collected mature seed capsules in paper bags between 1 and 27 August 2002, and I counted the seeds under a stereo microscope. Mature seed capsules are brown and dry. Mature seeds have a smooth and shiny surface and look swollen. Seeds that were wrinkled and shrunken were classified as aborted, together with those that were clearly not fully developed. I was not able to count the unfertilized ovules, because they were to numerous and too small to count accurately. I weighed the mature seeds on a microbalance (Precisa 205 A SCS), and obtained an average seed weight in milligram by dividing the total seed weight by the number of seeds weighed, and then multiply it with 1000.

Insect visitation rates

To examine if insect visitation rates differed between the two habitats, I measured visitation rate by counting the total number of flower visits to a group of plants during 10 minutes observation periods. The number of flowers during each observation period varied from 2 to 8, and I noted the total numbers of visits to individual flowers. I grouped the flower visitors into beetles (Coleoptera), flies (Muscidae), bumblebees (Apidae), solitary bees (Apidae), hoverflies (Syrphidae) and ants (Formicidae). Occasionally, a few spiders visited flowers, but I did not consider these as potential pollinators because they stayed for very long periods in single flowers.

I conducted visitation rate measurements on each of five days; 10, 11, 12, 14, 15 July 2002. On each day, I conducted five observation periods in the forest and five on the meadow, giving 25 measurements in each habitat. Within a day I alternated the observations between the two habitats, and I started the observations in the forest and on the meadow every other day. All observations were carried out between 10.00 and 14.00, during warm and sunny weather conditions.

The beetle *Miarus campanulae* represented a large proportion of the visits on the meadow. This small, hairy black beetle crawls to the bottom of the flower and lays the eggs in the ovary. The larvae develop in the seed capsule and feed on the fertilised ovules. Adult beetles feed on pollen from for example *C. persicifolia, C. rotundifolia* and *Phyteuma spicatum,* and individuals covered by pollen have been observed moving between flowers of *C. persicifolia* (Båtvik 2004, pers.com.). It is likely that the beetle contributes to pollination of *C. persicifolia,* but it is hard to say how important the beetle is as a pollinating agent because of the small size and behaviour. I have therefore chosen to analyse the data both with and without including the visits made by beetles.

Relationship between female reproductive success and floral and vegetative traits

I performed several morphological measurements to see if seed production, number of aborted seeds or seed weight was related to the measured traits, to examine if any of the relationships differed between the two habitats, and to see if there were morphological differences between the forest plants and the meadow plants. I randomly chose 43 individuals in the forest habitat and 34 on the meadow. Each selected plant had at least one bud or open flower. There were fewer plants on the meadow than in the forest, so I was not able to choose the same number of plants in both habitats. To increase sample size I included all the control plants from the pollen limitation experiment in this part of the study.

I counted the total number of flowers, and measured plant height as the length of the flower stalk from the ground and up to the lowest situated flower. I counted the number of leaves, and measured the length of four randomly chosen leaves. The average length of these leaves was used in the analysis. Leaves shorter than 2.5 cm was not included, because they were far from fully developed. Plant height and leaf length was measured to the nearest mm with a ruler. I used corolla height and corolla width as a measure of flower size. I conducted two measurements of corolla height on each flower; from the corolla bottom to the tip of one corolla lobe, and from the corolla bottom to the lowest part between to corolla lobes. The mean of these two measurements was used in the analysis. I also measured corolla width in two places on each flower by measuring the largest and the smallest width, and I used the mean of these two measurements in the analysis. Flower size measurement was conducted with a digital caliper to the nearest 0.1 mm. For all morphological measurements, except flower size, I conducted a second measurement one week after the first, to account for changes in morphological traits due to plant growth. I collected the mature seed capsules and counted and weighed the seeds as described above.

Data analysis

For each individual I calculated the mean number of seeds produced per flower, the mean number of aborted seeds per flower, and the mean seed weight in mg pr flower.

I used nested analysis of variance (ANOVA), with pair nested under habitat, to examine if number of seeds, number of aborted seeds, and seed weight differed between treatment groups (control and supplemental pollen) and habitats (forest and meadow), and to see if there were any interaction effects between the experiment and habitat. The nesting was done to account for variability within the pairs. I calculated F-values for the habitat factor using the formula $MS_{habitat} / MS_{pair(habitat)}$ (Sokal and Rohlf 1995). I regarded the experiment and habitat factors as fixed factors.

I performed ANOVA on the insect visitation rates data, both on the total number of visits and separately for each insect group, to examine if visitation rates differed between habitats and between the days that I conducted the measurements. The habitat factor was treated as fixed, while the day factor was treated as random. I calculated new F-values for the day factor, using the formula MS_{day} / MS_{error} (Zar 1984).

I performed simple regression analyses to see whether the number of flowers in each patch was related to the number of visits per flower. I did this separately for the two habitats.

I performed analysis of covariance (ANCOVA) to examine whether the relationship between seed number, number of aborted seeds and seed weight (responses), and the measured morphological variables (covariables) differed between the two habitats (categorical factors), as judged by a significant interaction between the categorical factor and a covariable. I then performed simple linear regressions for each response variable against each of the morphological variables, and also multiple regression for each response variable. The regression analyses were done separately for the two habitats.

I performed a two-sample t-test for each measured morphological trait to examine whether there were any morphological differences between individuals growing in the forest and on the meadow.

It was not necessary to transform the data to meet the assumptions of the statistic analyses. I performed analyses of variance (ANOVA), analyses of covariance (ANCOVA), and regression analyses in Minitab, version 14 (Minitab Inc.).

RESULTS

Pollen limitation on seed production

Number of seeds

Nested ANOVA showed that experimental pollen addition significantly increased seed number (Table 1). There was no significant difference in seed number between the forest and the meadow habitat. Moreover, there was no significant habitat by treatment interaction, showing that the treatment effect on seed number was similar in both habitats. Pooled across both habitats, pollen addition increased seed number by 82.6 % (Table 2), showing that female reproductive success of *C. persicifolia* was strongly pollen limited in the study year.

Table 1. *ANOVA results for number of seeds. Significant differences are marked *.*

Source	*df*	SS	MS	F	P
Experiment	1	278149	278149	20.08	< 0.000001*
Habitat	1	73830	73830	2.66	0.114
Habitat × Experiment	1	207	207	0.01	0.904
Pair(habitat)	29	803642	27712	2.00	0.033*
Error	29	401629	13849		
Total	61	1557257			

Table 2. *Mean ± SE for number of seeds, number of aborted seeds, and seed weight of control and supplemental pollen plants in forest and meadow.*

	Forest		Meadow	
	Control	Treatment	Control	Treatment
Mean no of seeds	195.1 ±32.9	332.8 ±31.2	129.7 ±32.0	260.1 ±46.9
Mean no aborted seeds	9.8 ±1.7	17.2 ±4.0	4.6 ±1.1	6.8 ±4.4
Mean seed weight	0.059 ±0.005	0.052 ±0.003	0.049 ±0.005	0.047±0.003

Number of aborted seeds

There was a significant difference in the number of aborted seeds between the open and forested habitat (Table 3), and pollen addition significantly increased the number of aborted seeds with 75.5 % in the forest and 47.8 % on the meadow (Table 2). As shown by the non-significant interaction effect, the effect of pollen addition on number of aborted seeds was the same in both habitats.

Table 3. *ANOVA results for number of aborted seeds. Significant differences are marked *.*

Source	*df*	SS	MS	F	P
Experiment	1	349.20	349.20	4.90	0.035*
Habitat	1	944.47	944.47	10.97	0.002*
Habitat × Experiment	1	107.46	107.46	1.51	0.229
Pair(habitat)	29	2496.31	86.08	1.21	0.307
Error	29	2065.63	71.23		
Total	61	5951.04			

Seed weight

Nested ANOVA showed that there was no significant difference in seed weight between the forested and open habitats, and that pollen addition had no significantly effect on seed weight (Table 4). In addition, there was no significant habitat by treatment interaction, indicating that pollen addition had similar effects on seed weight in both habitats.

Table 4. *ANOVA results for seed weight. Significant differences are marked *.*

Source	*df*	SS	MS	F	P
Experiment	1	0.00035	0.00035	1.868	0.183
Habitat	1	0.00102	0.00102	2.79	0.106
Habitat × Experiment	1	0.00010	0.00010	0.54	0.470
Pair(habitat)	29	0.00037	0.00037	1.93	0.041*
Error	29	0.00019	0.00019		
Total	61	0.01757			

Insect visitation rates

There were small differences in visitation rates between the two habitats (Table 6). Only the beetle *Miarus campanulae* had a significant different visitation rate, with the highest rate on the meadow (Table 5). The beetles performed about 75 % of the visits on the meadow. Total visitation rate and visitation rate of flies differed significantly among days. Total visitation rate was significantly higher in the open than in the forested habitat, but when the beetles were excluded there was no significant difference in visitation rate between habitats.

Table 5. *Mean visitation rates ± SE for the forest and the meadow.*

Visitors	Forest	Meadow
Beetles	0.0460 ± 0.0195	0.887 ± 0.145
Hoverflies	0.1893 ± 0.06	0.0608 ± 0.0219
Flies	0.11 ± 0.0393	0.1214 ± 0.0645
Bumblebees	0.0797 ± 0.0432	0.0528 ± 0.0262
Ants	0.0427 ± 0.0207	0.0183 ± 0.014
Total visitation rate	0.5097 ± 0.0752	1.173 ± 0.155
Tot.vis.rate, beetles excluded	0.4217 ± 0.073	0.2732 ± 0.0857

Table 6. *ANOVA F-values (p-values) for the visitation rates analyzed by the habitat factor, the period factor, and the interaction between these two factors. Significant differences are marked *.*

Visitors	Habitat	Period	Habitat × period
Beetles	133.53 (<0.0001)*	0.446 (0.082)	0.22 (0.925)
Hoverflies	2.28 (0.206)	1.264 (0.5379)	1.96 (0.120)
Flies	0.04 (0.885)	0.351 (0.036)*	0.54 (0.704)
Bumblebees	0.33 (0.598)	0.9 (0.365)	0.85 (0.503)
Ants	1.76 (0.255)	0.949 (0.392)	0.51 (0.726)
Bees	1.0 (0.374)	1.0 (0.419)	1.0 (0.419)
Total visitation rate	46.75 (0.002)*	0.182 (0.0013)*	0.28 (0.891)
Tot.vis.rate, beetles excluded	1.13 (0.347)	0.631 (0.1971)	1.53 (0.203)

The number of flowers in each patch used for measuring insect visitation rate was marginally significantly related to number of visits per flower only on the meadow with the beetles included ($F = 0.24$, $P = 0.05$). There was no significant relationship on the meadow with the beetles excluded, or in the forest with beetles included or excluded.

Relationship between floral and vegetative trait and female reproductive success

Number of seeds

Analysis of covariance revealed significant interaction effects between the habitat factor and the number of flowers and the number of leaves on number of seeds. This indicates that the relationship between these two traits and the number of seeds differed between the two habitats (see Table 7). I therefore performed separate regression analyses for the two habitats.

Table 7. *Analysis of covariance for number of seeds. Significant relationships are marked *.*

Source	*df*	SS	MS	F	P
Habitat	1	36660	36660	2.40	0.126
Number of leaves	1	5531	5531	0.36	0.549
Leaf length	1	86157	86157	5.64	0.020*
Mean height	1	9311	9311	0.61	0.438
Flower size	1	224068	224068	14.67	<0.0001*
Number of flowers	1	70968	70968	4.65	0.035*
Habitat × number of flowers	1	96940	96940	6.35	0.014*
Habitat × number of leaves	1	61797	61797	4.05	0.048*
Habitat × leaf length	1	11860	11860	0.78	0.381
Habitat × mean height	1	6961	6961	0.46	0.502
Habitat × flower size	1	15712	15712	1.03	0.314
Error	65	992643	15271		
Total	76	1821485			

For forest plants, the simple regressions showed that number of seeds produced was significantly positively related to all the measured morphological traits (Figure 1). In the multiple regression, number of flowers, leaf length and flower size all seemed to positively affect seed production, and they all had low VIF-values (Table 8). Number of leaves and plant height were not significantly related to seed number in the multiple regression.

For meadow plants, seed number was only significantly related to leaf length and flower size in the simple regressions, and the relationships were positive (Table 9). Seed number was not significantly related to the number of flowers, number of leaves or plant height. Only flower size was marginally significant, and had a low VIF-value, in the multiple regression. Seed number was not significantly related to any of the other traits in the multiple regression.

Table 8. *Forest plants: Standarized coefficients from simple and multiple regression analyses on number of seeds, and variance inflation factors (VIF) from multiple regression. P-value in parenthesis. Significant relationships are marked *.*

Variables	Simple	Multiple	VIF
No. of flowers	0.343 (0.024)*	0.463 (0,02)*	2.3
No. of leaves	0.296 (0.05)*	-0.356 (0.16)	3.9
Leaf length	0.349 (0.022)*	0.310 (0.05)*	1.5
Plant height	0.390 (0.01)*	-0.019 (0.93)	3.1
Flower size	0.507 (0.001)*	0.543 (0.001)*	1.6

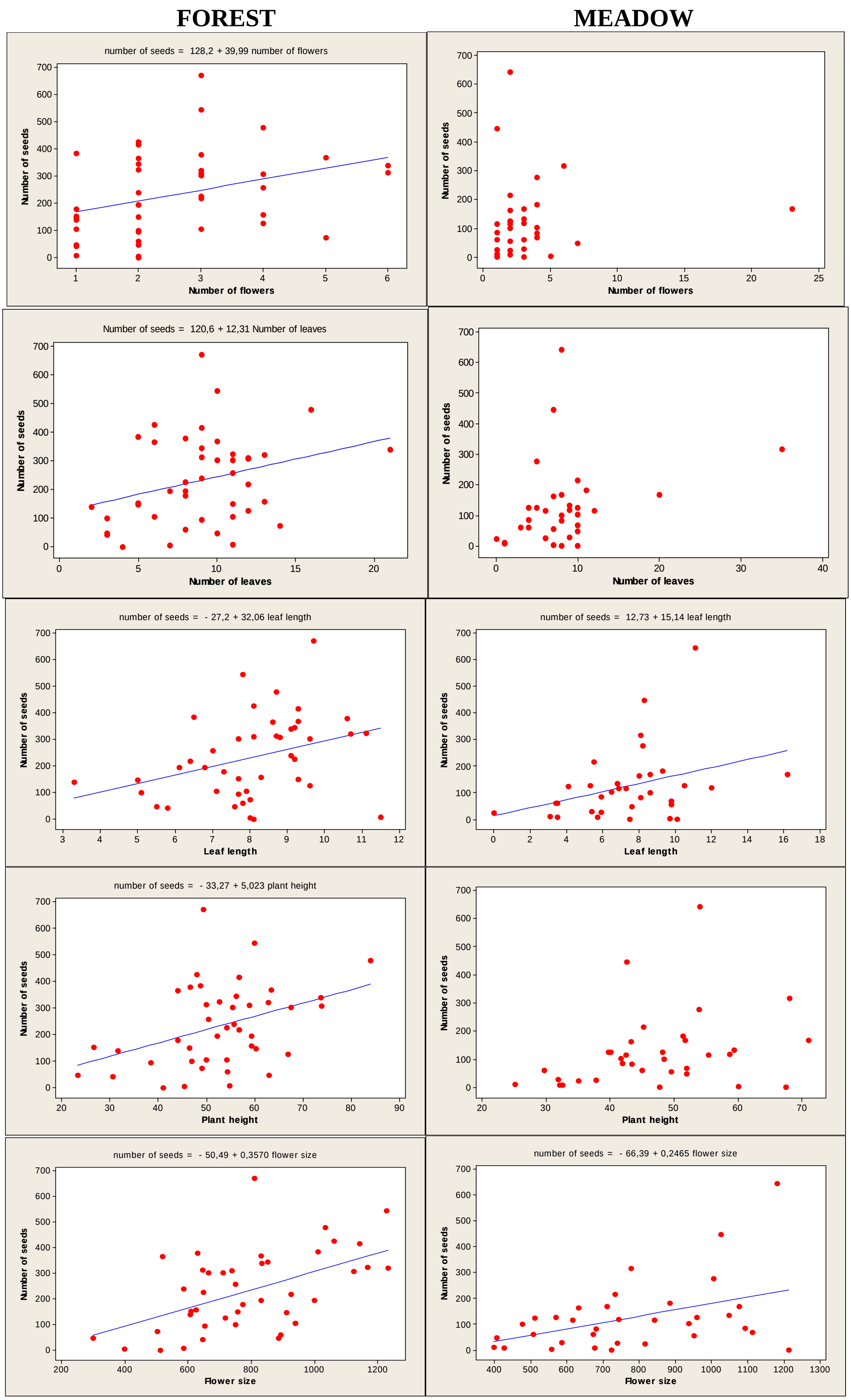

Figure 1. *Relationship between morphological traits and number of seeds. Line shown and equations above plots are from simple linear regressions.*

Table 9. *Meadow plants: Standarized coefficients from simple and multiple regression analyses on number of seeds, and variance inflation factors (VIF) from multiple regression. P-value in parenthesis. Significant relationships are marked *.*

Variables	Simple	Multiple	VIF
No. of flowers	0.068 (0.70)	-0.119 (0.54)	1.9
No. of leaves	0.329 (0.06)	0.365 (0.13)	2.1
Leaf length	0.345 (0.04)*	0.298 (0.23)	2.3
Plant height	0.297 (0.09)	-0.283 (0.37)	3.8
Flower size	0.430 (0.01)*	0.387 (0.05)*	1.5

Number of aborted seeds

Analysis of covariance showed no significant relationships between seed abortion and morphological traits, and none of the interactions were significant (Table 10). I therefore chose not to perform simple and multiple regressions for number of aborted seeds.

Table 10. *Analysis of covariance for number of aborted seeds.*

Source	*df*	SS	MS	F	P
Habitat	1	15.2	15.2	0.08	0.777
Number of leaves	1	154.8	154.8	0.83	0.367
Leaf length	1	39.8	39.8	0.21	0.646
Mean height	1	489.7	489.7	2.61	0.111
Flower size	1	25.0	25.0	0.13	0.716
Number of flowers	1	146.4	146.4	0.78	0.380
Habitat × number of flowers	1	642.0	642.0	3.42	0.069
Habitat × number of leaves	1	275.8	275.8	1.47	0.230
Habitat × leaf length	1	188.1	188.1	1.00	0.320
Habitat × mean height	1	0.7	0.7	0.00	0.952
Habitat × flower size	1	165.0	165.0	0.88	0.352
Error	65	12193.8	187.6		
Total	76	18489.7			

Seed weight

Analysis of covariance showed no significant relationships between seed weight and the morphological traits, and none of the interactions were significant (Table 11). I therefore chose not to perform simple and multiple regressions for seed weight.

Table 11. *Analysis of covariance for seed weight.*

Source	*df*	SS	MS	F	P
Habitat	1	0.0001662	0.0001662	0.38	0.541
Number of leaves	1	0.0004572	0.0004572	1.054	0.312
Leaf length	1	0.0002936	0.0002936	0.67	0.471
Mean height	1	0.0002270	0.0002270	0.52	0.475
Flower size	1	0.0007218	0.0007218	1.64	0.205
Number of flowers	1	0.0010465	0.0010465	2.38	0.128
Habitat × number of flowers	1	0.0010258	0.0010258	2.33	0.132
Habitat × number of leaves	1	0.0005337	0.0005337	1.21	0.275
Habitat × leaf length	1	0.0000183	0.0000183	0.04	0.839
Habitat × mean height	1	0.0001242	0.0001242	0.28	0.597
Habitat × flower size	1	0.0000000	0.0000000	0.00	0.996
Error	65	0.0285899	0.0004398		
Total	76	0.0329555			

Differences in morphological traits between habitats

Plant height was the only morphological trait that differed significantly between the two habitats (Table 12). Plants were higher in the forest than on the meadow.

Table 12. *Means ± SE for the measured morphological traits, and t-values and P-values from two-sample t-tests. Significant differences are marked **

Trait	Forest	Meadow	t-value	P-value
No. of flowers	2.581 ± 0.203	3.206 ± 0.651	0.92	0.365
No. of leaves	9.0 ± 0.569	8.03 ± 1.05	-0.81	0.42
Leaf length (cm)	8.065 ± 0.257	7.362 ± 0.523	-1.21	0.23
Plant height (cm)	52.7 ± 1.84	47.01 ± 1.9	-2.15	0.035*
Flower size (mm^2)	789.6 ± 33.6	773.1 ±40.1	-0.35	0.753

DISCUSSION

Haig and Westoby (1988) suggest that most pollen-addition experiments should not result in a major increase in seed set. Within a species that is consistently pollen limited, natural selection will favour individuals that allocate more of the resources to pollen attraction, while individuals that allocate less resources to pollen attraction will be favoured when resources are the limiting factor. The population thereby adapts to the environment and individuals allocate resources in an optimal way. Pollen availability can only be a limiting factor when pollen supply is highly variable. If pollen availability is relatively stable, the portion of available resources that needs to be allocated to pollen attraction also is stable. On the other hand, if pollen availability varies considerably, the optimal way of allocating resources is constantly changing. Their model is based on the economic principle that internal resources are optimally allocated among competing processes when each resource limits all processes to the same degree (Bloom et al. 1985).

Bateman`s principle states that female reproductive success, such as seed set or fruit set, usually is limited by resource availability, while male reproductive success usually is limited by the number of matings achieved (Burd 1994). This leads to the assumption that selection on floral traits arises mainly from effects on male fitness, because male reproductive success depends on efficient removal of pollen from the anthers and adequate delivery of pollen to stigmas. According to this principle, it should not be common that seed set or fruit set is limited by pollen availability. Nevertheless, several studies show that pollen availability can be a limiting factor for female reproductive success (e.g. Hainsworth et al. 1985, Fox 1992, Campbell and Halama 1993, Mitchell 1994, Parker 1997, Totland et al. 1998, Larson and Barret 2000). Wilson et al. (1994) argue that selection on flower attractiveness characters is often biased towards one gender, but it is just as likely the female as the male gender.

Seed production in the study population of *Campanula persicifolia* was indeed limited by pollen availability the year I carried out the study. The hand-pollinated flowers increased their number of seeds with about 82 % compared to the controls. This implies that variation in female reproductive success may affect selection on floral traits in *C. persicifolia*. Interestingly, there was no significant difference in pollen limitation between the plants in the forested habitat and on the open meadow, even though it is likely that the plants experience highly different environmental conditions in terms of light, in particular, but also nutrient and water availability.

Insect visitation rates did not differ between the forested and meadow habitat when the beetles were excluded, and this might explain that there was no difference in pollen limitation between habitats. When the beetles were included, visitation rate was significantly higher on the meadow than in the forest. The beetles have been seen in other areas covered by pollen and moving between flowers (Båtvik 2004, pers.com.). However, the beetles' contribution to pollination of *C. persicifolia* in the study area is uncertain, because seed production was not significantly different in the two habitats, despite the significant difference in visitation rate. The study population of *C. persicifolia* is relatively isolated from other *C. persicifolia* populations, and few other plant species with showy flowers grow together with the population. In addition, the study population is relatively small, about 140 individuals, so the flower visiting insects in the area likely have a restricted access to food. The insects may not "afford" to be critical to whom they visit, and consequently, they visit individuals both in the forest and on the meadow. Light and temperature may also affect the activity pattern of insects (Murcia 1990, Herrera 1997), and the lack of differences in visitation rate between the two habitats may be because the environmental differences between the forest and the meadow are not large enough to affect the insects activity pattern. Flower density in the patches used for measuring visitation rates was marginally significantly related to visits per flower only on the meadow with the beetles included. There was no relationship in the forest or on the meadow with the beetles included. This is in contrast to earlier findings by for example Thomson (1981), who found that insects concentrate the foraging in dense patches of flowers, but may be explained by the restricted access to food in the area.

Spatial or temporal variation in visitation rate or efficiency may cause variation in pollen supply. All the groups of visiting insects, except for the flies, appeared evenly distributed over the days that I conducted the measurements. All insect groups that appeared through the study period are common in the area. Pollen supply in terms of pollinator abundance should therefore be relatively stable. Still, it is known from other studies that pollinator abundance can change trough a season, and that the quality of each visit can vary between different pollinating species (Olsen 1997, Potts et al. 2001). *Campanula persicifolia* is visited by many groups of insects, so it is highly generalistic. This counteracts a possible large annual variation in visitation rate, but variation in relative abundance of each insect group may result in a temporal variation in pollination quality.

The number of seeds produced by *C. persicifolia* was not significantly different between the two habitats, despite that the plants in the forest and on the meadow probably experience different environmental conditions. Seed production is affected by pollinator visitation, environmental conditions and resource availability. Visitation rate was the same in both habitats, with the beetles excluded, and this may partly explain the result. With the beetles included, visitation rate was higher on the meadow than in the forest, but as mentioned above it is difficult to estimate how important the beetle is for pollination of *C. persicifolia*. I would expect light conditions to be one of the environmental factors differing most between the open and forested habitat, and light is perhaps the most important resource for the plants. But even though individuals experience different light conditions, seed production may not be significantly different. Sultan and Bazzaz (1993) showed that one genotype of *Polygonum persicaria* can produce the same number of fruits (one fruit is one seed unit) at different light intensities, because the plants adjust their resource allocation to be optimal. This may also be the case in my study population. Individuals probably share many of the same genes because of small population size and isolation, and should therefore have about the same genetic potential for seed production. The measured morphological traits are affected by the plants' access to resources like light, nutrients and water. Garbutt and Bazzaz (1987) examined individuals from a population of *Abutilon theophrasti* for different responses to a light gradient and a nutrient gradient. Their results showed significant effects of the resource state for all characters on both gradients. Total biomass was positively related to light intensity until a certain level, were biomass decreased with increasing light intensity. Total biomass was also positively related to nutrient state. The morphological traits may therefore be used as parameters for the plant resource status. Plant height was the only morphological trait in the study population that differed significantly between the two habitats, with the highest plants in the forest. Several factors acting together or alone might explain the difference. Enhanced length growth may be a compensatory response to shade (Lambers et al. 1998), or access to resources like nutrients and water may be higher in the forest. Scmitt (1993) included within-population morphological variation and life history traits in her study of *Impatiens capensis*. She found that different light levels caused morphological differences between individuals from the same population. When a set of phenotypes is produced by a genotype in response to diverse environmental conditions it is termed "norm of reaction" (Sultan and Bazzaz 1993).

The multiple regressions showed that there were some differences between habitats in the relationships between seed production and the measured traits. In the forest, number of seeds per flower was positively related to number of flowers on each individual, leaf length and flower size. On the meadow, number of seeds was not significantly related to any of the traits, although flower size had a marginally significant effect. The results might be explained by visitation rate and access to nutrients in the growing area. The number of flowers on each individual may affect pollinator behaviour, because pollinators forage optimally and may prefer to visit individuals with several flowers. Leaf length may be a response to resource availability in the area, since morphological traits reflect the access to resources in the plants growing area. Flower size and pollinator behaviour have been frequently studied, and the studies often show that large flowers receive more visits by potential pollinators than small flowers (Galen and Newport 1987, Cresswell and Galen 1991, Elle and Carney 2003). Pollinators probably prefer large flowers because nectar production and nectar sugar content often is positively related to flower size (Campbell et al. 1991, Cresswell and Galen 1991, Inoue et al. 1995). Pollen production has also been shown to positively relate to corolla length (Galen and Stanton 1989). It is reasonable to think that the largest flowers in the study population received more visits than the other flowers, and thereby received more pollen. Large flower size may be favoured by selection in the study population. However, it may not be an advantage to the plant if the flower is very large or very wide, because the pollinators may then reach the pollen or the nectar without making contact with the stigma. A large flower also implies a great cost for the plant, in terms of the nutrients and energy needed to build the flower. Increased flower size is only worth the effort up to a certain limit, and above the limit the cost exceeds the profit (Fægri and van der Pijl 1979).

Campanula persicifolia produces numerous ovules, and not all of them are fertilized (pers. obs.). Among the fertilized ovules, some are aborted. The large production of ovules may play an important role in controlling offspring quality through selective seed abortion. This occur when some genotypes are aborted more frequently than others, and it may lead to an increase in offspring quality (Korbecka et al. 2002). Selective abortion of fruits or seeds has been studied in several species, with different results. For example, Melser and Klinkhamer (2001) randomly removed ovules by hand of *Cynoglossum officinale* to simulate abortion. They collected randomly chosen seeds, and allowed them to germinate to test for offspring survival. *Cynoglossum officinale* seedlings from unmanipulated plants had a higher survival compared to seedlings from experimental plants. Andersson (1990), on the other hand, showed that there was no evidence for selective seed maturation in *Anchusa officinalis*. Obeso (1993) found that the ability to mature only high quality embryos may be limited in *Asphodelus albus*. The position of the fruit within the inflorescence and the seed number within each fruit seemed to be determining whether each fruit was allowed to ripe or was aborted. In Obeso`s experiment the abortion rate was unaffected by additional hand-pollination, but the probability that one-seeded fruits were retained increased. This suggests that genetic quality of the seeds might be improved through increased pollen supply.

To confirm selective embryo abortion, it has to be shown that viable embryos are aborted (Melser and Klinkhamer 2001). I have no evidence that the aborted seeds of *C. persicifolia* were viable, but it has been shown for several other species that viable seeds are aborted (for example Burd 1998, Korbecka et al 2001, Melser and Klinkhamer 2001). If this is the case also in *C. persicifolia*, the species has a large potential for selective embryo abortion. The abortion rate for *C. persicifolia* was higher in the forest than on the open meadow, maybe because there is a stronger selection for high quality offspring in the forest than on the meadow (Andersson 1993). The abortion rate increased in both habitats after supplemental pollination. A possible explanation might be that the plants are more selective in deciding which of the fertilized ovules that are allowed to develop to seeds when they are offered a large amount of pollen.

When considering the results of this study, it is important to keep in mind that I have only studied the population for one season, and that *C. persicifolia* is a perennial plant. It is known that enhanced seed set in some flowers on an individual may reduce seed set in other flowers on the same individual because of resource allocation. This can happen the same season or in a later one (Zimmerman and Pyke 1988). The most reliable results are obtained by studying lifetime seed production and pollen limitation.

CONCLUSIONS

The seed production of *Campanula persicifolia* in the study population was limited by pollen availability the year I carried out the study. There was no difference in seed production or pollen limitation between individuals from the forested and open habitat, despite conceivable large differences in abiotic environmental conditions between the two habitats.

Since female reproductive success in *C. persicifolia* was strongly limited by pollen availability, it is conceivable that pollinators play a decisive role in seed production. Thus, the lack of difference in pollen limitation may be explained by the fact that there were no significant differences in visitation rates of potential pollinators, except for the beetles, in the two habitats. The beetle *Miarus campanulae* visited significantly more flowers on the meadow than in the forest, but the pollination efficiency of this insect may be low.

Number of flowers, leaf length and flower size was positively related to seed production in the forest, indicating that access to resources may be positively related to seed production. Flower size may also increase seed production because this trait often positively affect pollinator visitation. On the meadow, only flower size was positively related to seed production.

Plant height was the only morphological trait that differed between the habitats, with the highest plants in the forested habitat. This may be a compensatory response to shade, or it may be caused by differences in nutrient or water availability.

REFERENCES

Andersson, S. 1990. No evidence for selective seed maturation in *Anchusa officinalis* (Boraginaceae). Oikos **57**: 88-93.

Andersson, S. 1993. The potential for selective seed maturation in *Achillea ptarmica* (Asteraceae). Oikos **66**: 36-42.

Anthony, K. R., Hoegh-Guldberg, O. 2003. Variation in coral photosynthsis, respiration and growth characteristics in contrasting light microhabitats: an anlouge to plants in forest gaps and understoreys? Functional Ecology **17**: 246-259.

Bell, G., Lechowicz, M. J. 1991. The ecology and genetics of fitness in forest plants. I. Environmental heterogeneity measured by explant trials. Journal of Ecology **79**: 663-685.

Bloom, A. J., Chapin, F. S., Mooney, H. A. 1985. Resource limitation in plants – an economic analogy. Annual Review of Ecological Systems **16**: 363-392.

Burd, M. 1994. Bateman`s Principle and Plant Reproduction: The Role of Pollen Limitation in Fruit and Seed Set. The Botanical Review **60**: 83-139.

Burd, M. 1998. “Excess” flower production and selective fruit abortion: a model of potential benefits. Ecology **79**: 2123-2132.

Campbell, D. R., Halama, K. J. 1993. Resource and pollen limitations to lifetime seed production in a natural plant population. Ecology **74**: 1043-1051.

Campbell, D. R., Waser, N. M., Price, M. V., Lynch, E. A., Mitchell, R. J. 1991. Components of phenotypic selection: Pollen export and flower corolla width in *Ipomopsis aggregata.* Evolution **45**: 1458-1467.

Cresswell, J. E., Galen, C. 1991. Frequency-dependent selection and adaptive surfaces for floral character combinations: the pollination of *Polemonium viscosum*. The American Naturalist **138**: 1342-1353.

Dudash, M. R. 1991. Plant size effects on female and male function in hermaphroditic Sabatia angularis *(Gentianecae). Ecology **70**: 1004-1012.*

Dudash, M. R. 1993. Variation in pollen limitation among individuals of *Sabatia angularis* (Gentianecea). Ecology **74**: 959-962

Elle, E., Carney, R. 2003. Reproductive assurance varies with flower size in *Collinsia parviflora* (Scrophulariaceae). American Journal of Botany **90**: 888-896.

Fox, J. F. 1992. Pollen limitation of reproductive effort in willows. Oecologia **90**: 283-287

Fægri, K., van der Pijl, L. 1979. The principles of pollination ecology. Third edition, Pergamon, Oxford, UK. 244 p.

Galen, C., Stanton, M. L. 1989. Bumble bee pollination and floral morphology: factors influencing pollen dispersal in the alpine sky pilot, *Polemonium viscosum* (Polemoniaceae). American Journal of Botany **76**: 419-426.

Galen C., Newport, M. E. A. 1987. Bumble bee behaviour and selection on flower size in the sky pilot, *Polemonium viscosum*. Oecologia **74**: 20-23.

Garbutt, K., Bazzaz, F. A. 1987. Population niche structure. Differential response of *Abutilon theophrasti* progeny to resource gradients. Oecologia **72**: 291-296.

Haig, D., Westoby, M. 1988. On limits to seed production. The American Naturalist. **131**: 757-759.

Hainsworth, F. R., Wolf, L. L., Mercier T. 1985. Pollen limitation in a monocarpic species, *Ipomopsis aggregata*. Journal of Ecology **73**: 263-270.

He, W. M., Dong, M. 2003. Physiological acclimation and growth response to partial shading in *Salix matsudana* in th Mu Us Sandland in China. Trees **17**: 87-93.

Herrera, C. M. 1997. Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. Oikos **78**: 601-611.

Heywood, V. H. 1978. Flowering plants of the world. Oxford University Press. 335 s.

Inoue, K., Maki, M., Masuda, M. 1995. Different responses of pollinating bees to size variation and sexual phases in flowers of *Campanula*. Ecological Research **10**: 267-273.

Korbecka, G., Klinkhamer, P. G. L., Vrieling, K. 2002. Selective embryo abortion hypothesis revisited – a molecular approach. Plant Biology **4**: 298-310.

Lagerberg, T., Holmboe, J., Nordhagen, R. 1958. Våre Ville Planter. Bind VI, 2. Revidert utgave. Reistad & Sønns Boktrykkeri. 279 p.

Lambers, H., Chapin III, F. S., Pons, T. L. 1998. Plant Physiological Ecology. Springer-Verlag. 540 p.

Larson, B. M. H., Barret, C. H. 2000. A comparative analysis of pollen limitation in flowering plants. Biological Journal of the Linnean Society **69**: 503-520.

Lechowicz, G. M., Bell, G. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. Journal of Ecology **79**: 687-696.

Lundberg, H. 1980. Effects of weather in foraging-flights of bumblebees (Hymenoptera, Apidae) in a subalpine/alpine area. Holoarctic Ecology **3**: 104-110.

Melser, C., Klinkhamer, P. G. L. (2001) Selective seed abortion increases offspring survival in *Cynoglossum officinale* (Boraginaceae). American Journal of Botany **88**: 1033-1040.

Mitchell, R. J. 1994. Effects of floral traits, pollinator visitation, and plant size on *Ipomopsis aggregata* fruit production. The American Naturalist **143**: 870-889.

Murcia, C. 1990. Effect of floral morphology and temperature on pollen receipt and removal in *Ipomoea trichocarpa.* Ecology **71**: 1098-1109.

Nicotra, A. B., Chazdon, R. L., Iriarte V. B. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecology **80**: 1908-1926.

Nyman, Y. 1992. Pollination mechanisms in six *Campanula* species (Campanulaceae). Plant Systematics and Evolution **181**: 97-108.

Obeso, J. R. 1993. Selective fruit and seed maturation in *Asphodelus albus* Miller (Liliaceae). Oecologia **93**: 564-570.

Olsen, K. M. 1997. Pollination effectiveness and pollinator importance in a population of *Heterotheca subaxillaris* (Asteraceae). Oecologia **109**: 114-121.

Parker, I. M. 1997. Pollinator limitation of *Cytisus scoparius* (scotch broom), an invasive shrub. Ecology **78**: 1457-1470.

Potts, S. G., Dafni, A., Ne'eman, G. 2001. Pollination of a core flowering shrub species Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire. Oikos **92**: 71-80.

Robertson, G. P., Huston, M. A., Evans, F. C., Tiedje, J. M. 1988. Spatial variability in a successional plant community: Patterns of nitrogen availability. Ecology **69**: 1517-1524.

Schmitt, J. 1993. Reaction norms of morphological and life-history traits to light availability in *Impatiens capensis*. Evolution **47**: 1654-1668.

Sokal, R. R., Rohlf, F. J. 1995. Biometry: The principles and practice of statistics in biological research. Third edition. W. H. Freeman and Company. 887 p.

Sultan, S. E., Bazzaz, F. A. 1993. Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. Evolution **47**: 1009-1031.

Thomson, J. D. 1981. Spatial and temporal components of resource assessment by flower-feeding insects. Journal of Animal Ecology **50**: 49-59.

Totland, Ø., Andersen, H. L., Bjelland, T., Dahl, V., Eide, W., Houge, S., Pedersen, T. R., Vie, E. U. 1998. Variation in pollen limitation among plants and phenotypic selection on floral traits in an early-spring flowering herb. Oikos **82**: 491- 501.

Wilson, P., Thomson, J. D., Stanton, M. L., Rigney, L. P. 1994. Beyond Floral Batemania: Gender biases in selection for pollination traits. The American Naturalist **143**: 283-296.

Zar, J. H. 1984. Biostatistical Analysis. Second Edition. Prentice-Hall International, Inc. 718 p.

Zimmermann, M., Pyke, G., H. 1988. Reproduction in *Polemonium*: Assessing the factors limiting seed set. The American Naturalist **131**: 723-738.

APPENDIX

Data set:

- Pollen limitation experiment
- Insect visitation rates
- Morphological traits and relation to number of seeds, aborted seeds and seed weight

POLLEN LIMITATION EXPERIMENT								
individual	**habitat**	**experiment**	**pair**	**plant**	**flower**	**seed number**	**ab. seeds**	**seed weight**
AEK 1	meadow	kon	1	1	1	55	1	0.063636364
	meadow	kon	1	snitt1		55	1	0.063636364
AEP 1	meadow	extrapoll	1	2	1	434	3	0.040322581
	meadow	extrapoll	1	snitt2		434	3	0.040322581
AEK 4	meadow	kon	2	3	1	439	16	0.054214123
	meadow	kon	2	3	2	45	2	0.062222222
	meadow	kon	2	3	3	66	7	0.051515152
	meadow	kon	2	snitt3		183.3333333	8.3333333	0.054545455
AEP 4	meadow	extrapoll	2	4	1	607	10	0.056177924
	meadow	extrapoll	2	4	2	152	4	0.065131579
	meadow	extrapoll	2	4	3	507	14	0.052859961
	meadow	extrapoll	2	4	4	174	2	0.054597701
	meadow	extrapoll	2	snitt4		360	7.5	0.055763889
AEK 6	meadow	kon	3	5	1	85	3	0.054117647
	meadow	kon	3	snitt5		85	3	0.054117647
AEP 6	meadow	extrapoll	3	6	1	300	9	0.051333333
	meadow	extrapoll	3	snitt6		300	9	0.051333333
AEK 7	meadow	kon	4	7	1	61	1	0.036065574
	meadow	kon	4	snitt7		61	1	0.036065574
AEP 7	meadow	extrapoll	4	8	1	50	3	0.038
	meadow	extrapoll	4	snitt8		50	3	0.038
AEK 8	meadow	kon	5	9	1	24	1	0.033333333
	meadow	kon	5	snitt9		24	1	0.033333333
AEP 8	meadow	extrapoll	5	10	1	33	2	0.012121212
	meadow	extrapoll	5	snitt10		33	2	0.012121212
AEK 9	meadow	kon	6	11	1	178	5	0.029213483
	meadow	kon	6	11	2	75	16	0.048
	meadow	kon	6	snitt11		126.5	10.5	0.034782609
AEP 9	meadow	extrapoll	6	12	1	398	8	0.05678392
	meadow	extrapoll	6	snitt12		398	8	0.05678392
AEK 10	meadow	kon	7	13	1	126	7	0.046031746
	meadow	kon	7	snitt13		126	7	0.046031746
AEP 10	meadow	extrapoll	7	14	1	344	3	0.053197674
	meadow	extrapoll	7	snitt14		344	3	0.053197674
AEK 11	meadow	kon	8	15	1	215	5	0.052093023
	meadow	kon	8	snitt15		215	5	0.052093023
AEP 11	meadow	extrapoll	8	16	1	99	9	0.055555556
	meadow	extrapoll	8	16	2	65	6	0.06
	meadow	extrapoll	8	snitt16		82	7.5	0.057317073
AEK 12	meadow	kon	9	17	1	406	1	0.067487685
	meadow	kon	9	17	2	293	3	0.06109215
	meadow	kon	9	17	3	251	0	0.054183267
	meadow	kon	9	snitt17		316.6666667	1.3333333	0.062
AEP 12	meadow	extrapoll	9	18	1	372	8	0.054301075
	meadow	extrapoll	9	18	2	287	7	0.056097561
	meadow	extrapoll	9	snitt18		329.5	7.5	0.05508346
AEK 13	meadow	kon	10	19	1	447	4	0.064205817
	meadow	kon	10	snitt19		447	4	0.064205817
AEP 13	meadow	extrapoll	10	20	1	545	18	0.058165138
	meadow	extrapoll	10	snitt20		545	18	0.058165138
AEK 16	meadow	kon	11	21	1	8	0	0.05
	meadow	kon	11	snitt21		8	0	0.05
AEP 16	meadow	extrapoll	11	22	1	33	7	0.039393939
	meadow	extrapoll	11	snitt22		33	7	0.039393939

individual	habitat	experiment	pair	plant	flower	seed number	ab. seeds	seed weight
AEK 17	meadow	kon	12	23	1	9	5	0
	meadow	kon	12	snitt23		9	5	0
AEP 17	meadow	extrapoll	12	24	1	27	5	0.02962963
	meadow	extrapoll	12	snitt24		27	5	0.02962963
AEK 18	meadow	kon	13	25	1	0	30	#DIV/0!
	meadow	kon	13	25	2	59	6	0.037288136
	meadow	kon	13	snitt25		29.5	18	0.037288136
AEP 18	meadow	extrapoll	13	26	1	277	2	0.051263538
	meadow	extrapoll	13	26	2	149	3	0.031543624
	meadow	extrapoll	13	snitt26		213	2.5	0.044366197
AEK 19	meadow	kon	14	27	1	10	1	0.08
	meadow	kon	14	snitt27		10	1	0.08
AEP 19	meadow	extrapoll	14	28	1	61	1	0.047540984
	meadow	extrapoll	14	28	2	56	3	0.035714286
	meadow	extrapoll	14	snitt28		58.5	2	0.041880342
AEK 21	meadow	kon	15	29	1	114	7	0.044736842
	meadow	kon	15	29	2	441	3	0.059863946
	meadow	kon	15	snitt29		277.5	5	0.056756757
AEP 21	meadow	extrapoll	15	30	1	474	9	0.049578059
	meadow	extrapoll	15	30	2	571	17	0.053765324
	meadow	extrapoll	15	snitt30		522.5	13	0.051866029
AEK 22	meadow	kon	16	31	1	72	2	0.075
	meadow	kon	16	31	2	132	4	0.05
	meadow	kon	16	snitt31		102	3	0.058823529
AEP 22	meadow	extrapoll	16	32	1	546	12	0.061538462
	meadow	extrapoll	16	32	2	451	15	0.071396896
	meadow	extrapoll	16	32	3	299	3	0.053511706
	meadow	extrapoll	16	snitt32		432	10	0.063117284
ASK 1	forest	kon	17	33	1	106	6	0.053773585
	forest	kon	17	snitt33		106	6	0.053773585
ASP 1	forest	extrapoll	17	34	1	456	21	0.047149123
	forest	extrapoll	17	snitt34		456	21	0.047149123
ASK 2	forest	kon	18	35	1	124	12	0.07016129
	forest	kon	18	35	2	86	29	0.059302326
	forest	kon	18	snitt35		105	20.5	0.065714286
ASP 2	forest	extrapoll	18	36	1	718	5	0.051392758
	forest	extrapoll	18	36	2	179	8	0.095530726
	forest	extrapoll	18	snitt36		448.5	6.5	0.060200669
ASK 3	forest	kon	19	37	1	5	0	0.08
	forest	kon	19	37	2	2	0	0.25
	forest	kon	19	snitt37		3.5	0	0.128571429
ASP 3	forest	extrapoll	19	38	1	465	8	0.053333333
	forest	extrapoll	19	snitt38		465	8	0.053333333
ASK 4	forest	kon	20	39	1	390	15	0.070769231
	forest	kon	20	39	2	257	21	0.071206226
	forest	kon	20	snitt39		323.5	18	0.070942813
ASP 4	forest	extrapoll	20	40	1	513	15	0.055555556
	forest	extrapoll	20	40	2	0	0	0
	forest	extrapoll	20	snitt40		256.5	7.5	0.055555556
ASK 5	forest	kon	21	41	1	194	7	0.058247423
	forest	kon	21	snitt41		194	7	0.058247423
ASP 5	forest	extrapoll	21	42	1	343	7	0.06180758
	forest	extrapoll	21	snitt42		343	7	0.06180758
ASK 6	forest	kon	22	43	1	391	19	0.063682864
	forest	kon	22	43	2	217	25	0.06359447

individual	habitat	experiment	pair	plant	flower	seed number	ab. seeds	seed weight
	forest	kon	22	43	3	66	7	0.075757576
	forest	kon	22	snitt43		224.6666667	17	0.064836795
ASP 6	forest	extrapoll	22	44	1	618	92	0.053074434
	forest	extrapoll	22	44	2	448	30	0.043080357
	forest	extrapoll	22	snitt44		533	61	0.048874296
ASK 8	forest	kon	23	45	1	46	4	0.039130435
	forest	kon	23	snitt45		46	4	0.039130435
ASP 8	forest	extrapoll	23	46	1	365	25	0.04109589
	forest	extrapoll	23	snitt46		365	25	0.04109589
ASK 10	forest	kon	24	47	1	44	13	0.056818182
	forest	kon	24	47	3	108	14	0.049074074
	forest	kon	24	47	4	71	27	0.05915493
	forest	kon	24	snitt47		74.33333333	18	0.053811659
ASP 10	forest	extrapoll	24	48	1	323	10	0.03869969
	forest	extrapoll	24	48	2	216	27	0.042592593
	forest	extrapoll	24	snitt48		269.5	18.5	0.04025974
ASK 12	forest	kon	25	49	1	99	16	0.034343434
	forest	kon	25	snitt49		99	16	0.034343434
ASP 12	forest	extrapoll	25	50	1	93	18	0.027956989
	forest	extrapoll	25	50	2	124	32	0.026612903
	forest	extrapoll	25	snitt50		108.5	25	0.02718894
ASK 17	forest	kon	26	51	1	193	7	0.058031088
	forest	kon	26	snitt51		193	7	0.058031088
ASP 17	forest	extrapoll	26	52	1	241	8	0.074688797
	forest	extrapoll	26	snitt52		241	8	0.074688797
ASK 18	forest	kon	27	53	1	416	12	0.047596154
	forest	kon	27	snitt53		416	12	0.047596154
ASP 18	forest	extrapoll	27	54	1	277	13	0.063898917
	forest	extrapoll	27	snitt54		277	13	0.063898917
ASK 19	forest	kon	28	55	1	147	3	0.051020408
	forest	kon	28	snitt55		147	3	0.051020408
ASP 19	forest	extrapoll	28	56	1	297	15	0.068686869
	forest	extrapoll	28	snitt56		297	15	0.068686869
ASK 20	forest	kon	29	57	1	268	4	0.054477612
	forest	kon	29	57	2	335	4	0.054328358
	forest	kon	29	snitt57		301.5	4	0.054394693
ASP 20	forest	extrapoll	29	58	1	26	60	0
	forest	extrapoll	29	58	2	346	36	0.037861272
	forest	extrapoll	29	58	3	398	30	0.037939698
	forest	extrapoll	29	58	4	268	19	0.035074627
	forest	extrapoll	29	snitt58		259.5	36.25	0.036223507
ASK 21	forest	kon	30	59	1	630	5	0.061269841
	forest	kon	30	59	2	483	5	0.054658385
	forest	kon	30	59	3	27	1	0.059259259
	forest	kon	30	snitt59		380	3.6666667	0.058421053
ASP 21	forest	extrapoll	30	60	1	621	3	0.055555556
	forest	extrapoll	30	60	2	330	4	0.047575758
	forest	extrapoll	30	snitt60		475.5	3.5	0.05278654
ASK 22	forest	kon	31	61	1	205	6	0.050243902
	forest	kon	31	61	2	324	5	0.065123457
	forest	kon	31	61	3	411	10	0.059367397
	forest	kon	31	61	4	313	23	0.046325879
	forest	kon	31	snitt61		313.25	11	0.056105347
ASP 22	forest	extrapoll	31	62	1	88	1	0.067045455
	forest	extrapoll	31	62	2	437	6	0.048512586

individual	habitat	experiment	pair	plant	flower	seed number	ab. seeds	seed weight
	forest	extrapoll	31	62	3	66	1	0.065151515
	forest	extrapoll	31	snitt62		197	2.6666667	0.053130288

MORPHOLOGICAL TRAITS AND RELATION TO NUMBER OF SEEDS, ABORTED SEEDS AND SEED WEIGHT

individual	habitat	plant	flower	seed number	ab seeds	seed weight	no flowers	leaves	leaf length	plant height	flower size
CE 1	meadow	1	1	55	1	0.06363636					950.16
	meadow	snitt1		55	1	0.06363636	2	7	9.8	49.55	950.16
CE 4	meadow	2	1	439	16	0.05421412					975.28
	meadow	2	2	45	2	0.06222222					769.95
	meadow	2	3	66	7	0.05151515					905.79
	meadow	snitt2		183.333333	8.33333333	0.05454545	4	11	9.3	51.35	885.12
CE 6	meadow	3	1	85	3	0.05411765					1093.05
	meadow	snitt3		85	3	0.05411765	1	4	5.9	41.95	1093.05
CE 7	meadow	4	1	61	1	0.03606557					506.88
	meadow	snitt4		61	1	0.03606557	1	3	3.5	29.75	506.88
CE 8	meadow	5	1	24	1	0.03333333					816.2
	meadow	snitt5		24	1	0.03333333	2	0	0	35.1	816.2
CE 9	meadow	6	1	178	5	0.02921348					953.37
	meadow	6	2	75	16	0.048					963
	meadow	snitt6		126.5	10.5	0.03478261	2	10	10.5	48.2	959.445
CE 10	meadow	7	1	126	7	0.04603175					570.24
	meadow	snitt7		126	7	0.04603175	2	4	5.3	4.1	570.24
CE 11	meadow	8	1	215	5	0.05209302					733.77
	meadow	snitt8		215	5	0.05209302	2	10	5.5	45.2	733.77
CE 12	meadow	9	1	406	1	0.06748768					880.8
	meadow	9	2	293	3	0.06109215					777.48
	meadow	9	3	251	0	0.05418327					680.13
	meadow	snitt9		316.666667	1.33333333	0.062	6	35	8.1	68	778.316667
CE 13	meadow	10	1	447	4	0.06420582					1024.76
	meadow	snitt10		447	4	0.06420582	1	7	8.3	42.55	1024.76
CE 16	meadow	11	1	8	0	0.05					675.92
	meadow	snitt11		8	0	0.05	1	1	5.7	32.5	675.92
CE 17	meadow	12	1	9	5	0					427.125
	meadow	snitt12		9	5	0	2	1	3.5	32.5	427.125
CE 18	meadow	13	1	0	30	0					477.18
	meadow	13	2	59	6	0.03728814					699.4
	meadow	snitt13		29.5	18	0.03728814	3	9	5.4	31.85	584.9175
CE 19	meadow	14	1	10	1	0.08					398.31
	meadow	snitt14		10	1	0.08	1	1	3.1	25.1	398.31

individual	habitat	plant	flower	seed number	ab seeds	seed weight	no flowers	leaves	leaf length	plant height	flower size
CE 21	meadow	15	1	114	7	0.04473684					1207.44
	meadow	15	2	441	3	0.05986395					817.44
	meadow	snitt15		277.5	5	0.05675676	4	5	8.2	53.85	1005.32
CE 22	meadow	16	1	72	2	0.075					1076.4
	meadow	16	2	132	4	0.05					804.94
	meadow	snitt16		102	3	0.05882353	4	10	6.5	41.7	936.9
CE 23	meadow	17	1	5	1	0.14					579.88
	meadow	17	2	1	0	0					674.45
	meadow	17	3	5	0	0.14					429.46
	meadow	snitt17		3.66666667	0.33333333	0.12727273	5	7	9.7	6.1	556.833333
CE 24	meadow	18	1	0	0	0					761.1
	meadow	18	2	126	7	0.07777778					882.34
	meadow	18	3	58	7	0.07068966					421.4
	meadow	snitt18		61.3333333	4.66666667	0.07554348	3	4	3.4	45	672.933333
CE 25	meadow	19	1	26	4	0.06923077					738.76
	meadow	snitt19		26	4	0.06923077	1	6	5.9	37.85	738.76
CE 26	meadow	20	1	163	0	0.0607362					631.62
	meadow	snitt20		163	0	0.0607362	2	7	8	43.3	631.62
CE 28	meadow	21	1	116	92	0.07413793					616.5
	meadow	snitt21		116	92	0.07413793	1	6	6.9	42.5	616.5
CE 29	meadow	22	1	167	83	0.06227545					620.23
	meadow	22	2	175	71	0.056					814.58
	meadow	22	3	90	162	0.06222222					746.816
	meadow	22	4	239	49	0.06485356					651.84
	meadow	snitt22		167.75	91.25	0.06154993	23	20	16.2	71	711.252
CE 31	meadow	23	1	100	6	0.05					476.37
	meadow	snitt23		100	6	0.05	2	8	8.6	48.4	476.37
CE 33	meadow	24	1	0	0	0					723.71
	meadow	snitt24		0	0	0	1	8	10.1	47.75	723.71
CE 34	meadow	25	1	35	6	0.03714286					547.428
	meadow	25	2	89	12	0.02247191					344.25
	meadow	25	3	34	6	0.03823529					428.48
	meadow	25	4	36	6	0.03888889					312
	meadow	snitt25		48.5	7.5	0.03092784	7	10	7.6	52	405.21975
CE 35	meadow	26	1	116	1	0.05431034					841.52

individual	habitat	plant	flower	seed number	ab seeds	seed weight	no flowers	leaves	leaf length	plant height	flower size
	meadow	snitt26		116	1	0.05431034	2	12	7.3	55.35	841.52
CE 36	meadow	27	1	123	1	0.07398374					804
	meadow	27	2	22	3	0.05909091					753.08
	meadow	27	3	39	6	0.04615385					578.88
	meadow	27	4	150	3	0.058					599.4
	meadow	snitt27		83.5	3.25	0.06257485	4	8	8.1	43.4	681.19125
CE 37	meadow	28	1	0	0	0					1212.9
	meadow	snitt28		0	0	0	3	10	7.5	67.45	1212.9
CE 38	meadow	29	1	93	2	0.05053763					1302.128
	meadow	29	2	44	3	0.04772727					936.39
	meadow	snitt29		68.5	2.5	0.04963504	4	10	9.8	51.95	1112.2165
CE 39	meadow	30	1	0	2	0					986.7
	meadow	30	2	268	18	0.03955224					1109.31
	meadow	snitt30		134	10	0.03955224	3	9	6.8	59.35	1047.2
CE 41	meadow	31	1	259	9	0.05521236					821.6
	meadow	31	2	43	4	0.05813953					786.31
	meadow	31	3	56	1	0.05178571					622.38
	meadow	snitt31		119.333333	4.66666667	0.05502793	3	9	12	58.65	743.344444
CE 45	meadow	32	1	110	2	0.05636364					487.56
	meadow	32	2	141	8	0.04255319					533.54
	meadow	snitt32		125.5	5	0.04860558	2	5	4.1	39.75	510.45
CE 48	meadow	33	1	644	3	0.05822981					1180.08
	meadow	snitt33		644	3	0.05822981	2	8	11.1	54.5	1180.08
CE 52	meadow	34	1	81	4	0.05308642					1022
	meadow	34	2	257	12	0.05564202					1128.47
	meadow	snitt34		169	8	0.05502959	3	8	8.6	51.7	1075.8825
CS 1	forest	35	1	106	6	0.05377358					938.4
	forest	snitt35		106	6	0.05377358	1	6	7.1	5	938.4
CS 2	forest	36	1	124	12	0.07016129					982.76
	forest	36	2	86	29	0.05930233					895.9
	forest	snitt36		105	20.5	0.06571429	3	11	7.9	54.2	939
CS 3	forest	37	1	5	0	0.08					437.39
	forest	37	2	2	0	0.25					361.8
	forest	snitt37		3.5	0	0.12857143	2	7	8	45.45	398.825
CS 4	forest	38	1	390	15	0.07076923					1364.2

individual	habitat	plant	flower	seed number	ab seeds	seed weight	no flowers	leaves	leaf length	plant height	flower size
	forest	38	2	257	21	0.07120623					986.38
	forest	snitt38		323.5	18	0.07094281	2	11	11.1	52.6	1167.8175
CS 5	forest	39	1	194	7	0.05824742					999.6
	forest	snitt39		194	7	0.05824742	2	7	6.1	52.25	999.6
CS 6	forest	40	1	391	19	0.06368286					889.17
	forest	40	2	217	25	0.06359447					599.44
	forest	40	3	66	7	0.07575758					482.4
	forest	snitt40		224.666667	17	0.0648368	3	8	9.2	54.2	646.566667
CS 8	forest	41	1	46	4	0.03913043					298.93
	forest	snitt41		46	4	0.03913043	1	3	5.5	23.35	298.93
CS 10	forest	42	1	44	13	0.05681818					546.1
	forest	42	3	108	14	0.04907407					346.94
	forest	42	4	71	27	0.05915493					622.72
	forest	snitt42		74.3333333	18	0.05381166	5	14	8	49.5	502.56
CS 12	forest	43	1	99	16	0.03434343					750.08
	forest	snitt43		99	16	0.03434343	2	3	5.1	46.95	750.08
CS 17	forest	44	1	193	7	0.05803109					830.76
	forest	snitt44		193	7	0.05803109	2	8	6.8	59.25	830.76
CS 18	forest	45	1	416	12	0.04759615					1141.65
	forest	snitt45		416	12	0.04759615	2	9	9.3	56.7	1141.65
CS 19	forest	46	1	147	3	0.05102041					911.84
	forest	snitt46		147	3	0.05102041	1	5	5	6.2	911.84
CS 20	forest	47	1	268	4	0.05447761					642.96
	forest	47	2	335	4	0.05432836					681.2
	forest	snitt47		301.5	4	0.05439469	3	11	9.6	55.45	663.95
CS 21	forest	48	1	630	5	0.06126984					827.75
	forest	48	2	483	5	0.05465839					497.5
	forest	48	3	27	1	0.05925926					582.4
	forest	snitt48		380	3.66666667	0.05842105	3	8	10.6	46.65	629.713333
CS 22	forest	49	1	205	6	0.0502439					529.62
	forest	49	2	324	5	0.06512346					776.58
	forest	49	3	411	10	0.0593674					908.82
	forest	49	4	313	23	0.04632588					415.2
	forest	snitt49		313.25	11	0.05610535	6	9	8.7	49.9	646.463125
CS 23	forest	50	1	292	11	0.06746575					1229.24

individual	habitat	plant	flower	seed number	ab seeds	seed weight	no flowers	leaves	leaf length	plant height	flower size
	forest	50	2	796	14	0.05138191					1224.17
	forest	snitt50		544	12.5	0.05569853	3	10	7.8	59.9	1226.88
CS 24	forest	51	1	615	7	0.05186992					864.2
	forest	51	2	122	4	0.05327869					795.24
	forest	snitt51		368.5	5.5	0.05210312	5	10	9.3	63.4	829.4
CS 25	forest	52	1	670	10	0.05402985					808.35
	forest	snitt52		670	10	0.05402985	3	9	9.7	49.3	808.35
CS 26	forest	53	1	309	17	0.06278317					736.88
	forest	snitt53		309	17	0.06278317	3	12	8.1	58.9	736.88
CS 27	forest	54	1	330	13	0.05030303					784.35
	forest	54	2	185	4	0.05351351					716.38
	forest	snitt54		257.5	8.5	0.05145631	4	11	7	5.4	749.98
CS 28	forest	55	1	425	6	0.05129412					1061.95
	forest	snitt55		425	6	0.05129412	2	6	8.1	47.95	1061.95
CS 29	forest	56	1	452	13	0.07588496					1076.683
	forest	56	2	237	20	0.07341772					637.56
	forest	snitt56		344.5	16.5	0.07503628	2	9	9.2	56.2	850.26725
CS 30	forest	57	1	151	12	0.03642384					610.4
	forest	snitt57		151	12	0.03642384	1	5	7.7	26.7	607.6
CS 31	forest	58	1	542	5	0.0699262					841.18
	forest	58	2	417	13	0.07386091					1229.28
	forest	snitt58		479.5	9	0.07163712	4	16	8.7	83.9	1033.73
CS 32	forest	59	1	149	42	0.03758389					756.96
	forest	snitt59		149	42	0.03758389	2	11	9.3	46.45	756.96
CS 34	forest	60	1	237	14	0.0464135					684.44
	forest	60	2	12	3	0.025					748.44
	forest	snitt60		124.5	8.5	0.04538153	4	12	9.6	66.8	717.44
CS 35	forest	61	1	485	21	0.04597938					401.76
	forest	61	2	248	14	0.05362903					646.98
	forest	snitt61		366.5	17.5	0.04856753	2	6	8.6	44	518.595
CS 36	forest	62	1	50	1	0.062					1376.7
	forest	62	2	43	1	0.07906977					494
	forest	snitt62		46.5	1	0.06989247	2	10	7.6	63	885
CS 37	forest	63	1	325	13	0.06523077					887.04
	forest	63	2	282	16	0.06205674					551.25

individual	habitat	plant	flower	seed number	ab seeds	seed weight	no flowers	leaves	leaf length	plant height	flower size
	forest	snitt63		303.5	14.5	0.06375618	3	10	7.7	67.5	710.2725
CS 38	forest	64	1	372	5	0.06532258					808.68
	forest	64	2	272	8	0.07205882					704.99
	forest	64	3	371	4	0.0638814					956.32
	forest	snitt64		338.333333	5.66666667	0.06660099	6	21	9.1	73.6	831.655556
CS 39	forest	65	1	8	2	0.075					585.64
	forest	snitt65		8	2	0.075	1	11	11.5	54.75	585.64
CS 40	forest	66	1	270	2	0.04925926					683.52
	forest	66	2	43	2	0.03255814					568.62
	forest	snitt66		156.5	2	0.04696486	4	13	8.3	59.25	624.75
CS 41	forest	67	1	179	45	0.07932961					771.65
	forest	snitt67		179	45	0.07932961	1	8	7.3	44.1	771.65
CS 42	forest	68	1	414	20	0.04951691					1320.22
	forest	68	2	203	4	0.05812808					941.28
	forest	snitt68		308.5	12	0.05235008	4	12	8.8	73.75	1122.77
CS 43	forest	69	1	19	1	0.04736842					1216.04
	forest	69	2	622	11	0.0511254					1245.74
	forest	snitt69		320.5	6	0.05101404	3	13	10.7	62.85	1231.07
CS 44	forest	70	1	385	20	0.05714286					1009.8
	forest	snitt70		385	20	0.05714286	1	5	6.5	48.75	1009.8
CS 45	forest	71	1	244	1	0.0704918					1018.96
	forest	71	2	192	29	0.06145833					831.6
	forest	snitt71		218	15	0.06651376	3	12	6.4	56.7	924.2125
CS 46	forest	72	1	145	52	0.08758621					627
	forest	72	2	55	9	0.04545455					407.66
	forest	snitt72		0	0	0	2	4	8.1	4.95	511.4875
CS 47	forest	73	1	106	4	0.06981132					1027.84
	forest	73	2	12	4	0.05					765.7
	forest	snitt73		59	4	0.06779661	2	8	7.8	54.3	892.045
CS 53	forest	74	1	138	11	0.02463768					605.8
	forest	snitt74		138	11	0.02463768	1	2	3.3	31.6	605.8
CS 55	forest	75	1	93	10	0.05483871					652.8
	forest	snitt75		93	10	0.05483871	2	9	7.7	38.5	652.8
CS 56	forest	76	1	240	6	0.06541667					584.63
	forest	snitt76		240	6	0.06541667	2	9	9.1	55.65	584.63

individual	habitat	plant	flower	seed number	ab seeds	seed weight	no flowers	leaves	leaf length	plant height	flower size
CS 59	forest	77	1	41	10	0.04878049					645.75
	forest	snitt77		41	10	0.04878049	1	3	5.8	3.6	645.75

INSECT VISITATION RATE (visit ^{2} = visits without beetles)

habitat	period	measurement	no flowers	beetles	hoverflies	flies	bumblebees	ants	bees	tot visits	visit/flower	visits ^{2}	visits ^{2}/flower
meadow	1	1	8	3	2	0	0	1	0	6	0.75	3	0.375
meadow	1	2	8	5	2	1	0	0	0	8	1	3	0.375
meadow	1	3	4	3	0	0	0	0	0	3	0.75	0	0
meadow	1	4	3	10	0	0	0	0	0	10	3.33333333	0	0
meadow	1	5	5	1	0	3	0	0	0	4	0.8	3	0.6
meadow	2	1	6	4	1	2	0	0	0	8	1.33333333	3	0.5
meadow	2	2	6	3	0	0	2	0	0	5	0.83333333	2	0.33333
meadow	2	3	7	7	0	0	2	0	0	9	1.28571429	2	0.28571
meadow	2	4	4	1	0	0	0	0	0	1	0.25	0	0
meadow	2	5	5	4	2	0	1	0	0	7	1.4	3	0.6
meadow	3	1	6	0	1	0	0	0	0	2	0.33333333	1	0.16667
meadow	3	2	4	6	0	0	0	0	0	6	1.5	0	0
meadow	3	3	7	5	1	1	0	0	0	7	1	2	0.28571
meadow	3	4	3	3	0	0	0	0	0	3	1	0	0
meadow	3	5	3	2	0	1	0	1	0	4	1.33333333	2	0.66667
meadow	4	1	4	3	0	0	2	0	0	5	1.25	2	0.5
meadow	4	2	5	11	0	0	0	0	0	11	2.2	0	0
meadow	4	3	3	1	0	0	0	0	0	1	0.33333333	0	0
meadow	4	4	23	2	0	0	0	0	0	2	0.08695652	0	0
meadow	4	5	2	2	0	3	0	0	1	6	3	4	2
meadow	5	1	4	3	0	0	0	0	0	3	0.75	0	0
meadow	5	2	7	7	1	0	0	0	0	8	1.14285714	1	0.14286
meadow	5	3	2	3	0	0	0	0	0	3	1.5	0	0
meadow	5	4	2	1	0	0	0	0	0	1	0.5	0	0
meadow	5	5	3	5	0	0	0	0	0	5	1.66666667	0	0
forest	1	1	5	0	0	0	0	0	0	0	0	0	0
forest	1	2	6	1	0	0	0	0	0	1	0.16666667	0	0
forest	1	3	4	1	0	0	0	0	0	1	0.25	0	0
forest	1	4	5	1	0	2	0	0	0	6	1.2	2	0.4
forest	1	5	5	1	0	2	0	0	0	4	0.8	2	0.4
forest	2	1	6	0	1	4	0	0	0	5	0.83333333	5	0.83333
forest	2	2	4	0	0	0	0	0	0	1	0.25	0	0
forest	2	3	8	0	0	0	1	0	0	1	0.125	1	0.125
forest	2	4	3	0	0	0	1	0	0	1	0.33333333	1	0.33333

rate beetles	rate hoverflies	rate flies	rate bumblebees	rate ants	rate bees
0.375	0.25	0	0	0.125	0
0.625	0.25	0.125	0	0	0
0.75	0	0	0	0	0
3.33333333	0	0	0	0	0
0.2	0	0.6	0	0	0
0.66666667	0.166666667	0.33333333	0	0	0
0.5	0	0	0.333333333	0	0
1	0	0	0.285714286	0	0
0.25	0	0	0	0	0
0.8	0.4	0	0.2	0	0
0	0.166666667	0	0	0	0
1.5	0	0	0	0	0
0.71428571	0.142857143	0.14285714	0	0	0
1	0	0	0	0	0
0.66666667	0	0.33333333	0	0.33333333	0
0.75	0	0	0.5	0	0
2.2	0	0	0	0	0
0.33333333	0	0	0	0	0
0.08695652	0	0	0	0	0
1	0	1.5	0	0	0.5
0.75	0	0	0	0	0
1	0.142857143	0	0	0	0
1.5	0	0	0	0	0
0.5	0	0	0	0	0
1.66666667	0	0	0	0	0
0	0	0	0	0	0
0.16666667	0	0	0	0	0
0.25	0	0	0	0	0
0.2	0	0.4	0	0	0
0.2	0	0.4	0	0	0
0	0.166666667	0.66666667	0	0	0
0	0	0	0	0	0
0	0	0	0.125	0	0
0	0	0	0.333333333	0	0

habitat	period	measurement	no flowers	beetles	hoverflies	flies	bumblebees	ants	bees	tot visits	visit/flower	visits ^{2}	visits ^{2}/flower
forest	2	5	6	0	2	0	0	0	0	2	0.33333333	2	0.33333
forest	3	1	6	0	2	0	0	0	0	2	0.33333333	2	0.33333
forest	3	2	5	0	0	0	1	1	0	2	0.4	2	0.4
forest	3	3	5	0	3	1	0	0	0	4	0.8	4	0.8
forest	3	4	5	0	4	0	0	1	0	5	1	5	1
forest	3	5	4	0	2	1	0	0	0	3	0.75	3	0.75
forest	4	1	3	0	0	0	0	0	0	0	0	0	0
forest	4	2	1	0	0	0	0	0	0	0	0	0	0
forest	4	3	3	0	2	0	0	1	0	3	1	3	1
forest	4	4	3	1	0	1	0	0	0	2	0.66666667	1	0.33333
forest	4	5	3	0	1	0	1	0	0	2	0.66666667	2	0.66667
forest	5	1	3	0	0	0	0	0	0	0	0	0	0
forest	5	2	2	0	2	0	0	0	0	2	1	2	1
forest	5	3	3	0	0	0	3	0	0	3	1	3	1
forest	5	4	2	0	0	1	0	0	0	1	0.5	1	0.5
forest	5	5	3	0	0	0	0	1	0	1	0.33333333	1	0.33333

rate beetles	rate hoverflies	rate flies	rate bumblebees	rate ants	rate bees
0	0.333333333	0	0	0	0
0	0.333333333	0	0	0	0
0	0	0	0.2	0.2	0
0	0.6	0.2	0	0	0
0	0.8	0	0	0.2	0
0	0.5	0.25	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0.666666667	0	0	0.33333333	0
0.33333333	0	0.33333333	0	0	0
0	0.333333333	0	0.333333333	0	0
0	0	0	0	0	0
0	1	0	0	0	0
0	0	0	1	0	0
0	0	0.5	0	0	0
0	0	0	0	0.33333333	0