Effects of fragmentation on pollen and gene flow in insect-pollinated plant populations
Velterop, Odilia
Do corridors increase pollen flow between patches of *Scabiosa columbaria* (Dipsacaceae)?

With M.M. Kwak and J. van Andel

**Summary**

Pollen flow between artificial patches of *Scabiosa columbaria*, mainly pollinated by syrphids, was studied in a semi-natural environment. Three linearly arranged patches of 30 heads each were used. The central patch served both as pollen donor and receptor patch (complete flowers), the other two patches served only as receptor patches (emasculated flowers and female flowers). The central patch was connected over a distance of 25m with one receptor patch by a corridor of flowers. The plant species of the corridor varied: either *S. columbaria* female heads, *S. columbaria* male heads, *Origanum vulgare* inflorescences or *Aster multiflorus* heads were used. The corridor species shared visitors with *S. columbaria*. The second receptor patch was not connected with the donor patch and served as a control. Experiments were performed with different arrangements of the corridor. The presence of a corridor did not influence the total insect visitation per patch. Syrphid species did not differ in hop size (distance between two subsequently visited heads) if the corridor consisted of *S. columbaria* female heads. In the Aster corridor syrphid species made larger hops than in the Scabiosa corridor. In the Aster corridor hop size of *E. arbustorum* differed significantly from the other two insect species. All together, insects flew larger distances between subsequently visited heads if the corridor contained Aster heads than when the corridor contained *S. columbaria* heads.

Despite the fact that a fair amount of pollen was deposited on the female heads in the corridor, pollen flow was increased significantly in 4 out of 10 experiments if the receptor patch was connected with a corridor containing *S. columbaria* male or female heads. In only one experiment a significant decrease in pollen deposition in the connected patch (connected with a female *S. columbaria* corridor) was observed. Pollen flow was significantly reduced in 3 out of 12 experiments with Aster or Origanum as corridor species and was increased significantly only once. A significant increase of heterospecific pollen deposition was observed if the corridor species was not conspecific.

Potential seed set (based on the number of stigmas with four or more *S. columbaria* pollen grains) showed the same overall pattern as mean number of pollen deposited, although the ratios in pollen deposition and potential seed set differed largely between experiments.
Introduction

Population genetic theory predicts that, as a consequence of genetic drift and inbreeding, small and isolated populations will have decreased levels of genetic variation. Even favourable alleles may be lost and the potential to adapt to a changing environment may be seriously diminished (Vrijenhoek 1985). This genetic erosion may lead to reduced fitness of individuals in a population and will ultimately increase the risk of extinction of populations and of species. However, the deleterious effects of genetic erosion can be counteracted by gene flow between populations. In plants, pollen flow in particular contributes to preservation of genetic variation. As a rule of thumb, the exchange of one migrating individual per generation should be sufficient to prevent genetic differentiation between subpopulations (Ellstrand and Elam 1993; Scott Mills and Allendorf 1996). Thus, management practices that prevent further isolation of plant populations or that increase pollen flow between populations or patches within a population may be important for genetic variation in small populations. Levin (1995) discussed the possible positive function of outliers, scattered plants, often occurring hundreds of meters or several kilometers beyond the limits of local populations. Outliers may form large, diffuse assemblages of interbreeding plants that fill gaps between local populations.

The hypothesis that habitat corridors or stepping-stones may increase migration of animals between populations is generally accepted (Opdam et al. 1993; Beier and Noss 1998). Several studies provided persuasive data regarding the utility of corridors, but few studies actually test the impact of the presence of a corridor on the mobility of animals and the value of these exchanges for the viability of the animal population (see review of Beier & Noss 1998). According to these authors, birds and mammals are target species in most studies and studies on insects are scarce with the exception of ground beetles (Vermeulen 1994). In the case of flower-visiting insects, visiting flowers in a corridor, we hypothesize that these movements may increase their foraging area, which has also an impact on the gene flow and seed set of plants. Restricted movements of flower-visiting insects will result in restricted pollen and gene flow of the plants. Thus, we need to know how flower-visiting insects are influenced not only by the arrangement of their food plants, but also by other characters of the landscape like the presence of bushes, forest, waterways etc. Fry & Robson (1994) found that hedgerows acted as barriers for butterflies. Powell & Powell (1987) found that males of four euglossine bee species did not cross 100m pasture clearings from continuous forest to forest fragments, even though bees can fly more than 20km per day from a release point (Janzen 1971). In contrast, Sutcliffe & Thomas (1996) found that open, grassy tracks were important as corridor for butterflies, acting as conduits between fields and glades.

The impact of the presence of a flower corridor on pollen flow of plants is the issue of this chapter. The consequences for the viability of insect populations of an increasing exchange among flower-visiting insects are left out of consideration. If an insect visits several patches of a target plant species within a larger area which contains flowers (same or different flowering species), these intervening flowers may serve as bridge or corridor. They may even become part of a fixed foraging route of flower visitors, for instance traplining as was found for bumblebees and euglossine bees (Janzen 1971; Heinrich 1975, 1976; Thomson et al. 1997; Williams and Thomson 1998; Comba 1999).
Three possibilities, not mutually exclusive, can be distinguished concerning the effects of a flower corridor on the amount of pollen exchange between two patches: 1. Pollen exchange is zero, although the patches may be within the possible action radius of the pollinators because each patch has its own pollinator guild; 2. Pollen exchange occurs if visitors cross the distance between two patches without loss of pollen because they are not visiting intervening flowers of the same or other species (guidance effect); 3. Pollen exchange occurs but, due to visits to the intervening flowers (guidance effect), pollen is lost. In the last case, pollen exchange between patches is dependent on the amount of switching of insects between the patches and the loss rate of pollen in the corridor. Loss rate in turn is dependent on the length (both in meters and in number of flowers) and on the plant species in the corridor. Visitation of another plant species forming the corridor may result in heterospecific pollen deposition in the connected patches.

In this chapter we present data on pollen flow between patches of *Scabiosa columbaria*, a species pollinated by syrphid flies and bumblebees in The Netherlands (Kwak and Velterop 1997). Artificial patches were connected with a corridor of the same plant species between a pollen source patch (either male or female heads as corridor species expecting a guidance effect and in the female corridor also a loss of pollen) and a receptor patch. As control, artificial patches not connected with a corridor were created. Also experiments were done with another flowering plant species in the corridor. A possible guidance effect with a pollen loss in the corridor and the chance of heterospecific pollen deposition in the receptor patch were expected. Pollen deposition in connected patches was compared with pollen deposition in control patches without a corridor. This study is part of a larger project in which the consequences of population fragmentation for pollen and gene flow by insects are studied in experimental situations in the field.
Material and methods

*Scabiosa columbaria* L. (Small scabious, Dipsacaceae), a perennial, outbreeding plant species, is rare in The Netherlands. It occurs in dry grassy places on calcareous soils. The small, blue-violet, tubular flowers are arranged in heads (30-100 flowers per head). Each flower is first male for about two days, then enters a neuter phase of varying length. After all flowers have passed the male phase, the whole head is female for about one day. Both anthers and stigmas protrude out of the flower and are easily touched by various species of insects.

In total, 22 experiments were conducted in unfertilized hay fields in the North of The Netherlands (Assen, 52°59'N, 6°35'E) in 1996 and 1997, from August till early October. Experiments were done at four neighbouring fields A (fietspad), B (boomstronk), C (bessenland) and D (buurman). Per day one or two experiments were conducted. Each experiment consisted of three patches arranged in a line (WNW-ESE orientated) with an interpatch distance of 25m. The distance of 25 meter between patches was chosen because earlier experiments (chapter 4) demonstrated that over this distance pollen flow from donor towards the receptor patch was reduced to about 25%. Moreover, the size of the fields did not permit much larger distances between patches. Each patch contained 10 female (virgin at the start of the experiment) and 20 male heads. Plants in pots were used. Only the central patch was allowed to deliver pollen and this patch served both as donor and receptor patch. The male flowers in the two distant patches were emasculated every half an hour, since the development of anthers continued during the day (see chapter 2). The central patch and one of the distant patches were connected with a corridor. This corridor contained either 30 female (virgin at the start of the experiment) *S. columbaria* heads, or 30 male (but emasculated) *S. columbaria* heads or 30 *Aster multiflorus* cv blue star heads or 30 *Origanum vulgare* inflorescences. *Origanum* was chosen since in natural populations of *S. columbaria*, insects often carried a pollen load that contained a large number of *Origanum* pollen (Kwak and Velterop 1997). Heads of *Aster* were chosen because their morphology enables the same group of insects to visit them and they were available later in the season when *Origanum* was out of flower.

The arrangement of heads or inflorescences within the linear corridor was either regular with a distance of about 80 cm between the individual heads or they were grouped in 6 clusters of each five heads or five inflorescences, at a distance of 1.5 m between each other. The position of the corridor was either parallel, along an imaginary axis connecting two patches or across this imaginary axis between the patches. Table 1 summarizes details of the experiments, performed on several census dates.
Table 1 Conditions during pollination experiments with corridors between patches of *Scabiosa columbaria* in 1996 and 1997. * Corridor direction reversed compared to all other experiments. Pollinating insects: Diptera, mainly Syrphidae and Apidae; *Siphona geniculata* and Lepidoptera excluded. Number of pollinating insects given per 60 observation surveys in the donor patch.

<table>
<thead>
<tr>
<th>Arrangement</th>
<th>Corridor species</th>
<th>Date</th>
<th>Field</th>
<th>Mean and (max) day temperature (°C)</th>
<th>Wind direction</th>
<th>Wind speed (m/s)</th>
<th>Duration experiments (h)</th>
<th>Observations on insect hop size</th>
<th>Number of pollinating insects</th>
<th>Bar letter in Figure 1</th>
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<td>a,b</td>
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<td>C*</td>
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<td>5</td>
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<td></td>
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<td>variable</td>
<td>3</td>
<td>5</td>
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<td>130</td>
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The experiments lasted between 4 and 6 hours. During the day, heads in each patch and in the corridors were screened for the presence of naturally occurring insects (no attempt was made to introduce particular insect species). This screening, called surveys, lasted about 2 minutes for the three patches and the corridor; screening was conducted 15-60 times per day. Insect species were classified as syrphids (most common species *Eristalis tenax, Eristalis pertinax, Eristalis intricarius, Eristalis arbustorum, Eristalis nemorum, Helophilus pendulus*), flies, small flies (most probably *Siphona geniculata*), bumblebees (*Bombus pascuorum Scop.*, mainly males and *Bombus terrestris L.*) and butterflies (*Autographa gamma, Thymelicus spec.*, *Inachis io, Pieris rapae*). All insect species are (very) common species in The Netherlands.

Visitation is given as the number of observed visits per 60 surveys per observation day.

In order to understand the results of pollen deposition, we followed foraging syrphids, visiting heads in the corridor. Each switch between heads in the corridor is called a hop and the distance between two subsequently visited heads was noted as hop size. Minimum hop size was 1 (see also Figure 2). The total number of observations of hop sizes per individual insect was called a bout. Hop sizes per insect species per corridor type and mean hop size per corridor type were calculated. Only bouts with a minimum of 3 hops (4 observed visits) were included.

At the end of each experiment, female heads were collected and the number of *S. columbaria* pollen grains per stigma was counted with a hand-lens of 20x. Either all stigmas or a random sample of 10-15 stigmas were counted and the mean deposition per stigma per head was calculated. After the direct counting of *S. columbaria* pollen in the experiments with *Aster* as corridor species, stigmas of all female heads in the receptor patches were cleaned with a piece of a sticky gel (Beattie 1972). The numbers of *S. columbaria* and *Aster* pollen per head were counted in this gel using a microscope and the fraction *Aster* pollen was calculated.

Effects of the corridors were tested for significance of the differences in the mean number of pollen grains per stigma, deposited in the connected and control patch, using a t-test or Mann-Whitney U test.

**Results**

**Visitation**

Visitation showed large variation; in some experiments very large numbers of insects visited the heads (experiments j and s in Figure 1, note the difference in scale of the Y-axis between the figures) while in others less than 50 efficient pollinators were recorded (species of Apidae and Diptera, the small fly species *S. geniculata* excluded): experiments h and l in Figure 1. Most frequent visitors on nearly all days were syrphid flies, especially the species *Eristalis tenax, Eristalis arbustorum* and *Helophilus pendulus*. Apidae, mainly bumblebees, were present in reasonable numbers in the experiments done with *Origanum* as corridor species. Butterflies were also regular visitors in these experiments, both on *Scabiosa* and *Origanum*. The small fly species *S. geniculata* was sometimes present in very large numbers, particularly in the experiments with *Aster* as corridor species.

In summary, *S. columbaria, Aster* and *Origanum* shared the same visitor species. Thus visitors of the donor patches of *S. columbaria* may use the corridor species in order to reach the other *S. columbaria* patch.
Figure 1. Frequency of insect visits to the donor patch of *Scabiosa columbaria* and the corridor consisting of various plant species, during 60 observation surveys during the day. Letters on X-axis indicate the date and field characteristics mentioned in Table 1. Note the different scales of Y-axes.

**Insect visitation of the corridor**

Some examples of long visitation bouts of individual syrphids in the corridor are given in Figure 2. Although the mean number of hops in a bout of an insect visiting an *Aster* corridor (5.3 ± 2.6, mean ± s.e.) was shorter than in the *Scabiosa* corridors (*Scabiosa* female and *Scabiosa* male, all regularly arranged, 6.8 ± 4.6, see Table 1), this difference was not significant (One way Anova P>0.05).
Figure 2. Examples of the behaviour of individual syrphids on a corridor. A and B. *Eristalis tenax* in a *Scabiosa columbaria* male corridor on September 18, 1997, C. *Helophilus pendulus* on a *S. columbaria* female corridor on September 11, 1997. S=start, E=end of the foraging bout.

Hop sizes were calculated for three syrphid species separately: *E. tenax*, *H. pendulus* and *E. arbustorum* visiting a *S. columbaria* female corridor where maximal guidance effect but also maximal pollen loss was expected, and an *Aster* corridor with an unknown guidance effect but with a pollen loss in the corridor and a possible heterospecific pollen deposition in the receptor patch. Syrphid species did not differ in hop size if the corridor consisted of *S. columbaria* female heads (Figure 3, One way Anova P>0.05). In the *Aster* corridor all three syrphid species made larger hops than on the *Scabiosa* corridor. On the *Aster* corridor hop size of *E. arbustorum* was significantly higher than hop size of the other two insect species (Mann-Whitney U test, P<0.005). With respect to the pollination of the plant (lumping the data of all insects), no difference in hop size was found between hop size on a corridor with female or male *S. columbaria* heads (Figure 4, SNK-test, P>0.05) but hop size in the *Aster* corridor was significantly larger than in the other two corridors (SNK-test P<0.05). Making large hops on an *Aster* corridor (compared with *Scabiosa* corridors) may result in a quick arrival in the receptor patch, with probably a smaller loss of *S. columbaria* pollen in the *Aster* corridor compared to a conspecific corridor. However, in the presence of an *Aster* corridor, deposition of *Aster* pollen in the receptor patch of *S. columbaria* is possible.
Figure 3. Hop size (mean ± s.e.) of the three most important insect species in corridors of different plant species (observations of 4 dates lumped, see Table 1). Values differed significantly if indicated by different letters (SNK test, P<0.05). Insect species did not differ in hop size in a *Scabiosa columbaria* corridor.

Figure 4. Hop size (mean ± s.e.) as the plant (*Scabiosa columbaria*) experienced (insect species lumped). Only hop size on the *Aster* corridor differed significantly from hop size on the other two corridors (SNK test, P<0.05).
Pollen deposition in corridor

Deposition of *S. columbaria* pollen in the corridor may have occurred in all experiments but it was only measured if *S. columbaria* female or *Aster* was used in the corridor. The total number of pollen grains in the *S. columbaria* female corridor equaled the number found in the receptor patches. In general, a decrease in the numbers of pollen on heads in the corridor was found from the donor patch towards the receptor patch (Figure 5). Figure 5A shows the large difference in pollen deposition between two experiments done on the same day but in different fields. Figure 5B shows that *S. columbaria* pollen was also deposited in the *Aster* corridor but the numbers were smaller and the decrease with distance to the donor patch was sharper than in *S. columbaria* female corridors.

Pollen deposition in receptor patches

Depending on the plant species in the corridor, we expected an effect on the guidance of insects, a loss of *S. columbaria* pollen in the corridor and/or heterospecific pollen deposition. Pollen deposition in the receptor patches is expressed as the ratio of deposition in the receptor patch connected with a corridor and the receptor patch not connected with the donor patch, the control receptor patch (Figure 6A). A ratio higher than 1 indicates that the presence of a corridor had a positive effect on the number of *S. columbaria* pollen deposited in the connected receptor patch. In those cases where *S. columbaria* was the corridor species, the presence of a corridor increased the pollen flow significantly towards the receptor patch in 4 out of 10 experiments. In only one case (a female corridor) we observed a significant negative effect. In the experiments with *Aster* or *Origanum* as corridor species only once a significant positive effect on pollen deposition was found. In 3 out of 12 experiments the presence of an *Aster* or *Origanum* corridor resulted in a lower pollen deposition. Overall, pollen deposition tended to be lower compared to the control patch, in patches connected with the donor patch with a heterospecific corridor (Figure 6A).

Four experiments with heads arranged in clusters were done (see Table 1). The data were insufficient to allow reliable conclusions on the effect of clustering of heads or inflorescences within a corridor due to the fact that also three plant species as corridor species were used. Only three experiments were done with a corridor situated in an across position instead of a parallel position. In all three experiments pollen deposition was decreased, with one experiment showing a significant decrease (Figure 6A).
Figure 5. A. Deposition of *Scabiosa columbaria* pollen number of pollen per stigma per head (mean ± s.e.) in a *S. columbaria* female corridor in two experiments done on September 29, 1997. Head number 1-6 are close to the donor patch, 25-30 most distant from donor patch. B. Deposition of *S. columbaria* pollen in an *Aster* corridor on September 25, 1997.
Figure 6. A. Ratio between the number of *Scabiosa columbaria* pollen per stigma per head in receptor patches connected with a corridor between the donor and receptor patch and in control patches. r=regular, c=clustered arrangement of heads or inflorescences. Stars indicate significant differences in pollen deposition per stigma between the two patches (t-test, at least P<0.05). B. Ratio between the percentages of potential seed set of *S. columbaria* in connected patches and control patches. Stars indicate significant differences in pollen deposition per stigma between the two patches (t-test, at least P<0.05).
In an earlier experiment we found that at least 4 pollen grains per stigma were needed to achieve the maximal seed set of one seed per flower (chapter 3). Applying this threshold of at least 4 pollen grains per stigma, we calculated the ratio between potential seed set in the receptor patch connected with a corridor and the control receptor patch (Figure 6B). The same pattern was found as observed for the mean number of S. columbaria pollen deposited, although the ratios in pollen deposition and potential seed set could differ largely in some experiments.

Variation in the number of visiting insects and deposition of S. columbaria pollen was very large. Since high visitation frequencies in the donor patch were not related with high pollen deposition in the donor patches (a non-significant negative relation was found with $r^2=0.28$, $P>0.1$, Figure 7A), a relation between visitation frequency and deposition in control receptor patches, where pollen deposition was depended also on visitation in the donor patches, was not to be expected. However, pollen deposition in the donor patch was positively correlated with pollen deposition in the control receptor patch (Figure 7B, $r^2=0.57$, $P<0.01$).

**Figure 7.** A. Visitation (number of visits of Apidae and larger Diptera per 60 observation surveys) and pollen deposition per stigma per hour in donor patches of Scabiosa columbaria ($y=2.3-0.0036x$, $r^2=0.28$, $P>0.1$). B. Pollen deposition (number of S. columbaria grains per stigma per head) in donor patches and control receptor patches of S. columbaria ($y=-0.3+0.35x$, $r^2=0.57$, $P<0.01$).
Heterospecific pollen deposition

The percentages Aster pollen in receptor patches were significantly higher if patches were connected with an Aster corridor than without corridor (Table 2). Control receptor patches received Aster pollen, but the numbers were much lower although still reasonable.

Table 2 Percentages Aster pollen (mean ± s.e.) as fraction of the total number of Aster and Scabiosa columbaria pollen per head in control patches and patches connected with an Aster corridor; * P<0.05, ** P<0.01, *** P<0.005.

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<th>Date (1997)</th>
<th>Percentage Aster in control patch</th>
<th>Percentage Aster in connected patch</th>
<th>Statistics</th>
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<td>September 8</td>
<td>21.5 ± 4.0</td>
<td>51.2 ± 5.8</td>
<td>t-test 4.25 ***</td>
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<td>12.2 ± 3.4</td>
<td>39.0 ± 5.2</td>
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<td>September 11</td>
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<td>36.8 ± 5.2</td>
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<td>35.3 ± 3.7</td>
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<td>t-test 2.11 *</td>
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Discussion

This study shows how insect pollinators may react on a corridor of heads or inflorescences of the same or another plant species and describes what the consequences are for pollen exchange between patches.

Visitation of the patches varied due to differences in years and dates of experiments during the season. Especially the experiments with Origanum as corridor species were done early in the season with a substantial amount of visits of bumblebees and butterflies. Visitation of S. columbaria patches and pollen deposition within the same field on the same day varied very much and in an unpredictable way. Therefore, no effect of the presence of a corridor on insect visitation could be detected. Possibly only a fraction of the visitors of the donor patch will reach the receptor patches. Other insects that did not visit the donor patches may have visited the corridor and/or the receptor patches. The last category was counted as visitors but apparently had no contribution as vector of S. columbaria pollen.

Differences between pollinator guilds of S. columbaria donor patches and S. columbaria corridors may be due to differences in head density. Scabiosa female corridors had fewer visitors than the donor patches, whereas Scabiosa male corridors received the same number of visitors as the donor patches (Figure 1). Differences in pollinator guilds of Scabiosa donor patches and Aster or Origanum corridors are much larger due to differences in both head or inflorescence density and plant species.

Insects that do not have absolute flower constancy can use a corridor consisting of another plant species. In our experiments we considered syrphids and to a lesser extent bumblebees as important visitors and pollinators. Both syrphids and bumblebees (mostly males) did switch between plant species. Little is known about the flower constancy of syrphid flies (but see Goulson & Wright 1998), but considering the composition of pollen loads on the bodies of insects visiting natural populations of S. columbaria, only 15-37% of the grains were conspecific (see chapter 2), their flower constancy is not high. Also bumblebees foraging in natural Dutch populations carried a low percentage conspecific pollen (0.5-10.6%, chapter 2).
In our experiments, it was clear that insect species differ in hop size (see Figure 3). Differences in hop size may influence conspecific pollen flow and heterospecific pollen deposition. Thus, in experiments with mainly *E. arbustorum* as visitor other results can be expected than in those where *E. tenax* or *H. pendulus* are the only visitors. However, such a difference could not found in our data because various species simultaneously were responsible for the pollen flow.

Only in four cases with *S. columbaria* as corridor species we found a significant increase in pollen deposition in patches connected with a corridor; a significant decrease in pollen deposition in the presence of a corridor was found once. However, the mean ratios of pollen deposition using a *S. columbaria* corridor were 1.52-1.60 for male and female *S. columbaria* corridors respectively (a positive effect) while for *Aster* and *Origanum* corridors were 0.79 and 0.89 respectively (a negative effect). The expected loss of pollen in a corridor, especially in a *S. columbaria* female corridor, does not to be important, as shown by the comparison of the data of male and female corridors). Guidance of insects by conspecific flowers in the corridor was much more important than pollen loss in the corridor. It seems that the presence of different plant species in the corridor may have a negative effect on pollen flow. Pollen deposition in the receptor patches was significantly influenced, in three occasions negative and only once positive. The presence of these corridors of another plant species may work in two ways: first, insects may be deterred by the corridor flowers and don't visit them. Secondly, flowers in the corridor may receive so much *S. columbaria* pollen that few grains are left on the insect's bodies in order to reach the other patch. Because we estimated that the pollen loss in an *Aster* or *Origanum* corridor was not greater than in a *S. columbaria* female corridor (see Figure 5 A and B) and we found that pollen deposition in the connected receptor patch was lower after an *Aster* or *Origanum* corridor, we conclude that corridors with another plant species had a deterrent effect on the behaviour of insects visiting *S. columbaria*.

No conclusion could be drawn about the effect of head or inflorescence arrangement in the corridor (in clusters or regularly distributed) on pollen flow because of shortage of data. In a similar experiment, Manasse (1992) and Cresswell (1997) could not demonstrate a net effect of clumping on gene flow, although the behaviour of pollinators changed. In two experiments, done on August 8, 1996, with a parallel corridor of *Origanum* in clusters, gene flow of *S. columbaria* pollen was measured by analysing the dispersal of allozyme marker alleles (using non-emasculated patches, data not presented in this chapter). No significant effect of the corridor on gene flow was found. The mere distance effect of 25m was much larger than the effect of the presence of the corridor. Fluorescent dye powder was also used in those experiments and despite a considerable loss within the corridor, similar amounts were deposited in connected and control patches. We did not find a relation between wind direction and/or wind speed and the ratio of pollen deposition in donor and receptor patches.

In several species, fruit and/or seed set was decreased after heterospecific pollen deposition (Galén and Gregory 1989; Kwak and Bergman 1996). Thus, visitation of a corridor containing another plant species may result in heterospecific pollen deposition, which may have a negative effect on seed set. Even if a corridor of a heterospecific plant species has a positive effect on the guidance of pollinating insects visiting the corridor species and increases pollen flow, the net impact of the corridor on seed set may still be negative. In those situations where a corridor has a negative guidance effect on insects, an additional negative effect, that of heterospecific pollen deposition, may occur. We found a reasonable percentage of *Aster* pollen (37-51%) in connected patches. The effect of *Aster* pollen on seed set was not studied.
Our study shows that the impact of a corridor on the behaviour of insects and the resulting pollen flow depends on the plant species present in patches and in corridors as well as on the pollinator species. Thus, the quality of the corridor influences the behaviour of the pollinating insects. Results of the present study are much more variable than in earlier experiments with *Phyteuma nigrum* and bumblebees as pollinators (Kwak 1994; Kwak et al. 1998; Kwak and Vervoort 2000). Behaviour of syrphids is different from that of bumblebees concerning traplining and possibly flight distances. Recapture percentage of marked bumblebees was 80-100 while the percentages of recaptures of marked syrphid individuals visiting *S. columbaria* amounted to only 4% (n=160) indicating the continuous replacement of flies.

Summarizing, the presence of a conspecific corridor has a more positive effect on pollen flow than a heterospecific corridor despite the loss of conspecific pollen in a *S. columbaria* female corridor. The visitation by insects of a heterospecific corridor results in a considerable amount of heterospecific pollen deposition. The scale of our experiments permits only conclusions on interpatch movements and not on interpopulation movements.

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