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Amygdalin in almond nectar and pollen – facts and possible roles

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Abstract. Nectar and pollen within flowers are usually the primary attractants to floral visitors. Chemical analysis of almond nectar and pollen in this study revealed that they contain the secondary compound amygdalin. Floral display often reflects pollinator characters, and almond flowers are accordingly designated as "bee flowers". A previous study in Israel showed that when almonds bloom early in the season they attract honeybees, but later in the season the bees shift toward other species that start blooming. In this study, we offered honeybees sugar solutions containing various concentrations of amygdalin. These preference experiments revealed that in mid-summer bees were not selective, whereas early in the summer they were more discriminating, and consumed faster the sugar solutions with the lower amygdalin concentrations. Possible roles of amygdalin in almond nectar and pollen are discussed.

Key words: Almond, *Amygdalus communis* L., secondary compounds, honeybees, nectar, pollen, pollination, amygdalin.

Introduction

Almond (*Amygdalus communis* L.) is a self-incompatible crop that requires cross-pollination for nut set (Tufts and Philip 1922, Kester and Griggs 1959, Thorp 1978, Delaplane and Mayer 2000). In Israel almonds are characterized by early blooming in the winter (February-March) and are mainly pollinated by honeybees (*Apis mellifera* L.). Eisikowitch and Lupo (1989) observed honeybees foraging in an almond orchard surrounded by fields of wild flowers, mainly white mustard (*Sinapis alba* L., Brassicaceae). In the beginning of the season, when no other species of plants were flowering, bees tended to visit the almond trees and to collect both nectar and pollen. However, later in the season, when wild flowers co-bloomed with the almonds, some of the honeybees abandoned the almonds and shifted to the wild flowers.

Such competition for honeybees is also known in other crops. Stephen (1958) found that pear (*Pyrus* spp.) orchards surrounded by *Sinapis alba* and *Stellaria* spp. flowers had low fruit set. The nectar of the latter two species contains a higher sugar concentration than that of the pear flowers and was preferred by honeybees. A similar competitive effect was seen in plum (*Prunus* spp.) orchards growing next to *Sinapis alba* (Vansell 1952).

The almond flower is entomophylic; its fragrant petals attract insects, especially honeybees, with nectar located at a depth suitable for the proboscis length of the honeybee, and

pollen that can be easily collected (Faegri and van der Pijl 1979). Almond nectar is of low and variable sugar concentration, composed exclusively of glucose and fructose. Nevertheless, it is considered to be in the range consumed by honeybees (Baker and Baker 1983b).

The almond is a member of the Rosaceae, a family that is characterized by cyanogenic glycosides (Tewe and Iyayi 1989), which are typical secondary plant products with protective functions against herbivory (Raven et al. 1986, Selmar et al. 1988, Tewe and Iyayi 1989). When treated with acid or appropriate hydrolytic enzymes, these compounds produce toxic hydrocyanic acid (HCN). Most plants containing cyanogenic glycosides, also possess the enzymes necessary for their hydrolysis. Substrates and enzymes that are usually compartmented come together when the plant tissues are injured. Therefore, the products of hydrolysis are thought to be the actual toxicants for herbivores (Nahrstedt 1988).

It has been known since the early 19th century that wild almonds contain the cyanogenic glycoside amygdalin in their seeds and fruit pulp (Lechtenberg and Nahrstedt 1999). Secondary compounds are also found in the pollen and nectar of other species (Baker and Baker 1975, Adler 2000a). For example, digestion by honeybees of the nectar of *Astragalus miser* var. *serotinus* (Fabaceae) releases the toxic compound 3-nitro-1-propanol (Majak et al. 1980, Majak and Pass 1989). Sharma et al. (1986) noticed that the toxic nectar of tea plants (*Camellia thea* L.) caused the death of honeybee colonies. *Sophora microphylla* (Fabaceae) (Clinch et al. 1972) and *Senecio jacobaea* (Asteraceae) (Deinzer et al. 1977) contain alkaloids in their nectar. The pollen and nectar of *Tilia* spp. (Tiliaceae) contain mannose, a sugar toxic to insects (Vogel 1978). The pollen of *Zygadenus paniculatus* (Liliaceae) causes severe intoxication to honeybees and can also lead to the death of the colony (Goolsbey 1998).

It seems that bees refrain from visiting almond flowers when other flowers are available, so we decided to examine whether amygdalin is also present in the nectar, pollen and honey of almond flowers. We also tested how various concentrations of amygdalin in sucrose solution affect the attractiveness to honeybees.

Material and methods

Research site

Field observations were conducted in a commercial almond orchard in Kibbutz Yizrael in the Yizrael Valley, Israel. The area of the orchard is 120 hectares. We focused on three of the most common cultivars: Ne-Plus Ultra (NPU), Mem-Dalet (MD) and Um-El-Phahem (UEP).

Nectar, pollen and honey collection

Newly opened almond flowers of three cultivars were covered with ventilated plastic bags at 08:00. Nectar was collected at noon on 3, 5, 8 and 10 March 2000 by using 1 µl microcapillaries (Bardram, CHR Denmark). Ten µl, from as many flowers as were required, were pooled to one Eppendorf test tube containing 90 µl of 50% ethanol and stored at 4°C until chemical analysis. Nectar of white mustard flowers was collected by the same method on 7 and 11 April 2000, when the white mustard started to bloom. Twenty test tubes were collected from the MD and NPU almond cultivars, eleven from the UEP almond cultivar, and thirteen from white mustard.

Pollen pellets were collected from pollen traps placed at the entrance of a honeybee hive. Almond and white mustard pollen were identified and separated under a microscope, and kept at room temperature until chemical analysis. In order to determine the amygdalin content in honey, we collected ripe and fresh liquid honey from three hives. These hives were not supplemented with sugar feeding during the entire season. Honey samples were kept frozen (−10°C) until chemical analysis.

Chemical analyses

Sugar concentration in nectar of almond and white mustard flowers

HPLC chemical analysis was performed according to the Bio-Rad Company protocol for sugar identification. Nectar samples of 50 µl were taken

from each of ten test tubes of MD and NPU almond nectar, one test tube of UEP almond and nine test tubes of white mustard nectar. Samples were passed through a 0.2 μm syringe filter into an autosampler vial before HPLC analysis. Analysis was done at 55°C, with 0.01 N sulfuric acid eluant in a Biorad Aminex HPX-87H column, at a flow rate of 0.6 ml/min, for 50 minutes. A refractive index detector was used.

Amygdalin concentration in nectar and pollen

Ten nectar samples from each almond cultivar and four of white mustard were analyzed. A pollen sample from each plant source was powdered with mortar and pestle just prior to chemical analysis. The pollen powder was extracted into water in an ultrasonic bath for 15 minutes, mixed and filtered through a 0.45 μm membrane filter. The clear samples were injected to the HPLC. Nectar samples that were stored with 50% ethanol were injected to HPLC. Amygdalin concentrations in nectar and pollen were determined by HPLC according to Wasserkrug and El Rassi (1997). Concentrations were determined by comparing with known 5 ppm standards of amygdalin (Sigma, D-Amygdalin from apricot kernels, 99% A-6005).

Amygdalin concentration in almond honey

The larger volume of honey samples, relative to nectar and pollen, allowed using a colorimetric method, which is more sensitive than HPLC. One gram of almond honey was extracted with 1 M phosphate buffer. In order to perform the enzymatic reaction, 2.6 ml of the extract was placed in a Conway diffusion dish with 1.25 ml of beta-glucosidase and 2 ml of 0.1 M NaOH. The dishes were covered with paraffin and incubated for 4 h at 35°C. After incubation the solution was transferred to an Ehrlenmeyer flask with phosphate acetate buffer, pH 4.5, chloramine-T and pyridine reagent. A violet color appeared as a result of the reaction and its absorption at 578 nm was determined with a spectrophotometer.

Preference experiments with honeybees

Experiments with honeybees were performed in order to determine their preferences for solutions of the same sucrose concentration that differed in amygdalin content.

Early summer experiments

Early summer experiments were conducted in the Botanical Gardens of Tel-Aviv University on 6–9 June 2000, while bees could forage on a large variety of nectar sources. These experiments simulated the situation at almond orchards when competition from wild flowers is most intense. The consumption rates by honeybees of sucrose solutions with various amygdalin concentrations were examined. Four experiments were performed, each with a different range of amygdalin concentrations: 0–10,000, 0–1,000, 0–100, and 0–10 ppm. We added 2.5 g of amygdalin to 250 ml of a 25% w/w sucrose solution to form a stock solution of 10,000 ppm amygdalin. The stock solution was diluted with 25% w/w sucrose solution to form the lower concentrations of amygdalin.

Honeybees were trained on a table a few meters from their hives. In each experiment, five containers (8.5 cm in diameter, 3.5 cm deep) were placed randomly in a circle on the table: four of them with an increasing concentration of amygdalin, and one containing only sucrose solution with no amygdalin, as a control. The containers were weighed before the experiment and at regular intervals during the experiment. After each weighing, they were replaced on the table in random order, in order to prevent the bees from associating the containers with a certain position. The experiment ended when the bees had consumed all the solution in one of the containers. We regularly checked around the hives for bee mortality, for up to several days after the end of the experiments.

Mid-summer experiments

To simulate the situation at the beginning of the almond blooming season, when only few other nectar sources are available, we repeated preference experiments with honeybees in the Botanical Gardens of Tel-Aviv University on 25 July and 1 August 2000. This season was characterized by a shortage in nectar sources, and when provided with a 25% sucrose solution, bees soon crowded the containers and showed robbing behavior. We therefore conducted the experiments with a 15%

sucrose solution. We examined the rate at which honeybees consumed amygdalin concentrations in the range of 0–200 ppm. On each of the two days in which the experiment was conducted, we presented three tables simultaneously (total of six replicates), each holding five containers with an increasing range of amygdalin, and one control container with no amygdalin.

Since replicates lasted different lengths of time, for each replicate we calculated a rate of consumption for each amygdalin concentration relative to the duration of that replicate. We then calculated mean relative consumption rates for the six replicates after 30%, 60% and 90% of the duration of each replicate.

Results

Chemical analysis of nectar, pollen and honey

Sugar concentrations in nectar of almond and white mustard flowers

The nectar of all almond cultivars and of white mustard contained glucose and fructose in a 1:1 ratio. No sucrose was detected in either species. One-way ANOVA revealed a significant effect of nectar origin on the concentration of glucose ($F_{2,26} = 10.4$, $P = 0.0005$) and fructose ($F_{2,26} = 11.0$, $P = 0.0003$). Tukey test ($p < 0.05$) revealed that the concentrations of both fructose and glucose in MD almond were greater than those in NPU almond and white mustard. UEP almond was not included in the statistical analysis since we had only one sample (which was composed of many flowers), but its sugar concentration was similar to that of NPU almond (Fig. 1).

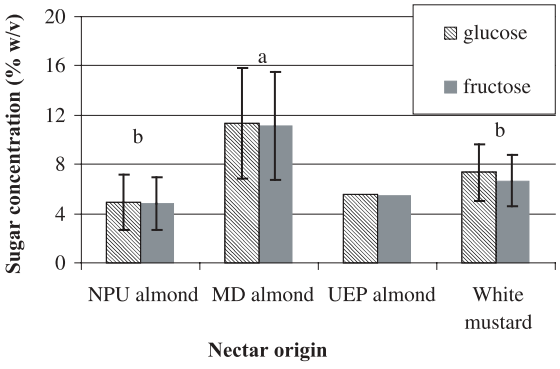

Fig. 1. Mean glucose and fructose concentration (w/v) in nectar of three almond cultivars and white mustard as measured by HPLC. Vertical lines represent standard errors

Amygdalin concentration in nectar, pollen and honey

The highest amygdalin concentration detected in almond nectar was that in MD, next was UEP, and the lowest was NPU, although these differences were not significant. Fresh almond honey contained lower amygdalin concentrations than the nectar. The amygdalin content of ripe almond honey was intermediate between those of nectar and fresh honey. An extremely high concentration of amygdalin was found in almond pollen. No amygdalin was found in white mustard nectar or pollen (Table 1).

Preference experiments with honeybees

Early summer experiments

In the three early summer experiments with the higher ranges of amygdalin, the control solution with no amygdalin and the lowest con-

Table 1. Mean, standard error and coefficient of variation of amygdalin concentrations in nectar, pollen and honey. Sample size, N, is the number of test tubes analyzed

Origin of sample	Amygdalin Content			
	Mean (ppm)	N	SE	Coefficient of variation
MD almond nectar	6.7	10	3.11	1.47
NPU almond nectar	4.9	10	1.52	0.98
UEP almond nectar	5.5	10	1.54	0.89
Fresh almond honey	2.9	2	0.14	0.05
Ripe almond honey	3.17	3	0.67	0.21
Almond pollen	1889	1		
White mustard nectar	0	4		
White mustard pollen	0	1		

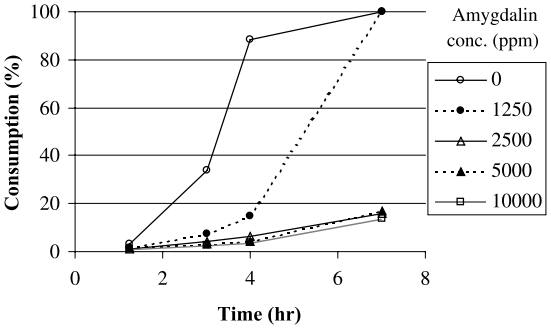

Fig. 2. Consumption by honeybees of sucrose solutions containing amygdalin concentrations of 0–10,000 ppm in the early summer experiments

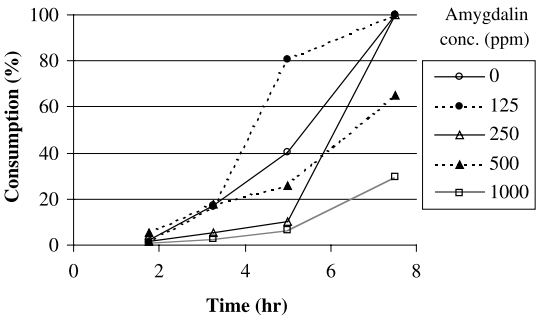

Fig. 3. Consumption by honeybees of sucrose solutions containing amygdalin concentrations of 0–1,000 ppm in the early summer experiments

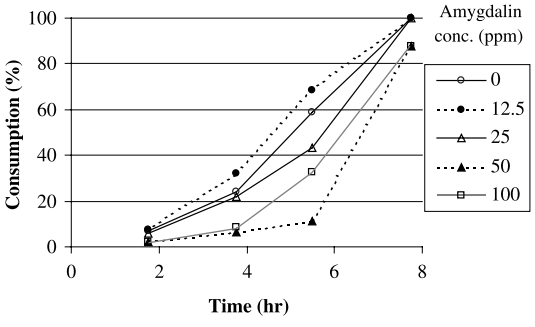

Fig. 4. Consumption by honeybees of sucrose solutions containing amygdalin concentrations of 0–100 ppm in the early summer experiments

centration of amygdalin were consumed the fastest, and the highest concentrations of amygdalin were consumed the slowest

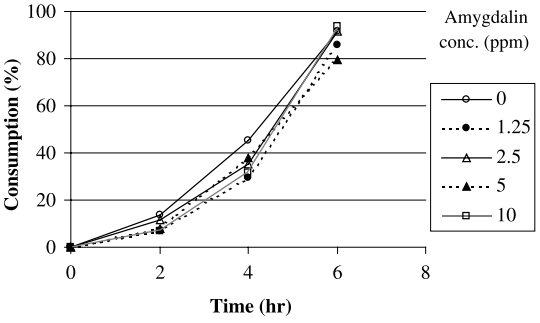

Fig. 5. Consumption by honeybees of sucrose solutions containing amygdalin concentrations of 0–10 ppm in the early summer experiments

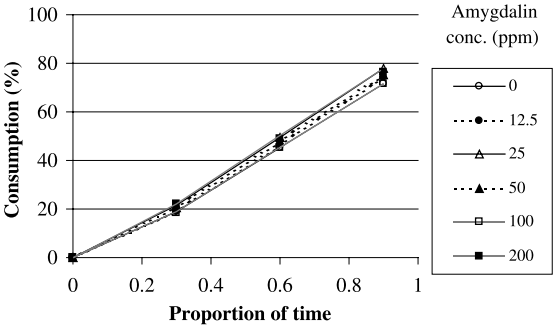

Fig. 6. Consumption by honeybees of sucrose solutions containing amygdalin concentrations of 0–200 ppm (n = 6) in the mid-summer experiments

(Figs. 2–4). The differences in consumption rates tended to be most pronounced for the largest amygdalin concentration range (1–10,000 ppm), and to decrease as the amygdalin concentration range narrowed. For the limited range of 1–10 ppm, there were no clear differences in consumption rates, except that the control was still consumed the fastest (Fig. 5). No dead bees were found near the hives during the experiments, and no decrease in the bee population was apparent.

Mid-summer experiments

Though the sucrose concentration in the containers in the mid-summer experiments (15%) was less than that in the early summer experiments (25%), bees consumed the solution in mid-summer in less than half the time (< 3 hr) it

took them in early summer (> 6 hr). There were no differences in relative consumption rates of the various amygdalin concentrations in the mid-summer experiments (Fig. 6).

Discussion

Chemical analysis of nectar, pollen and honey

Floral nectars are mixtures of natural products consisting primarily of sugars, with lesser amounts of amino acids, proteins, lipids, salts, and organic acids (Baker and Baker 1983a). Benedek and Nyeki (1997) found that the rate at which bees visited flowers was positively correlated with the nectar sugar concentration in various cultivars of Rosaceae. Sugar concentration, volume and caloric value of the nectars of several almond cultivars has been found to be positively correlated with honeybee foraging levels (Abrol 1995). We found the highest sugar concentration in the MD cultivar, which is also the most attractive cultivar to honeybees (London 2001). This cultivar also had higher sugar concentrations than white mustard. The other almond cultivars that we tested had similar sugar concentrations to those of white mustard. Hence, the lesser attractivity of almond relative to white mustard cannot be due to differences in sugar concentration.

The nectars of the three almond cultivars contained glucose and fructose in a 1:1 ratio, and did not contain any sucrose. This composition is typical for nut fruits that bloom early in the spring (Orosz-Kovacs et al. 2000). These monosaccharides are favorable to bees because they are easy to digest (Harborne 1982). Therefore, it does not appear that the sugar composition of almond nectar should reduce its attractivity to bees. Furthermore, white mustard nectar was also found to contain a 1:1 ratio of glucose and fructose, and no sucrose. The lesser attractivity of almond relative to white mustard cannot be due to differences in the composition of these sugars in the nectar.

Specific constituents of nectars, such as phenols and alkaloids, can influence the preferences of foragers (Waller et al. 1972, Hagler and Buchmann 1993). We found the cyano-glycoside amygdalin in the nectar of all three almond cultivars tested, and not in the nectar of white mustard. There was also amygdalin in the honey of colonies that foraged in the almond orchard. The amygdalin levels in the nectar and in the honey were below the lethal threshold for honeybees, since we did not detect any unusual levels of bee mortality. We suspected, however, that amygdalin deters bees, and that these concentrations are high enough to explain the preference for white mustard flowers over almond in the almond orchard.

Preference experiments with honeybees

In early summer bees consumed the solutions with the lower amygdalin concentrations more quickly than those with the higher amygdalin concentrations, whereas in midsummer the bees did not differentiate among various amygdalin concentrations. We offer the hypothesis that the difference in the behavior of honeybees between these two seasons results from differences in pollen and nectar supplies; the summer is much poorer in floral resources than the preceding season. The preference experiments showed that honeybees are able to distinguish among various concentrations of amygdalin, and prefer not to consume it as long as they have alternatives.

The highest coefficient of variation of amygdalin concentration was found in the MD almond, which is also the most attractive cultivar (London 2001). Honeybees prefer less variable nectar volumes to more variable ones (Shafir et al. 1999) and, in general, animals prefer constant amounts of food to variable ones, even if the mean amounts are similar (Shafir 2000). The preference for the cultivar that is most variable in amygdalin concentration may be explained by the fact that animals prefer the more variable option when the variation involves an aversive parameter, such as reward delay (Kacelnik and Bateson 1996). Thus, the higher variability of amygdalin levels in the MD cultivar may reduce its deterrent effect on bees.

The highest concentration of amygdalin was found in almond pollen: 1,889 ppm on average. It is possible that the amygdalin found in the nectar originated from pollen grains that fell into the nectar (Harborne 1982, Gottsberger et al. 1989, Erhardt and Baker 1990). Such an explanation is consistent with the large variability in amygdalin concentration found in almond nectar samples (Table 1), and the absence of amygdalin in some samples. No amygdalin was found in white mustard pollen or nectar.

The presence of secondary compounds in nectar and pollen suggests several hypotheses. Adler (2000b) claimed that resistance traits of plants, such as secondary compounds, can increase plant fitness, directly by reducing herbivore attack and indirectly by increasing pollinator visitations to defended plants. The presence of secondary compounds in nectar and/or pollen may also enhance plant fitness by attracting more specialized pollinators. Monocrotaline, a pyrrolizidine alkaloid, attracts specialist butterflies that seek these compounds for mate attraction and defense, while it deters other more generalist species of butterflies (Masters 1968, 1991). Similarly, Stephenson (1981, 1982) showed that iridoid glycosides of *Catalpa speciosa* increase floral constancy by inhibiting nectar thieves but not legitimate pollinators. These findings suggest that the presence of cyanogenic glycosides in nectar and pollen of almond flowers might inhibit inefficient pollinators or nectar "robbers". Honeybees, as the most efficient pollinators of almonds, can probably tolerate the toxicity of amygdalin, up to a certain level.

Izhaki (1992) found that frugivorous birds could shift from one fruit to another to avoid ingesting excessive levels of a single secondary compound. Similarly, it may be that the toxic effect of amygdalin forces the bees to increase their pattern of movements between trees, and thus improving the chance of the almond tree for cross-pollination.

It seems that in comparison with other flower species, the ability of almond flowers to attract honeybees is low. It may be that when floral nectar resources are scarce, bees have no alternative but to collect their food even from almond flowers. However, when other species start to bloom, bees will prefer to visit them, and will neglect the almond flowers.

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References

Abrol D. P. (1995) Energetics of nectar production in some almond cultivars as a predictor of floral choice by honeybees *Apis cerana indica* F. and *Apis mellifera* L. (Hymenoptera: Apidae). Proceedings of the Indian National Science Academy Part B Biological Sciences 61: 285–289.

Adler L. S. (2000a) The ecological significance of toxic nectar. Oikos 91: 409–420.

Adler L. S. (2000b) Alkaloid uptake increases fitness in hemiparasitic plant via reduced herbivory and increased pollination. Amer. Nat. 156: 92–99.

Baker H. G., Baker I. (1975) Studies of nectar-constitution and pollinator-plant coevolution. In: Gilbert L. E., Raven P. H. (eds.) Coevolution of plants and animals. University of Texas Press, Austin, pp. 100–140.

Baker H. G., Baker I. (1983a) Floral nectar sugar constituents in relation to pollinator type. In: Jones C. E., Little R. J. (eds.) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp. 117–141.

Baker H. G., Baker I. (1983b) A brief historical review of the chemistry of floral nectar. In: Bentley B. L., Elias T. (eds.) The biology of nectaries. Columbia University Press, New York, pp. 126–152.

Benedek P., Nyeki J. (1997) Considerations on the nectar production and the honeybee visitation of fruit tree flowers. Hort. Sci. 29: 117–122.

Clinch P. G., Palmer-Jones T., Forster I. W. (1972) Effect on honey bees of nectar from yellow

kowhai (*Sophora microphylla* AIT) N.Z.J. Agric. Res. 15: 194–201.

Deinzer M. L., Thomson P. A., Burgett D. M., Isaacson D. L. (1977) Pyrrolizidine alkaloids – Their occurrence in honey from tansy ragwort (*Senecio Jacobaea* L.) Science 195: 497–499.

Delaplane K. S., Mayer D. F. (2000) Crop pollination by bees. CABI, Cambridge, UK.

Eisikowitch D., Lupo A. (1989) Wild flowers as competitors for pollinators in almond orchards. Alon Hanotea 12: 1307–1312 (In Hebrew).

Erhardt A., Baker I. (1990) Pollen amino acids – an additional diet for a nectar feeding butterfly? Plant Syst. Evol. 169: 111–121.

Faegri K., van der Pijl L. (1979) The principles of pollination ecology, 3rd revised edition. Pergamon Press, Oxford.

Goolsbey A. (1998) Poison pollen from *Z. paniculatus*. Amer. Bee J. 138: 459–460.

Gottsberger G., Arnold T., Linskens H. F. (1989) Variation in floral nectar amino acids with aging of flowers, pollen contamination, and flower damage. Israel J. Bot. 39: 167–176.

Hagler J. R., Buchmann S. L. (1993) Honey bee (Hymenoptera: Apidae) foraging responses to phenolic-rich nectars. J. Kansas Entomol. Soc. 66: 223–230.

Harborne J. B. (1982) Introduction to ecological biochemistry. 2nd edition. Academic Press, London.

Izhaki I. (1992) A comparative analysis of the nutritional quality of mixed and exclusive fruit diets for yellow-vented bulbuls. Condor 94: 912–923.

Kacelnik A., Bateson M. (1996) Risky theories – the effects of variance on foraging decisions. Amer. Zool. 36: 402–434.

Kester D. E., Griggs W. H. (1959) Fruit setting in the almonds: The effect of cross pollinating various percentages of flowers. Proc. Amer. Soc. Hort. Sci. 74: 206–213.

Lechtenberg M., Nahrstedt A. (1999) Cyanogenic glycosides. In: Ikan R. (ed.) Naturally occurring glycosides. John Wiley and Sons, Chichester, pp. 147–191.

London I. (2001) Competition for pollination between cultivated almonds and wild flowers. M.Sc. Thesis, Tel Aviv University, Israel. (In Hebrew).

Majak W., Pass M. A. (1989) Aliphatic nitrocompounds. In: Cheeke P. R. (ed.) Toxicants of plant origin. Volume II. CRC Press, Boca Raton, pp. 143–159.

Majak W., Neufeld R., Corner J. (1980) Toxicity of *Astragalus miser* v. *serotinus* to the honeybee. J. Apic. Res. 19: 196–199.

Masters J. H. (1968) Collecting Ithomiidae with heliotrope. J. Lepidop. Soc. 22: 108–109.

Masters A. R. (1991) The dual role of pyrrolizidine alkaloids in nectar. J. Chem. Ecol. 17: 195–205.

Nahrstedt A. (1988) Cyanogenesis and the role of cyanogenic compounds in insects. In: Ciba Foundation Symposium 140: Cyanide compounds in biology. John Wiley and Sons, Chichester.

Orosz-Kovacs Z., Szabo L. G., Buban T., Farkas A., Bukovics P. (2000) Sugar composition of floral nectar in sour cherry cultivars. Int. J. Hort. Sci. 6: 109–113.

Raven P. H., Evert R. F., Eichhorn S. E. (1986) Biology of Plants. Fourth edition. Worth Publishers, Inc., New York, pp. 616–618.

Selmar D., Lieberei R., Biehl B. (1988) Mobilization and utilization of cyanogenic glycosides. Plant Physiol. 86: 711–716.

Shafir S., Wiegmann D. D., Smith B. H., Real L. A. (1999) Risk-sensitive foraging: choice behaviour of honeybees in response to variability in volume of reward. Anim. Behav. 57: 1055–1061.

Shafir S. (2000) Risk-sensitive foraging: the effect of relative variability. Oikos 89: 663–669.

Sharma O. P., Raj D., Garg R. (1986) Toxicity of nectar of tea (*Camellia thea* L.) to honeybees. J. Apic. Res. 25: 106–108.

Stephen W. P. (1958) Pear pollination studies in Oregon. Bull. Ore. Agric. Exp. Stn. 43.

Stephenson A. G. (1981) Toxic nectar deters nectar thieves of *Catalpa speciosa*. Am. Midl. Nat. 105: 381–383.

Stephenson A. G. (1982) Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. J. Chem. Ecol. 8: 1025–1034.

Tewe O. O., Iyayi E. A. (1989) Cyanogenic glycosides. In: Cheeke P. R. (ed.) Toxicants of plant origin. Volume II. CRC Press, Boca Raton, pp. 43–60.

Thorp R. W. (1978) Honey bee foraging behavior in California almond orchards. Proc. IVth symp. on pollination Md. Agric. Exp. Sta. Spec. Misc. Publ. 1: 385–392.

Tufts W. P., Philip G. L. (1922) Almond pollination. California Ag. Exp. Stn. Bull. no. 346.

Vansell G. H. (1952) Variations in nectar and pollen sources affect bee activity. Amer. Bee J. 92: 325–326.

Vogel S. (1978) Floral ecology. Progress in Botany 40: 453–481.

Waller G. D., Carpenter E. W., Ziehl O. A. (1972) Potassium in onion nectar and its probable effect on attractiveness of onion flowers to honey bees. J. Amer. Soc. Hort. Sci. 97: 535–539.

Wasserkrug K., El Rassi Z. (1997) High performance liquid phase separation of glycosides. 1. Reversed phase chromatography of cyanogenic glycosides with UV and pulsed amperometric detection. J. Liq. Chromatog. Rel. Technol. 20: 335–349.

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