Phyton (Horn, Austria)	**Vol. 44**	Fasc. 1	155–165	9. 7. 2004

Pollination Problems in Styrian Oil Pumpkin Plants: Can Bumblebees be an Alternative to Honeybees?

By

Renate FUCHS and Maria MÜLLER*)

With 1 Figure

Received January 28, 2004

Key words: *Cucurbita pepo*, Styrian oil pumpkin, bumblebees, honeybees, pollination efficiency.

Summary

FUCHS R. & MÜLLER M. 2004. Pollination problems in Styrian oil pumpkin plants: Can bumblebees be an alternative to honeybees? – Phyton (Horn, Austria) 44 (1): 155–165, 1 figure. – English with German summary.

The Styrian oil pumpkin (*Cucurbita pepo* L. subsp. *pepo* var. *styriaca* GREB.) has an important regional importance since the European Union protected the Styrian oil pumpkin seed salad oil as a selected European speciality in 1995. In recent years the production of the Styrian oil pumpkin listed severe losses, one of the reasons is a decreased availability of pollinators. Since a great loss of bee colonies (decrease of about 200.000 beehives in the last ten years) and wild bees can be observed in Austria and worldwide, an adequate pollination cannot be guaranteed any longer. Strategies to find alternative pollinators and to ensure sufficient pollination are important. In this study we determined the pollination efficiency of bumblebees (*Bombus terrestris*) compared to honeybees (*Apis mellifera*). Further we investigated the pollination behaviour (flower visit rate, visit frequency and forage distances) of bumblebees in the open field, to see if they can be used as an alternative, if honeybee colonies continue to decline, or honeybee pollination alone is not sufficient, for example at adverse weather. These studies of bumblebees in *Cucurbita* fields are the first ones in Austria, as up to now bumblebees were only used in glasshouses or orchards. Our studies showed that bumblebees can be used in the open field and can lead to a general improvement in pollination, as bumblebees visited four to five times more flowers in a minute and foraged at adverse weather, even during rain. But the use of

*) Mag. Renate FUCHS (corresponding author), Ao. Univ.-Prof. Dr. Maria MÜLLER, Institute of Plant Physiology, Schubertstrasse 51, 8010 Graz, Tel.: +43-316-380-5641 / 8785; e-mail: maria.mueller@uni-graz.at, fuchsren@gmx.at

commercial bumblebees in Styrian pumpkin fields, as already used in tomato or pepper greenhouses, can not be a solution for the pollination problems as at least four to five hives / hectare are needed. They can only be an alternative if the natural populations can be increased again, this means habitat and food resources must be conserved.

Zusammenfassung

FUCHS R. & MÜLLER M. 2004. Zur Bestäubungsproblematik beim Steirischen Ölkürbis: Stellen Hummeln eine Alternative zu Honigbienen dar? – Phyton (Horn, Austria) 44 (1): 155–165, 1 Abbildung. – Englisch mit deutscher Zusammenfassung.

Der Steirische Ölkürbis besitzt aufgrund der von der Europäischen Union seit 1995 geschützten Marke des „geographisch geschützten“ steirischen Kernöls eine große Bedeutung für die regionale Landwirtschaft. Der Anbau des Steirischen Ölkürbisses führte in den letzten Jahren aber immer wieder zu hohen Ertragseinbußen; ein Grund dafür ist die ständig rückläufige Zahl an Bestäubern. Aufgrund des starken Rückgangs an Bienenstöcken in den letzten zehn Jahren in Österreich aber auch weltweit, kann eine ausreichende Bestäubung nicht länger garantiert werden. Daher müssen Strategien entwickelt werden um dennoch eine gute Bestäubung sichern zu können. Dies beinhaltet vor allem den Einsatz von alternativen Bestäubern wie etwa Wildbienen. In dieser Studie werden die Bestäubungsleistungen der Erdhummel (*Bombus terrestris*) mit denen der Honigbiene (*Apis mellifera*) verglichen. Zusätzlich wird das Bestäubungsverhalten von Erdhummeln im Kürbisfeld (Blütenbesuchrate, Verweildauer in der Blüte und Flugdistanzen) untersucht um zu sehen ob sie eine Alternative zu den Honigbienen darstellen, falls deren Zahl weiter sinkt oder die Bestäubung allein durch sie nicht ausreicht, wie zum Beispiel bei Schlechtwetter. Derartige Studien über einen möglichen Einsatz von Hummeln in Kürbisfeldern sind in Österreich das erste Mal durchgeführt worden, da bislang Hummeln nur in Glashäusern oder in Obstgärten genutzt wurden. Diese Untersuchungen zeigten, dass Hummeln generell zu einer guten und verbesserten Bestäubungsleistung beitragen können, da sie in der Minute 4- bis 5-mal so viele Blüten besuchen wie Honigbienen und sie vor allem auch bei Schlechtwetter bestäuben. Alleine der Einsatz von gezüchteten Hummelvölkern, wie sie bereits seit langem in Glashäusern für Tomaten oder Paprika genutzt werden, stellt jedoch keine Lösung für die derzeitige Bestäubungsproblematik beim Steirischen Ölkürbis dar, da zumindest mehr als drei Stöcke pro Hektar benötigt werden. Vor allem der Schutz von Nistmöglichkeiten und Nahrungsangeboten kann den Rückgang an Hummeln in der Steiermark stoppen um sie so zu einer Alternative zu Honigbienen für die Bestäubung nutzen zu können.

Introduction

In recent years the production of the Styrian oil pumpkin (*Cucurbita pepo* L. subsp. *pepo* var. *styriaca* GREB.) recorded a dramatic yield loss. Although many factors such as climate, drought, and the infection with zucchini yellow mosaic virus also affect crop yield, pollination is a very critical factor as *Cucurbita* plants are monoecious, which means they have separate male and female flowers on the same plant (MCGREGOR 1976, FREE 1993). Each flower is about 7–8 cm wide, male flowers occurring at the end of a slender peduncle and they have three anthers. Each female flower occurs at the end of a short peduncle and has a thick style and three two lobed stigmas; the ovary occurs at the base of the corolla. Male flowers produce nectar and pollen, female only nectar. Flowers are not wind- or self-pollinated (McGREGOR 1976), so that fruit and seed set depends on insect pollination and only honeybees and other bees like bumblebees are qualified for pollen transfer, because of the large size of the pollen grain (100–200 µm), their stickiness and the way they are released from the anthers (NEPI & PACINI 1993). Pollination is critical because flowers of *Cucurbita pepo* are only open for a single day (6 hours) (NEPI & PACINI 1993) and never reopen again; therefore pollination time is very short. Thus, it is important for a female flower to be pollinated as early as possible while pollen is still viable. As the number of seeds/fruit increases if the number of pollen deposited on a stigma increases (WINSOR & al. 1987), a high number of bee visits to flowers is necessary for adequate pollination and high seed set. Honeybees are today the most important pollinators in *Cucurbita* crops, but their number, in fact, declined rapidly in the past in Styria (KINDLER 2002) and worldwide (ALLEN-WARDELL & al. 1998). Other bees, like bumblebees or squash bees, can be alternative species for crop pollination, as they can be equal or better pollinators than honeybees (WESTRICH 1990, CANTO-AGUILAR & PARRA-TABLA 2000, KEVAN & ROBINSON 2001, MAYFIELD & al. 2001). They make more stigma contact, work faster and work earlier in the morning, but their numbers declined in the past, too, because of the changes in modern agricultural practises, which leads to a reduction of habitat and food resources for many pollinators (KEVAN 1999, SVENSSON & al. 2000, RICHARDS 2001). These habitat changes influences pollination system worldwide (KREMEN & RICKETTS 2000). Consequently, interest has grown in search for alternative pollinators and pollination strategies to secure adequate pollination worldwide (TORCHIO 1990). Particularly bumblebees can be an option for pollination in many crops, so that many studies of their pollination efficiency, pollination behaviour and the effect on fruit and seed production were made in the past, most of them in greenhouses (DRAMSTAD & FRY 1995, MORADIN & al. 2001, THOMSON & GOODELL 2001). Bumblebees are already an important option to complete the pollination community in orchards and in greenhouse produced tomato and pepper plants (SHIPP & al. 1994, HAVENITH 2000, CALZONI & SPERANZA 1998). There are no studies about bumblebee pollination behaviour in *Cucurbita* fields in Austria so far. Consequently, the objective of this study was to determine the pollination effectiveness of bumblebee visiting *Cucurbita pepo* flowers compared to the effectiveness of honeybees, which are almost the only visitors in *Cucurbita* fields in Styria. The study also included pollination behaviour; visit frequency and foraging distances of bumblebees in the open field. The main questions for practical use in agriculture are: 1) can bumblebees be good pollinators for *Cucurbita* plants and 2) can they be an alternative to honeybees, when pollination conditions for them are bad, especially at adverse weather?

Material and Methods

Plant Material

Plants of *Cucurbita pepo* L. subsp. *pepo* var. *styriaca* GREB. grew from May to September. Sowing was done at the end of April / beginning of May, first bloom was observed in the mid of June.

Study Sites

The study was done between June and September over two planting periods in 2002 and 2003. The study sites were located in Styria and consisted of three pumpkin fields, located in Kalsdorf (in the south of Graz), in Pölten (southeast Styria) and in Stainz (southwest Styria). The geographical coordinates and climate characteristics in these regions are shown in Table 1.

Table 1. Geographical coordinates altitudes, average temperatures, climate characteristics, field sizes and characterisation of their surroundings of the three investigation fields Kalsdorf, Pölten and Stainz. All three fields were mostly surrounded by other pumpkin fields or cornfields, but also by small woods.

	Kalsdorf	Pölten	Stainz
Geographical coordinates	46 °97′ N 15°48′ E	46°75′ N 15°98′ E	46°89′ N 15°25′ E
Altitude	324 m	290 m	300 m
Predominantly soil (study fields)	clay	clay	clay
Average temperature in July in °C	17.8–18.8	17.8 – 18.8	18.5
Average temperature of the year in °C	7.8–9.8	7.8–9.8	9.0–9.5
Vegetation (d / year)	228–235	222–243	225–240
Clime during growth period	Frequently foggy, less wind (950–1000 mm/ year)	Frequently foggy, less wind, (800 mm/year)	More climate differences, (1104 mm/year)
Field size in hectare	3	0.5	1
Surrounding areas	forest and cornfields	pumpkin fields	grassland and forest

Pollinators

Honeybees: At least 5 honeybee hives were positioned within a radius of one kilometre, each hive has >10.000 individuals. The distances of the hives to the investigation fields were: Stainz (directly on the field), Pölten (500 m) and Kalsdorf (>1 km).

Bumblebees: commercial bumblebee hives were bought at Austrosaat, one hive per tunnel (70 m^2) in 2002 and three hives per acre in 2003; at least >50–70 individuals (see below);

Insects were introduced at beginning of blossoming (in the middle of June) in the fields.

Investigations of 2002: Pollination Efficiency of Bumblebees in Tunnels

In 2002 the pollination efficiency of bumblebees compared to honeybees were evaluated. In order to analyse the effect of bumblebees, one area (70 m^2) of each field was isolated by caging it under insect-proof fine meshed net. The material of the nets was pervious to light, water and air. Measurements of the conditions in and outside the tunnels showed the same results. The pollination efficiency of bumblebees was evaluated in these tunnels, whereas the honeybee's pollination efficiency was evaluated in the open field as more than 95% of *Cucurbita*-pollination, in these regions, is done by honeybees. For this purpose the same area of about 70 m^2 was used as control and showed the natural pollination in these fields.

At harvest in September 2002, all mature fruits in the tunnel and from the control area were counted and harvested by hand and the total number of fruits and seed number per fruit were documented and compared.

Investigations of 2003: Pollination Behaviour of Bumblebees Compared to Honeybees in Open Field Studies

During flowering period in 2003, the same three fields as described above were investigated over a period of five weeks. We estimated flower visit rates, visit frequency and pollination behaviour in connection with the visit begin in the morning, visit frequency at adverse weather and bee-behaviour during pollen and nectar collecting. Three commercial bumblebee hives (at least 50 individuals) per field were placed in the middle of the three *Cucurbita pepo* acres (see Table 1) and at least 5 honeybee hives were positioned at different distances to the fields (see pollinators).

Insect visit rate of bumblebees and honeybees was estimated visually by counting legitimate visits; i.e. only bees with anther or stigma contact. Counting was performed for five hours each day (5.30–10.30 o'clock) as follows: ten flowers were observed for ten minutes, this was done three times per hour at different places in the field for a total of 30 minutes of counting / 30 flowers. The number of visits per flower a bloomy day was evaluated as follows:

Counts of 30 minutes / 30 flowers * 2 = Visit rate / hour and 30 flowers

This was repeated five times (5.30–10.30) and added up = Visit rate / bloomy day and flower.

The investigations were performed for three days at each field and the mean visit rates were calculated.

The visit time of bumblebees in flowers was evaluated with a stopwatch and the average of more than 150 stops was compared to the visit frequency of honeybees.

Results

Pollination Efficiency of Bumblebees in Tunnels

In the year 2002, the pollination efficiency of bumblebees was evaluated in a tunnel of about 70 m^2 each pumpkin field and compared to the honeybees in the open field (also 70 m^2). In Pölten, most fruits were rotten, because of the great hotness and drought in this summer. In 2002 rainfall from April to August was similar to average rainfall in the years before (up to 350 mm – equal distribution), but in the year 2002 rainfall distribution in this region was quite different: 80% of the rainfall could be measured in August that led to a maceration of the fruits. The total harvest / hectare was only 200 kilogram of pumpkin seeds, therefore the number of fruits could not be compared to the two other areas. In Kalsdorf and Stainz rainfall distribution from April till August was nearly equal over the whole period (about 400 mm). The different pollination efficiency between bumblebees and honeybees in these fields (Kalsdorf and Stainz) showed an increase in the total number of fruits of about +30 % when pollination was done by bumblebees. Therefore the weight of seeds was elevated in Kalsdorf (+19 %) and in Stainz (+38 %), too (Table 2).

Table 2. The effect of different pollinators in K: Kalsdorf and S: Stainz; Pollination efficiency of honeybees (control) and bumblebees (tunnels) were compared. Differences in % = increase in the tunnel.

	Control areas		Tunnels		Differences in %	
	K	S	K	S	K	S
Total number of fruits / 70 m^2	51	48	73	69	+ 30.1	+ 30.4
Weight of seeds (kg) / 70 m^2	2.8	2.7	3.5	4.3	+ 19.3	+ 38.3

Open Field Studies of Bumblebees and Honeybees

The visit rates, visit frequency and pollination behaviour of bumblebees and honeybees were observed on the same three acres as in the year 2002.

The honeybee hives (each >10.000 individuals) were positioned, as described in material and methods, in different distances to each field. The bumblebee hives (each >50 individual) were positioned in the middle of each acre. The investigations were performed in an area of one hectare each field, because preliminary investigations showed, that visit rates of the bumblebees out of this area were not frequently enough. Therefore, the data in table 3 expressed the counts of visits of honeybees and bumblebees of our hives on sunny days. Visits of other wild bees could be ignored, because of the extreme low number of these individuals. With an average number of about 10.000 plants / hectare, at least 60.000 flowers are bloomy at the same time. The number of visit rates / flower and day of bumblebees was similar in all fields and showed that each flower was visited at least 2 to 2.5 times a day. The number of visits by honeybees was different between the three fields, depending on the distance from the hives to the acres. Honeybees showed a visit rate between 10–20 times per flower and day. Although the visits by bumblebees seem to be lower, they pollinated more effectively comparing the number of individuals: while 200 bumblebees visited each flower / day for 2 times, at least >10.000 honeybees visited each flower / day only for 10 to 20 times (table 3).

Measurements of the visit frequency showed that bumblebees visited flowers more frequently than honeybees. The average time, calculated from more than 150 stops, of flower visits by bumblebees was about 15 seconds (± 12), whereas honeybees stayed about 55 seconds (± 25) per visit.

Pollination behaviours in the open field showed that bumblebees pollinated earlier in the morning, they started at about 5 o'clock, whereas honeybees started at about 7 o'clock. Bumblebees also foraged at adverse weather (windy, clouded) and even at rain, whereas honeybees only showed the high visit rate at sunny days.

Table 3. Average number (three days of counts at each field) of visit rates per flower and day of bumblebees and honeybees. Bumblebee hives were positioned in the middle of each field, whereas honeybee hives were positioned at different distances to each field (Kalsdorf: >1 km distance to the investigation plot, Pölten: 500 m distance and Stainz: directly at the plot).

	Number of individuals		Visit rate / flower and day	
	Bumblebees	Honeybees	Bumblebees	Honeybees
Kalsdorf	150–200	>10.000	2	10.2
St. Pölten	150–200	>10.000–20.000	2.5	15.3
Stainz	150–200	>10.000–30.000	2.4	20

Observations of pollinating bees showed that most of the bumblebees (>90 %) approached female flowers directly by landing on the reproductive parts. The honeybees most often collected nectar without stigma contact, because of their smaller bodies, which significantly reduced the pollination success. Both bee species typically collected pollen by scrabbling at the anthers. Out of the male flowers, honeybees often rest on a leaf to remove some of the pollen with their legs, whereas bumblebees flew more frequently from flower to flower. Therefore bumblebees have more pollen loaded on their hairs when visiting female flowers.

Discussion

The efficiency of a pollinator depends on the fit between floral characteristics and pollinator foraging behaviour. Many parameters, such as pollen viability, stigma receptivity, visit frequency or pollen deposition on stigma can adequately explain the pollination efficiency of floral visitors (HERRERA 1989). In evaluating pollination behaviour for *Bombus terrestris* and *Apis mellifera* in *Cucurbita pepo*, the results in our studies as a whole, indicate that bumblebees can be more efficient pollinators. The investigations in the tunnel show that bumblebees have great potential to pollinate pumpkins and they can, additionally to honeybees, lead to a better pollination. This fact should be taken into consideration, e.g. when honeybees available for rental are limited or when the pollination conditions, for example at adverse weather, are unfavourable for them. This better pollination efficiency (see table 2) leads to an increase in the total number of fruits and total weight of seeds / 70 m^2.

Further studies in the open acres confirm the better efficiency of bumblebees in all three investigated fields, too. Bumblebees start foraging at least one to two hours earlier than honeybees and they visit more flowers per minute. Similar results have also been described in studies with cucumber and watermelon by STANGHELLINI & al. 2002. Especially in the pollination of *Cucurbita pepo* plants this fact seems to be very important, as the flowers are only open for six hours and pollen viability and its receptivity to stigma is highest in the early morning (NEPI & PACINI 1993, PACINI & al. 1997). Further observations show that bumblebees forage at adverse weather conditions and even at rain, because they are far less sensitive to unfavourable climatic conditions, i.e. low temperature, wind and rain, and they will continue to forage under conditions unacceptable to honeybees (FUSSEL & CORBET 1992, WILLMER & al. 1994). This is especially of great importance when the weather conditions in the first two flowering weeks are not ideal for honeybees, because only the fruits, which are pollinated in the first two to three blooming weeks, are regular in size and of commercial value for the production of the Styrian pumpkin oil. Therefore, the position of bumblebee hives in pumpkin fields or the protection of native bumblebees, this means to conserve habitat and food resources (mouse nests, hedges, biotopes . . .) can prevent a possible crop loss due to an inadequate pollination of honeybees. Further, our studies point out that bumblebees do not only forage close to their nest, as sometimes documented, but up to a circumference of one hectare. These results are confirmed by different other studies, especially in orcharding, where radar techniques and / or marked bumblebees are used (OSBOURNE & al. 1999, DRAMSTAD & SCHAFFER 2003).

The total number of bumblebee visit rates / flower and day (Table 3) seems to be low in comparison to honeybees visit rates, but these visits were only done by about 200 bumblebees per hectare. Compared to this, for example in Stainz, five honeybee hives with at least >10.000 bees each hive were positioned near the field. The pollination efficiency of bumblebees is very high, when we realize that only 200 bumblebees can visit each flower / hectare field two times. With an average number of about 10.000 plants / hectare, at least 60.000 flowers are bloomy at the same time. For an adequate pollination in *Cucurbita*, every flower should be visited at least 12 to 15 times a day by honeybees (McGregor 1976), this means 1 to 2 strong honeybee hives / hectare. But our results suggested that despite the better pollination efficiency of bumblebees, three commercial hives / hectare are not enough when no other pollinators occur, i.e. commercial bumblebee hives can only be used additionally to honeybees.

Summing up these results indicate that *Bombus terrestris* can be an important pollinator for *Cucurbita pepo* crops. But the commercial use of cultured hives is not economically, because of the present price per hive (about 70 €). Therefore it will be important to stop the decline of the natural populations of bumblebees and to increase intensively their occurrence, by protecting their habitat and food resources. They need local access to suitable nesting and hibernation sites, as well as alternative food sources during periods when pumpkins are not blooming. Under these conditions they might be an adequate alternative additionally to honeybees. However, nowadays the protection of native pollinators is critical and difficult (Kevan 1999, Barron & al. 2000), because of modern agricultural techniques. Finally we are concerned to underline that in the future bumblebees and other wild bees should play once again an important role for the production of pumpkins.

Acknowledgements

The authors thank the land owners F. Fuchs, Mag. Ch. Konrad and „Fachschule für Landwirtschaft" in Stainz for allowing the project to take place on their acre. Thanks to Dr. A. Kindler and Ing. H. Pelzmann for useful discussing and helping in questions for field studies. Thanks to „Versuchsanstalt für Spezialkulturen Wies" and „ Landwirtschaftskammer Graz" for their financial support.

References

Allen-Wardell G., Bernhard P., Bitner R., Burquez A., Buchmann S., Cane J., Cox P. A., Feinsinger P., Ingram M., Inouye D., Jones E., Kennedy K., Kevan P., Koopowitz H., Medellin R., Medellin-Morales S. & Nabhen G. P. 1998. The potention consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. – Conservation Biology 12: 8–17.

Barron M. C., Wratten S. D. & Donovan B. J. 2000. A four year investigation into the efficacy of bumble bee populations. – Agricultural and Forest Entomology 2: 141–146.

Calzoni G. L. & Speranza A. 1998. Insect controlled pollination in Japanese plum (*Prunus salicina* Lindl.). – Scientia Horticulturae 72: 227–237.

Canto-Aguilar M. A. & Parra-Tabla v. 2000. Importance of conserving alternative pollinators: assessing the pollination efficiency of the squash bee, *Peponapis limitaris* in *Cucurbita moschata* (*Cucurbitaceae*). – Journal of Insect Conservation 4: 203–210.

DRAMSTAD W. & FRY G. 1995. Foraging activity of bumblebees (Bombus) in relation to flower resources on arable land. – Agriculture, Ecosystems and Environment 53: 123–135.

— & SCHAFFER M. J. 2003. Bumblebee foraging – is closer really better? – Agriculture, Ecosystems and Environment 95: 349–357.

FREE J. B. 1993. Insect pollination of crops. 2nd edition. – Academic Press London. p. 684.

FUSSEL M. & CORBET S. A. 1992. Flower usage by bumblebees: a basis for forage plant management. – Journal of Applied Ecology 29: 451–565.

HAVENITH CH. 2000. Bestäubung durch Wildbienen – eine Option für den Obstbau. – Erwerbsobstbau 42: 44–50.

HERRERA C. M. 1989. Pollinator abundance, morphology and flower visitation rate: analysis of the quantity component in a plant pollinator system. – Oecologia 80: 241–248.

KEVAN P. G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. – Agriculture, Ecosystems and Environment 74: 373–393.

— & ROBINSON M. 2001. Secrets of the hoary squash bee uncovered. – Fruit & Vegetable Magazine, Januar/Februar: 42–43.

KINDLER A. 2002. Aktuelles zum Steirischen Ölkürbis. – Landwirtschaftliche Mitteilungen 10: 13.

KREMEN C. & RICKETTS T. 2000. Global perspectives on pollination disruptions. – Conservation Biology 14 (5): 1226–1231.

MAYFIELD M. M., WISER N. M. & PRICE M. V. 2001. Exploring the most effective pollinator principle with complex flowers: bumblebees and *Impomopsis aggregata*. – Annals of Botany 88: 591–596.

MCGREGOR S. E. 1976. Insect pollination of cultivated crop plants. – Agriculture Handbook No 496. U. S. Government Prinitng Office. Washington D. C. p 411.

MORADIN L. A., LAVERTY T. M. & KEVAN P. G. 2001. Bumble bee (Hymenoptera: Apidae) activity and pollination levels in commercial tomato greenhouses. – Journal of Economic Entomology 94: 462–467.

NEPI M. & PACINI E. 1993. Pollination, pollen viability and pistil receptivity in *Cucurbita* pepo. – Annals of Botany 72: 527–536.

OSBOURNE J. L., CLARK S. J., MORRIS R. J., WILLIAMS I. H., RILEY J. R., SMITH A. D., REYNOLDS D. R. & EDWARDS A. S. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. – Journal of Applied Ecology 36 (4): 519–529.

PACINI E., FRANCHI G. G., LISCI M. & NEPI M. 1997. Pollen viability related to type of pollination in six angiosperm species. – Annals of Botany 80: 83–87.

RICHARDS A. J. 2001. Does low biodiversity resulting from modern agricultural practise affect crop pollination and yield? – Annals of Botany 88: 165–172.

SHIPP J. L., WHITFIELD G. H. & PAPADOPOULOS A. P. 1994. Effectiveness of the bumble bee, *Bombus impatiens* Cr. (Hymenoptera: Apidae), as a pollinator of greenhouse sweet pepper. – Scientia Horticulturae 57: 29–39.

STANGHELLINI M. S., AMBROSE J. T. & SCHULTHEIS J. R. 2002. Diurnal activity, floral visitation and pollen deposition by honey bees and bumble bees on field grown cucumber and watermelon. – Journal of Apicultural Research 41: 27–34.

SVENSSON B., LAGERLÖF J. & SVENSSON B. G. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. – Agriculture, Ecosystems and Environment 77: 247–255.

THOMSON J. D. & GOODELL K. 2001. Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. – Journal of Applied Ecology 38: 1032–1044.

TORCHIO P. F. 1990. Diversification of pollination strategies for U. S. Crops. – Environmental Entomologie 19 (6): 1649–1656.

WESTRICH P. 1990. Die Wildbienen Baden-Württembergs, 2 Auflage. – Ulmer Verlag, Stuttgart p. 292–297.

WILLMER P. G., BOTANE A. A. M. & HUGHES J. P. 1994. The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. – Ecological Entomology 19: 271–284.

WINSOR J. A., DAVIS L. E. & STEPHENSON G. 1987. The relationship between pollen load and fruit maturation and the effect of pollen load on offspring vigor in *Cucurbita pepo*. – The American Naturalist 129: 643–656.