

SILENE OTITES (CARYOPHYLLACEAE) POLLINATED BY NOCTURNAL LEPIDOPTERA AND MOSQUITOES

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SUMMARY

Indications of the existence of plants of *Silene otites* in the dunes in The Netherlands (Coastal plants), with wind pollination additional to insect pollination, gave rise to this study. Morphological evidence, such as stickyness of pollen, together with field observations on the wind dispersal of pollen and experiments with bagged flowers, prove the absence of wind pollination. Insect visitors mainly belonged to the Lepidoptera (Microlepidoptera, Geometridae and Noctuidae) and to the Diptera (Culicidae). Observations of the dusting with pollen and of the flower visiting behaviour indicate that insects of these two types pollinate. This has finally been proved by experimental confinement of insects with bagged flowers. Neuroptera are visitors but are not pollinators. The pollination of flowers by mosquitoes is new for Europe.

1. INTRODUCTION

There are indications that in The Netherlands, in the dunes along the coast, *Silene otites* (L.) Wibel might have developed anemophilic races (FAEGRI & VAN DER PIJL 1971, p. 44) as an adaptation to the strong sea winds, which are of substantial hindrance to pollinating insects.

Van der Pijl (pers. comm.) based his opinion on the observed absence of visitors. Scarcity of visitors was also noted by Schulz, Warming and Knuth, as was reviewed by SCHULZ (1905). They all decided on additional wind pollination. However, Schulz changed his opinion after VERHOEF (1893), on the island Norderney, discovered the nocturnal anthesis of *S. otites*, and the intensive visitation during the night. New observations (being now nocturnal) revealed to Schulz that small Lepidoptera were dominating visitors.

However, anemophilous races remained possible, and even more so because several characteristics of the flower might be adaptive to wind pollination:

1. The gregarious growing habit of *S. otites*.
2. Diclony is often regarded to be functional in anemophiles for the separation of the functions of issue and reception of pollen. Dioecy might even be more profitable, because it nullifies the to anemophiles substantial danger of self-pollination.
3. The fact that staminate flowers in Holland outnumber the pistillate ones by 6 to 1 (FAEGRI & VAN DER PIJL 1971).

4. The low number of ovula (48 per flower) in comparison to different *Silene* species.
5. Shedding of pollen might be promoted by the pendulous movements of the whole flower. In this way the stiffness of the filaments is compensated.
6. The large receptive surface on long extruding stigmas seems fit for the reception of windborne pollen.
7. In both types of flowers the small recurved petals are out of the way.
8. The dull petal colours (yellow-green) might be interpreted as absence of visual means of attraction.

For clarifying the still existing controversial opinions about the mode of pollination of the ancestral angiosperms "Anemophily or entomophily?", the possible coexistence of plants with both modes of pollination offers a good opportunity to study the process of the evolution.

We studied the pollination of *S. otites* in The Netherlands, to find out which insects are involved and to check the existence of additional wind pollination.

2. MATERIALS AND METHODS

The plants used originated from seeds of two different populations: A: From the collection of the Botanical Garden, University, Nijmegen, ("Continental plants") and B: The "Coastal plants" were from the dunes near The Hague. All plants were from seeds.

In 1973 the observations on visitors and pollination were made in the nature reserve "De Wylerberg" at Beek in the vicinity of Nijmegen involving continental plants. In 1975, additional observations on plants from both populations were made in the Botanical Garden of the University, Nijmegen.

Determination of the Lepidoptera was by Dr. A. L. Cox. Nomenclature is according to LEMPKE (1953-1970).

3. RESULTS

3.1 Description of the flowers

The flowers stand in condensed dichasia in the axils of the leaves on flower stalks. Stalks produce about 150 flowers on pistillate and 1000 on staminate plants. There are about 20 days between anthesis of the first and the last flower on a stalk. New flower stalks are produced from May until November. Flowering is from June until November.

Staminate flowers are functional for 2 nights and wither thereafter. Pistillate flowers remain functional until they become pollinated. A very detailed account, similar to our observations, of the morphology and of the flowering process is given by SCHULZ (1905).

Sex-ratios are dependant on the mode of expression, *table 1*. Two ratios are of interest. Firstly, the ratio for the flower stalks (1:4.5) suggests that, in case

Table 1. Sex ratios of *S. otites* (continental plants).

	pistillate	staminate	ratio
Number of plants obtained from seeds	17	30	1:2
Number of flower stalks with flowers			
18. July	4	23	
30. July	7	25	
22. August	18	74	1:4.5
5. September	16	73	
Average number of flower stalks produced per plant			
until 30. July	0.3	1	
until 22. August	1	2.5	1:3
Average number of flowers produced per plant	150	1000	1:7
Total number of flowers available per night			1:30

pistillate and staminate flower stalks are equally attractive, each visitor has a probability of about 0.2 of landing on a pistillate one. But when landing on a pistillate stalk, the probability that the visitor comes from a staminate flower stalk and, therefore is loaded with pollen, is 0.8. Secondly, in case the number of flowers determines the frequency of landings, the visitors have a probability of 0.03 to visit a pistillate flower.

There are some morphological differences between the two populations, *table 2*. The continental plants are stouter compared to the coastal plants. The rosette leaves are longer and broader. Petals of the coastal plants are smaller, (*fig. 2a*). In pistillate plants they do not often extend beyond the calyx. The petals seem to produce most of the scent.

Table 2. Differences between plants of two populations.

The plants were grown under identical conditions, in the Botanical Garden, University, Nijmegen.

	Coastal pl.	Continental pl.
Both types		
Height of the flower stalks, cm	30–45	55–80
Number of nodes in the stalks	7–10	9–12
Rosette leaves	few, small	many, large
Staminate plants		
Length of petals mm	6.2	8.1
Width of petals	0.4	0.8
Colour of petals	whitish-yellow	yellow

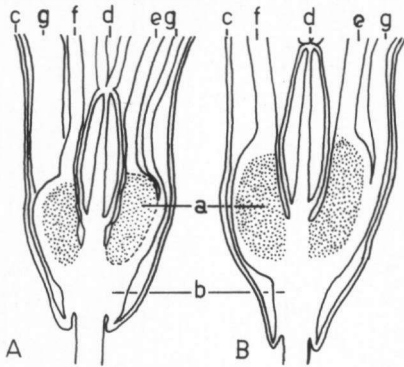


Fig. 1. Longitudinal section through the base of pistillate flowers of *S. otites*.

A: continental plant, B: coastal plant.

a: nectarium, b: internodium, c: calyx, d: rudimentary ovary, e: epipetal anther, f: episepal anther, g: petal.

The pollen grains, filaments and anthers are identical (*fig. 2a*).

The nectary is large both in pistillate and in staminate flowers of both populations (*fig. 1*). During the night nectar production is so rich that in flowers protected from insects it often flows out of the calyx.

Scent emission and nectar secretion follow the cyclic rhythm of anthesis of *S. otites*. The human nose cannot distinguish between flowers of the two populations. The scent and nectar production in the coastal plants indicate basical entomophily, as in the genus.

3.2 Field observations

3.2.1 Wind pollination

The occurrence of wind pollination was tested by checking the pollenrain, *table 3*. During the period of observation the weather conditions (dry, windy) seemed favourable for wind pollination.

At daytime, under staminate plants and at some distance from them no pollen appeared. This must be caused by the time of dehiscence of anthers, being in the evening.

During the night may clots of pollen appear on the slides, but hardly any isolated pollen grains. Aggregation is due to their stickyness, an argument in favour of entomophily (KNOLL 1930).

Fig. 2. A: Staminate flowers of *S. otites*. Left continental, right coastal plants.

B-F: Flowers on De Wylerberg with visitors.

B: *Leiobunum rotundum* drinking from a pistillate flower.

C, D: *Culiseta annulata* females.

E: *Chrysopa carnea* on a pistillate flower.

F: *Culiseta annulata* male, dusted with pollen.

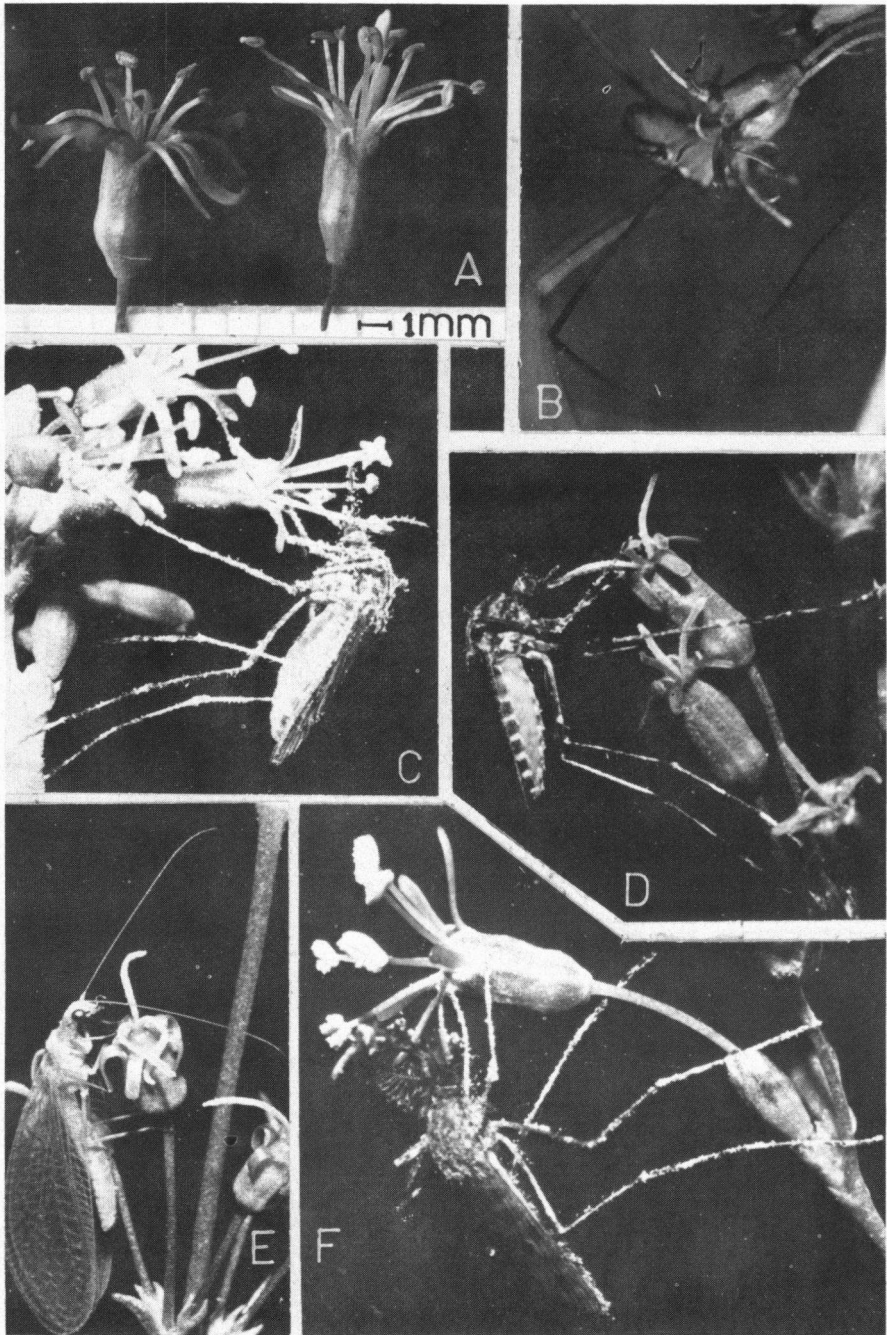


Table 3. Pollen-grains under *S. otites* plants.

	Day-time 14.15–15.45 dry, 30°C. low wind velocity	Night-time 21.00–22.30 dew, 17°C. low wind velocity
Underneath staminate plants	0	400, 370, 300
25 cm from staminate plants	–	600, 470
50 cm from staminate plants	0	450
100 cm from staminate plants	0	250
300 cm from staminate plants	0	–
Underneath pistillate plants	–	470, 280, 30

Pollen-grains are collected on sticky microscopic slides (7.5 × 2.5 cm), layed on the ground, and are counted under the microscope.

When a staminate flower stalk was touched, the pollen rain was visible. Even with wind, the clots fell straight downwards. Therefore, the clots on the slides at some distance from the staminate plants, and under the pistillate plants, *table 3*, cannot be explained by wind dispersal. The numerous, nocturnal visitors are responsible.

Enveloping pistillate flower stalks on the plants with netting, with openings of 1 mm², allowing passage of wind, prevented seed production (*fig. 3 d, f*), both in De Wylerberg and in the Botanical Garden with plants from the two populations. Therefore, both groups of plants are obligate entomophiles.

3.2.2 Visitors

Almost daily, from 2nd August until 6th September 1973, on De Wylerberg visitors were collected from the plants. The proboscis length, as measured in mm, is in brackets.

Lepidoptera, Microlepidoptera:

Catoptria falsella D&S (4), *Metriostola betulae* Goeze (3–5), *Evergestis forficalis* L. (5–8), *Haritata ruralis* Scop. (8–12), *Udea prunalis* D&S.

Macrolepidoptera, Plutellidae:

Plutella maculipennis Curt.,

Pterophoridae:

Aleucita pentadactyla L.

Geometridae:

Cyclophora linearia Hübner, *Idaea seriata* Schrank (3–5), *I. aversata* L. (6), *Xanthorhoë spadicearia* D&S (4–8), *X. designata* Hufnagel (6), *X. ferrugata* Clerck, *X. fluctuata* L. (6), *Epirrhoë alternata* Müller (5), *Campptogramma bilineata* L. (7–8), *Cosmorhoë ocellata* L. (5), *Chloroclysta truncata* Hufnagel (7–12), *Thera obelisca* Hübner (7), *Perizoma alchemillata* L. (3), *P. flavofasciata* Thunberg (5), *Eupithecia centaureata* D&S (6), *E. goossensiata* Mabille (3), *E. icterata* Villers (5), *E. succenturiata* L. (5), *Gymnoscelis rufifasciata* Haworth (4), *Apocera eiformata* Guenée (7), *Semiothisa notata* L. (5), *S. liturata* Clerck,

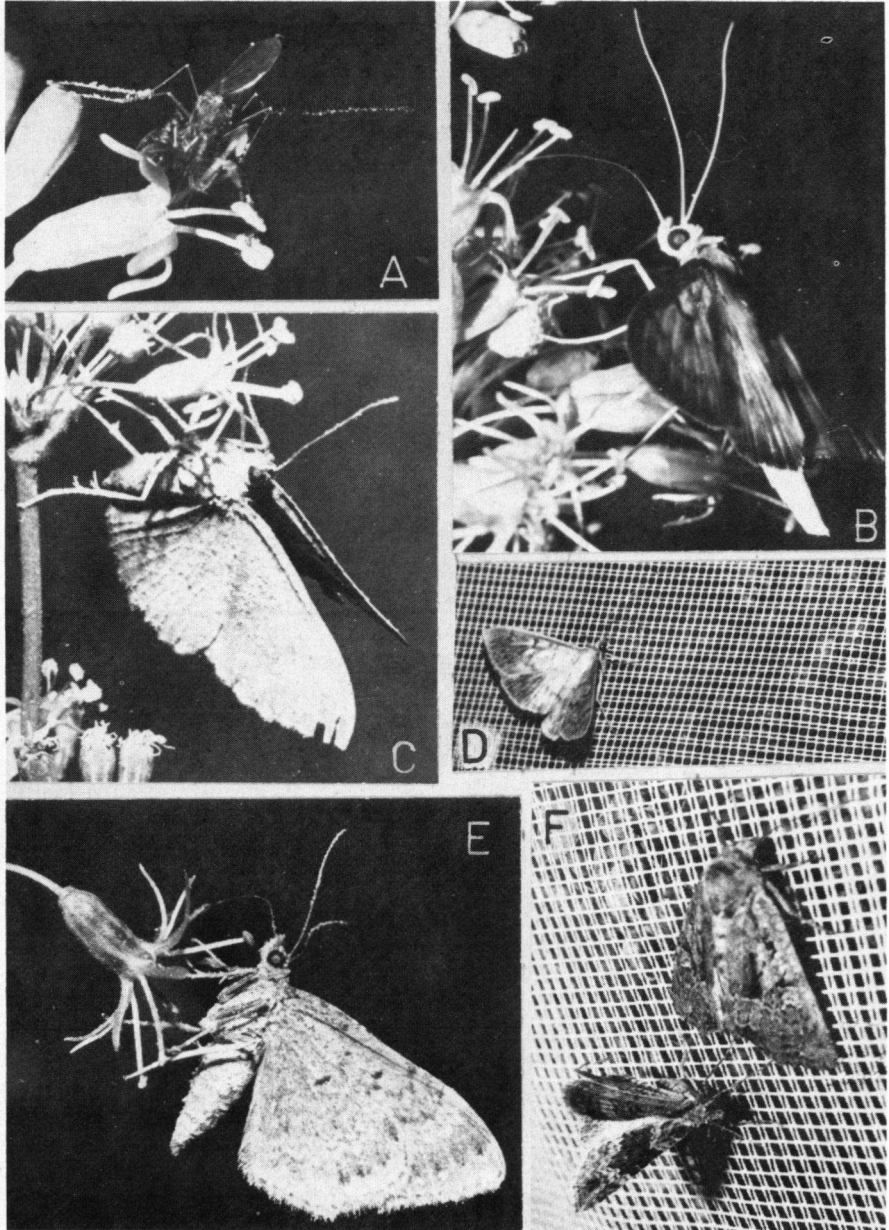


Fig. 3. A-C, E: *S. otites* staminate flowers on De Wylerberg with visitors.
 D, F: Moths sitting on the netting over pistillate flowers, trying to insert the proboscis
 A: *Culex pipiens* male with pollen on the legs.
 B, D: *Haritata ruralis*.

Opisthoptis luteolata L. (5–7), *Epione repandaria* Hufnagel (4), *Campaea margaritata* L. (6–8), *Lithosia complana* L. (6),

Noctuidae:

Euxoa obelisca Schiff., *Scotia segetum* Schiff., *Ochropleura plecta* L. (5–6), *Noctua pronuba* L. (15), *Dicestra trifolii* Hufnagel (9), *Mamestra brassicae* L. (8–12), *Hadena rivularis* Fabr. (9), *Mesapamea secalis* L. (7), *Mesoligia furunculata* Schiff. (4–5), *Phlogophora meticulosa* L. (12), *Caradrina clavipalpis* Scop. (6), *Cosmia trapezina* L., *Autographa gamma* L. (16–18), *Plusia chrysitis* L. (14), *Rivula sericealis* Scop. (4–5), *Hypaena proboscidalis* L. (5),

Diptera:

Calliphora subalpina (Ringd.), *Culex pipiens* L., *Culiseta annulata* Schrank,

Neuroptera:

Chrysopa carnea Stephens.

Sometimes Opilionidae and ants were drinking from flowers (*fig. 2b*).

To determine the relative importance of the species, on several nights an estimation was made of their numbers on the plants, *table 4*. Both the species composition and the total number of visitors were different on each night.

Campaea margaritata and *Autographa gamma* were observed each night. Only the insects with rank numbers from 1 till 15 can be regarded to be substantial visitors.

In the Botanical Garden, plants from both the continental and from the coastal populations were frequented by Lepidoptera, Neuroptera and Diptera.

3.2.3 Pollinators

In how far visitors actually pollinate was not regarded in older literature on *S. otites*, so therefore, the pollinating potencies of the animals were now checked, A, by counting the pollen grains adhering to their body, *table 5*, and B, by encaging animals with plants (to be discussed under pollination experiments).

At arrival on the location, our insects had hardly any pollen on their bodies, *table 5, column 1*. Therefore, they did not obtain pollen from other plant species, or they did not visit other flowers before.

Visitors of staminate flowers were found to be dusted with pollen, *table 5, column 2*, so the transport capacity of the insects is good. Insects on pistillate plants or on the netting over the plants had many pollen grains, *column 3, 4*. Therefore, they visited staminate plants before, and moved between the plants.

Often the insects walk over the flowering side branches without taking a fixed position on each flower. All body parts come into close contact with the extruding anthers. Pollen grains were found on all body parts, *table 6*. Therefore, deposition on the insect was not precise. However, there were differences in relative pollen load of the body parts for different groups of visitors. The legs and wings were most important.

The behaviour of the insect determines the number and distribution of pollen grains on the body parts. This is clearly illustrated by *Opisthoptis luteolata*. After landing this moth folds up its wings. Compared with other Geometridae,

Table 4. Frequency of visitors of *S. otites*.

	August					September		Rank number of importance
	18.	20.	21.	26.	31.	3.	6.	
<i>Evergestis forficalis</i>	D	D	D					13
<i>Haritata ruralis</i>	B	B	C				D	3
<i>Plutella maculipennis</i>			D				D	
<i>Idaea seriata</i>			D		D		D	14
<i>Xanthorhoë spadicearia</i>	C	B	D					5
<i>X. designata</i>	D	D						
<i>X. ferrugata</i>		D						
<i>X. fluctuata</i>	B	D	B					4
<i>Camptogramma bilineata</i>	D	D	C	D	D	D		7
<i>Cosmorhoë ocellata</i>			C					15
<i>Chloroclysta truncata</i>			D				D	
<i>Thera obelisca</i>				D			D	
<i>Perizoma alchemillata</i>			D					
<i>P. flavofasciata</i>		D	B					6
<i>Eupithecia centaureata</i>	B							11
<i>E. goossensiata</i>	D							
<i>E. icterata</i>			B				D	10
<i>E. succenturiata</i>			B				D	9
<i>Semiothisa liturata</i>	D							
<i>Opisthoptis luteolata</i>	C	D	C	C				8
<i>Campaea margaritata</i>	B	D	C	B	B	B	C	1
<i>Euxoa obelisca</i>	D							
<i>Scotia segetum</i>							D	
<i>Phlogophora meticulosa</i>			D					
<i>Mesoligia furunculata</i>	D							
<i>Caradrina clavipalpis</i>			D					
<i>Autographa gamma</i>		D	B	C	D	B	D	2
<i>Rivula sericealis</i>		B						12
<i>Mosquitoes</i>	A	B	B		B	C	D	
<i>Chrysopa carnea</i>						D	D	

The number of insects was determined at approx. 10 p.m. A > 50, B = 50 - 10, C = 9 - 5, D = 4 - 1.

The importance is obtained from a combination of the number of nights the species is observed, and from its abundance.

which keep the wings in a spread position, the number of pollen on the wings is low: 4% for *O. luteolata*, while other Geometridae have an average of 33%.

Pollen of *S. otites* adheres well to the insects. For deposition on the stigma it has to separate from the insect. Actually the grains remain in clots on the insect. These clots desintegrate easily and so many grains fall off onto the stigmas or onto the ground, as it is recorded in table 3.

Table 5. Total pollen counted on the visitors of *S. otites*.

Capture	shortly after arrival	Sitting on:		
		staminate flowers	pistillate flowers	netting
Lepidoptera				
Microlepidoptera				
<i>Haritata ruralis</i>	10	295	1435	
Geometridae				
<i>Camptogramma bilineata</i>			250	
<i>Eupithecia goossensata</i>			400	
<i>Opistograptis luteolata</i>			170	
<i>Xanthorrhoe ferrugata</i>		740		
<i>X. spadicearia</i>			270	
<i>Campaea margaritata</i>		3425, 1980		
Noctuidae				
<i>Noctua pronuba</i>	65			
<i>Autographa gamma</i>	10			
Diptera				
<i>Culex pipiens</i> male	0	310, 145, 29	150	200, 105, 13
<i>Culex pipiens</i> female	0, 0		840, 205	250
<i>Culiseta annulata</i> male		2260, 625, 59	130	
<i>Culiseta annulata</i> female		57, 200, 254	90	
<i>Calliphora subalpina</i>		360		
Neuroptera				
<i>Chrysopa carnea</i>		250, 595		

The insects were individually trapped by keeping a clean glass jar over it, in which they were killed thereafter, and subsequently transported to the laboratory. The adhering pollen-grains were counted under a stereo microscope the following day. Some loss of pollen from the body, therefore, was inevitable.

Table 6. Location of the pollen-grains on the insect body.

	Micro- lepidoptera	Geome- dridae	Mosqui- toes	Neuro- ptera
Observed number of individuals	3	7	9	2
Average number of grains	580	1034	211	423
Average % of grains on the body parts:				
Head	5	7	3	3
Proboscis and palp	1	4	10	—
Antennae	5	7	12	5
Wings	21	33	6	62
Legs	59	27	37	16
Thorax	8	12	15	3
Abdomen	2	10	18	14

Collection and handling of the insects as in *table 5*.

From the intense dusting with pollen, and the shedding from the insects, together with the frequent moves of the visitors between flower stalks, we can conclude that the observed visitors pollinate *S. otites*.

3.2.4 Behaviour and pollination

The effectiveness of the pollinators depends on the number of visited flowers. Because of the dioecy, also the frequency of moves from pistillate to staminate plants determines the pollination. *Table 7* gives an impression of these behavioural characteristics. On this occasion, the behaviour was much like that on other nights.

The behaviour of the Microlepidoptera and of the Geometridae is much alike; The moths land on a cluster of flowers and walk, with stationary wings, over the flowers, while probing the flowers with the proboscis and drinking from them. All body parts contact anthers and pistils, and become loaded with pollen, *table 5*. The pistillate and staminate plants are visited in an irregular sequence with a high frequency, *table 7*. The Microlepidoptera as well as Geometridae are effective pollinators, and because of their great number on most nights, their contribution to the pollination of *S. otites* will be substantial.

Autographa gamma does not visit the individual flowers separately, but moves fluttering over the flower stalk, clinging to groups of flowers and probing them with the proboscis. Mainly legs, proboscis and underside of the body contact anthers and stigmas, and are dusted with pollen. Because of the high number of visited flowers, *table 7*, and because in August and September *A. gamma* becomes very abundant it is a very important pollinator of *S. otites*.

Apart from the pollinating capacity of each visiting species the number of visitors relative to the number of flowers is decisive for the total seed production. On most evenings there were abundant visitors, *table 4*. At 9 p.m. on one night, which can be taken as example for all other nights, we observed on all

Table 7. Activity of insects on *S. otites* plants.

	number of indi- duals	visits to the flower stalk	visited flowers	visited flowers per visit to a stalk	activity period in seconds	time per flower in seconds
<i>Evergestis forficalis</i>	1	2	31	16	1615	52 (15-72)
<i>Evergestis forficalis</i>	1	4			1840	
<i>Campaea margaritata</i>	8	9	163	18	3930	24 (10-60)
<i>Autographa gamma</i>	10	14	90	6	355	4 (1-8)
<i>Chrysopa carnea</i>	1	1	20	20	660*)	

At 10.30 p.m. observations are made during 24 minutes on one flower stalk.

*) Remained on the flower stalk until the end of the observation period.

Table 8. Visitors of several flowers on De Wylerberg.

	<i>Silene otites</i>	<i>Melandrium album</i>	<i>Salvia pratensis</i>	<i>Lamium maculatum</i>	<i>Lamium album</i>
<i>Haritata ruralis</i>	B	O	O	D	O
<i>Camptogramma bilineata</i>	B	D	D	D	O
<i>Mamestra brassicae</i>	D	D	O	O	O
<i>Hadena rivularis</i>	D	D	O	O	O
<i>Autographa gamma</i>	B	B	C	C	D

Explanation as in table 4.

flower stalks together: 3 *A. gamma*, 14 *Campaea margaritata* and two more Geometridae, 3 Neuroptera and 20 Mosquitoes. Later on (10.30 p.m.) the mosquitoes had disappeared. Then, in 24 minutes, 10 *A. gamma* and 8 *C. margaritata* moths visited 272 out of a total of 500 flowers on one stalk, table 7. Therefore, that evening, each flower will have been visited several times. In this way, the night flying Lepidoptera give an explanation for the good seed production of *S. otites* in our location.

The behaviour of the insects also determines specificity of pollination. Plant species, growing next to the bed of *S. otites* plants, were checked for visitors during three nights, table 8. Only five moth species, also known from *S. otites* plants, were visiting these flowers. Therefore, all other visitors of *S. otites* exhibit fidelity. This might be imposed on the Geometridae and Microlepidoptera by the relation between the proboscis length (see list of visitors) and the position of the nectar in the flowers studied.

Of the Noctuidae *Mamestra brassica* and *Hadena rivularis* only a few individuals were observed on *M. album*, and these species visit *S. otites* only occasionally. As is known, *A. gamma* visits a wide variety of flowers, but develops constancy (Schremmer 1941). Because of the constancy the pollination is specific.

On all evenings in August and in September many mosquitoes, both males and females (several females with blood in their abdomen) were drinking on the flowers of *S. otites*. They sit motionless with the thin proboscis dipped into the nectar droplet on the flower or inserted into the narrow slit between petals and calyx, figs. 2 c, d, f and 3a.

The mosquitoes visit several flowers in succession. They walk to nearby flowers or, less frequently fly to another flower stalk. It has often been observed that mosquitoes are disturbed easily by the approach of a moth, and thereafter fly to another stalk. The observer was also disturbing to mosquitoes. Lepidoptera were less sensitive.

The mosquitoes visit several flowers in succession. They walk to nearby flowers, figs. 2c, d and 3a. Many insects sitting on pistillate plants were bearing pollen. Therefore, they must have been on staminate flowers before. This indicates that such mosquitoes are capable of pollinating *S. otites*, as was confirmed by

experimental confinement of mosquitoes with bagged flowers, which is described in the next chapter.

Unless disturbances by other insects promote movements, the mosquitoes were observed to move infrequently between different stalks. Therefore, the quantity of pollination effected by one insect will not be very large. Because of the high number of mosquitoes, active on the flowers on most evenings, this compensates for low individual effectiveness. The mosquitoes might be an important category of pollinators of *S. otites*.

Many mosquitoes were found on the netting bags over the flower stalks, mostly on the leeward side. For long periods the insects were piercing their mouthparts through the openings, too small for their heads, even when the flowers were out of reach. It seems that the flower scent, though not emanating from animals, attracted the mosquitoes and induced this piercing behaviour.

3.3 Pollination experiments

The pollination capacities of the visitors were tested, because adherence of pollen and the moving over the flowers indicate but do not prove pollination.

Whole pistillate plants with only flower buds were bagged with netting – with openings of 1 mm² – or with plastic bags. After the start of anthesis, a staminate flower stalk was added into the bag. In certain bags an insect was added during some nights. Afterwards the seed production was checked.

Untreated plants produced many seeds, bagged plants did not. Because the wind was able to move freely through the netting, the absence of seed set indicates that no wind pollination occurred.

In all those bags provided with insects, seed production was good, although less than in unshielded plants possibly due to the experimental set-up. Therefore, the pollination capacities of the insects have been proved. The insects tested were: *Haritata ruralis*, of which 2 individuals produced 146 and 309 seeds; *Xanthorhoë spadicearia*, 1 resp. 462; *Camptogramma bilineata*, 3 resp. 131, 36, 33; *Euxoa obelisca*, 1 resp. 453; mosquitoes, 2 resp. 0 and 66.

4. DISCUSSION

In the dunes near The Hague the pollination of coastal plants of *S. otites* was good. G. J. de Bruyn, a student of Professor Dr. L. van der Pijl, observed an average seed production of 27 per flower. On De Wylerberg, we found an average of 30 for continental plants. Therefore, the only differences between the two populations, the petal size and the plant size, appear not to harm the pollination.

Because in the pollination experiments wind pollination was absent, the coastal plants are not transitional to anemophily. Therefore, ecotypes based on mode of pollination, cannot be defined.

The production of sticky pollen, scent and nectar, and the intense visitation of coastal plants, when grown in the Botanical Garden, Nijmegen, confirm that

these plants did not lose their entomophilic characteristics.

Flowers of *S. otites* were found to be visited by many insects. As they do not move between flower stalks, the ants, the Opilionidae and the Neuroptera will not pollinate. The nocturnal, small Lepidoptera and the mosquitoes were pollinating, as was concluded from the adherence of pollen and the moving around and from the experimental encaging with flowers.

The flower characteristics are adaptive to these hemitropic visitors:

Aggregation of many small flowers on the stalks, so that the sexual parts form brushes, promotes a good contact of anthers and stigmas with the visitors, which walk irregularly around.

S. otites plants grow gregarious. Is this adaptive for the pollination, because the visitors fly relatively short distances, and the clots of pollen fall off easily? Or is only absence of seed dispersal, causing the seedlings to grow together, responsible for it?

Because mosquitoes tried to reach flowers, which were hidden behind netting, even in the presence of unshielded flowers, the nocturnal scent of *S. otites* seems to be an important means of orientation. Also Lepidoptera were often observed to land on the netting, *fig. 3d, f*, but their visits did not last for long. At De Wylerberg most Lepidoptera were seen to arrive downwind of the group of plants. This suggests scent directed orientation, or anemotaxis.

Visual cues seem to play a minor role. The flowers are rather inconspicuous with their small yellow to green petals. U.V.-absorption or reflexion is absent. Because of the absence of function for visual attraction and for providing a landing platform, the petals seem to be pure osmophores. A comparable reduction of the perianth to green osmophores has the likewise phalaenophilous *Narcissus viridiflorus* (VOGEL & MÜLLER-DOBLIES 1975).

The discovering of the pollinating capacity of mosquitoes is new for Europe. In arctic environments mosquitoes can act as pollinators (HOCKING 1968, KEVAN 1972). A record of small Lepidoptera and mosquitoes as pollinators in the American temperate zone is the pollination of *Habenaria obtusata* (DEXTER 1913, THIEN & UTECH 1970). In the present case the two orders are found in combination. From observations to be published elsewhere, it seems that this combination is common.

The importance as pollinators of the mosquitoes relative to the Lepidoptera, differs for each locality and for the season. Here, on *S. otites*, mosquitoes were scarce in July, but were dominating the picture in September. Under conditions adverse for Lepidoptera, the mosquitoes might be able to take over the pollination job. In the same way as day-time-Diptera substitute for the Hymenoptera in the Faroes (HAGERUP 1951).

Many mosquitoes are of medical interest. But although the necessity of sugar meals for energy (CLEMENS 1963), and for autogenous species (SPIELMAN 1971), is evident, astonishing little is known about the flower visiting behaviour (DOWNES 1958). This contrasts with the vast amount of research done on the blood feeding behaviour (CLEMENS l.c., HOCKING 1960).

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REFERENCES

- CLEMENTS, A. N. (1963): *The physiology of mosquitoes*. Int. Ser. Monogr. Pure Appl. Biol., Pergamon, London.
- DEXTER, J. S. (1913): Mosquitoes pollinating orchids. *Science*: 867.
- DOWNES, J. A. (1958): The feeding habits of biting flies. *Ann. Rev. Ent.* 3:249–266.
- FAEGRI, K. & L. VAN DER PIJL (1971): *The principles of pollination ecology*. (2nd ed.) Pergamon, Oxford.
- HAGERUP, O. (1951): Pollination in the Faroes – in spite of rain and poverty in insects. *Kgl. Danske Vidensk. Selsk. Biol. Medd.* 18:15.
- HOCKING, B. (1960): Northern biting flies. *Ann. Rev. Ent.* 5: 135–152.
- (1968): Insect-flower associations in the high arctic, with special reference to nectar. *Oikos* 19:359–387.
- KEVAN, P. G. (1972): Insect pollination of high arctic flowers. *J. Ecol.* 60:831–847.
- KNOLL, FR. (1930): über Pollenkitt und Bestäubungsart. *Zeitschrift für Botanik* 23:609–675.
- KNUTH, P. (1898): *Handbuch der Blütenbiologie*. Engelmann Verl., Leipzig, Bd 2.
- LEMPKE, B. J. (1953–1970): Catalogus der Nederlandse Macrolepidoptera, (Suppl. 1-Suppl. 15). *Tijdschr. Ent.* 96–112.
- SCHREMMER, F. (1941): Sinnesphysiologie und Blumenbesuch des Falters von *Plusia gamma* L., *Zool. Jahrb. Syst.* 74:375–435.
- SCHULZ, A. (1905): Das Blühen von *Silene otites* (L.). *Beih. Bot. Centralbl.* 18:433–446.
- SPIELMAN, A. (1971): Bionomics of autogenous mosquitoes. *Ann. Rev. Ent.* 16:231–248.
- THIEN, L. B. & F. UTECH: The mode of pollination in *Habenaria obtusata* (Orchidaceae). *Amer. J. Bot.* 57:1031–1035.
- VERHOEFF (1893): Blumen und Insecten der Insel Norderney und ihre Wechselbeziehungen. *Nova Acta Ksl. Leop. Carol. Deutsch. Akad. Naturforscher* 61:41–44.
- VOGEL, ST. & D. MÜLLER-DOBLIES (1975): Eine nachtblütige Herbst-Narzisse. Zwiebelbau und Blütenökologie von *Narcissus viridiflorus* Shousboe. *Bot. Jahrb. Syst.* 96:427–447.