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Pollinator attraction of Vitis vinifera subsp. silvestris

by

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Die Anlockung blütenbesuchender Insekten durch Vitis vinifera subspec. silvestris

Zusammenfassung. — Der Pollen der morphologisch hermaphroditen Blüten der Wildrebe *Vitis vinifera* L. subspec. *silvestris* (C. C. Gmelin) Hegi ist steril; die Art muß daher als funktionell diözisch betrachtet werden. Der (sterile) Pollen ist für die Insekten die einzige „Belohnung". Die optisch auffälligen Antheren sind eine notwendige Voraussetzung für die Attraktion der Halictiden (Schmal- oder Furchenbienen) und Syrphiden (Schweb- oder Schwirrfliegen); für Käfer haben sie jedoch keine Signalfunktion. Käfer werden durch Duftorientierung zu den Blüten hingeführt. In den Blüten finden sich Strukturen, die "Nektarien" genannt werden, jedoch keinen Nektar produzieren. Es handelt sich dabei um Duftdrüsen. Es ist anzunehmen, daß die Duftdrüsen abgewandelte Nektarien sind, die eine neue Funktion angenommen haben.

Introduction

The wild plants of *Vitis vinifera* L. subsp. *silvestris* (C. C. Gmelin) Hegi are supposed to be androdioecious but most European varieties have only hermaphrodite flowers and are thought to be self-pollinating. There are, however, several varieties which have pollination difficulties (Free 1970). Many varieties are either self or partly self-sterile due to the existence of sterile pollen. For these, the interplanting of a pollinizer species is recommended. Cross-pollination, therefore, becomes either a necessity or a means by which fruit yield can be increased. In cultivated plants where natural cross-pollination is poor, several modes of artificial pollination are used: hand pollination, spraying with pollen suspended in water, blowing air currents containing pollen or touching with bouquets from pollinizer species.

Because the mode of pollination of vine flowers is still a matter of some dispute (Zohary and Spiegel-Roy 1975[1]), it was decided to study this occurrence in a natural habitat.

Results

Description of the flower

The petals are united at their top and form a cap that is shed as a complete unit at anthesis. Each hermaphrodite flower has a single slender-necked pistil at the base of which are five yellow structures, commonly called "nectaries". Five stamens are located outside the "nectaries". Most cultivated varieties have stiff stamens,

[1]) Observations were made in the spring of 1977 in the Alsace region of France. The plants grew at the edge of a forest, about 5 km outside the vine culture district but within the natural habitat of *Vitis vinifera* subsp. *silvestris*.

whereas, in several cultivated varieties and in wild plants the stamens of the hermaphrodite flowers are curled. The male flower has a reduced or even aborted ovary. The grape flower has a strong sweet fragrance.

Prof. Dr. H. F. LINSKENS and Prof. Dr. R. LINDER (pers. comm.) found that pollen from the curled anthers is sterile. Therefore, those flowers, apparently hermaphrodite, are in fact functionally female. The wild *Vitis vinifera* can be regarded as dioecious instead of androdioecious. This pollen sterility causes the absence of fruit set after selfing and not the existence of self-sterility in the "hermaphrodite" flowers as stated by FREE (1970).

Wind pollination

In the cultivated grape, the shedding of the petal cap often causes self-pollination because pollen can be pushed from the anthers onto the stigmas. Movements of the flowers caused by wind also promotes the falling of pollen grains. The pollen grains, however, sink very fast and since in the location concerned the sexual forms of the wild *Vitis* plants grow some 50 m apart, the possibility of cross-pollination by wind can be excluded.

Pollinators

In contrast to a scarcity of insects visiting the flowers in the vineyards, a large number was observed in the wild situation: Coleoptera (Cerambycidae, Mordellidae and several beetles of about 2 mm in length), Hymenoptera (Halictidae, *Apis mellifica)* and Diptera (Syrphidae). Temperature was a key factor affecting the composition of the visitor spectrum. On hot days ($t >$ ca. 20 °C), the Coleoptera outnumbered the others; on cool days ($t <$ ca. 20 °C) the Diptera and Hymenoptera formed the majority; honey bees *(Apis mellifica)* were always rare.

The Coleoptera worked on the anthers; the Halictidae collected pollen on the venter; the Syrphidae licked the anthers. The "nectary" was never licked and the bees *(Apis mellifica)* never extended their proboscis.

In order to obtain information about the attracting value of pollen and scent of the various flowertypes, some experiments were carried out:

Influence of the flower type on flower visitors

Equal-sized bunches of cultivated varieties with hermaphrodite flowers were suspended together with bunches of male and of female flowers from the wild plants. The number of landings, the duration of the insect visits and the behaviour of the visitors were similar for the three flower types. The sterile pollen was also consumed. Therefore, the three flower types have equal attractive value for insects. For the wild, dioecious plant this is, of course, necessary in order to ensure the movement of pollinators between the two types of the flowers.

Influence of pollen on flower visitors

The anthers were removed from clusters of functionally female wild flowers and this group and untreated clusters of equal sizes were exposed simultaneously to insects. Although Halictidae and Syrphidae approached the two types with equal frequency, they landed less often on the emasculated flowers (Table 1). In their approach to a cluster of flowers the insects always hovered in front of it for a few seconds. They subsequently left the emasculated flowers without landing, but did land on the untreated ones. The presence of anthers also influenced the duration of

Table 1

Influence of the anthers on the attractive value of the flowers to bees and flies
Bedeutung der Antheren für die anlockende Wirkung der Blüten auf Bienen und Fliegen

Insect groups	Number of landings on flower clusters	
	Intact flowers	Emasculated flowers
Syrphidae	24	5
Halictidae	8	4

Duration of the visits (s)	Number of visits to	
	Intact flowers	Emasculated flowers
<10	3	4
10—30	3	1
30—120	11	2
>120	23	0
undetermined	0	1

For 30 min, 6 equal-sized clusters of female flowers (3 intact, 3 emasculated) were exposed simultaneously between the leaves of wild *Vitis vinifera* plants.

Table 2

Influence of the anthers on the attractive value of flowers to beetles and bees
Bedeutung der Antheren für die anlockende Wirkung der Blüten auf Käfer und Bienen

Insect groups	Number of landings on flower clusters	
	Intact flowers	Emasculated flowers
Halictidae	4	3
Coleoptera	6	5

Duration of the visits by beetles (s)	Number of visits to	
	Intact flowers	Emasculated flowers
<10	1	1
10—30	1	0
30—120	1	2
>120	3	2

For 30 min, 6 equal-sized clusters of hermaphrodite flowers (3 intact, 3 emasculated) were exposed simultaneously between the leaves of wild *Vitis vinifera* plants.

the visits to a flower cluster and also, in this way, the probability of effective pollination. For the beetles such a difference was not found (Table 2): Absence of anthers was no obstacle affecting the number and the duration of visits.

Influence of scent on flower visitors

With the removal of the "nectary" the flower becomes odourless, at least to the human nose. The isolated "nectary" has the characteristic odour of the grape flower.

Clusters of flowers were hidden in a box with only one opening. After 15 min the box contained several beetles which obviously had oriented to the flowers by means of flower odour. The behaviour of the Cerambycidae also indicated an odour-directed orientation: The beetles arrived from downwind of the flowers. Mostly they landed on a leaf near the flower cluster, walked around over this leaf and moved their antennae. After walking around for a short time, the beetles resumed flight from the edge of the leaf that was closest to the flowers and landed on a new leaf yet closer. In this manner the beetles slowly approached the clusters.

Discussion

Since the absence of pollen had no effect in attracting the beetles, any odour from the pollen must not have any signal function. The odour must, therefore, originate from another part of the flower: the so-called "nectary". This "nectary" does not produce nectar, but instead produces the flower odour. It is a scent gland, not a nectary. The classical concept about the grape flower, as given in all handbooks on viticulture and in Free (1970), needs to be corrected.

Because of the location of the scent gland, inside the circle of stamens, the glands are not derived from reduced petals or sepals as is the case in *Silene otites* (Brantjes and Leemans 1976) and in *Narcissus viridiflorus* (Vogel and Müller-Doblies 1975). Most likely the scent gland is a modified nectary.

The pollen is eaten by all insects visiting the flowers. They perceive the anthers after their approach to the flower and the presence of the anthers induces landings by the Halictidae and Syrphidae. In this way the sterile pollen in the female flowers compensates for the absence of other rewards due to the modification of the "nectary" into a scent gland.

The attractive value of the flowers lies in the anthers. The flower, therefore, is a "pollen flower".

The observed equal attractive value of the cultivated and the wild flowers contrasts with many statements in literature where the low frequency of visits by insects is ascribed mainly to low attractive value of the flowers of cultivated plants. One of the factors which are held responsible for this is the nectar, which, however, is always absent.

The scarcity of visits can also be explained by the absence of insects in the vineyards due to spraying and the removal of weeds, and to the scattering over large areas of the few flying insects into the large mass of grape flowers which all bloom in the same few days.

Summary

The pollen from the morphologically hermaphrodite flowers of wild grape is sterile. Subsequently, *Vitis vinifera* L. subsp. *silvestris* (C. C. Gmelin) Hegi is functionally dioecious. The sterile pollen of these wild-growing plants is the only food source for many insects. While the presence of visually conspicious anthers is necessary in order to attract Halictidae and Syrphidae, they do not appear to have a signal function for beetles. Beetles arrive at the flowers by scent orientation. There are structures in the flowers, called "nectaries", which do not produce nectar and are, in actual fact, odour glands. These structures may be derived from the true nectary.

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