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POLLINATION OF SUNFLOWER BY HONEY BEE: REVIEW

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Sunflower oil importance, cultivation history, floral anatomy, flowering physiology, evolutionary adaptations of sunflower for insect cross-pollination and behavior of honey bees at its visiting are described. This plant has long, interesting and confusing history with rediscovering its seed oility and repatriation in form of big headed oil cultivars in North America. Sunflower inflorescence consists of unisexual sterile ray florets with showy big petals that attract pollinators and bisexual fertile disc florets that produce seed. Its flowering develops by gradually opening of florets rows with transition from staminate male to pistillate female stage. In nature sunflower is an insect cross-pollinated plant. Quantity and quality of sunflower seed yield still strongly depend on honey bee pollination even in case of modern autofertile hybrids and significantly increases under presence of this ecosystem service. Disk florets produce nectar and pollen which play role of reward for pollination. Sunflower nectaries are located at style base directly above floret ovary. They secret nectar which bees use as raw for honey production. Sunflower anthers produce large quantities of pollen. In addition to reproductive function it is used for bee foraging too. This pollen has high energy value due to fatty acids presence (mainly lauric, palmitic and α-linolenic) but deficit of proteins and essential amino acids (methionine and tryptophan) makes low its total nutrient value. Ultraviolet target pattern of sunflower inflorescence guides bees from side to center of inflorescence. They deposit pollen which collected from another heads when move among stigmas of pistillate stage florets rows and then reach staminate stage florets rows for nectar and pollen collection. In addition, permanently are being breeded a lot of new autofertile sunflower hybrids that requires estimation their melliferous potential and also its comparing with old cross-pollinated cultivars. *Key words:* sunflower, honey bee, pollination.

Запилення соняшника медоносною бджолою: огляд. Шпак Я.В., Сосновський К.С., Буркут В.І., Зароченцева О.Д., Жук А.В., Федоряк М.М.

Описано значення соняшникової олії, історію вирощування, квіткову анатомію, фізіологію цвітіння, еволюційні пристосування соняшника для перехресного комахозапилення та поведінку бджіл при його відвідуванні. Ця рослина має довгу, цікаву й заплутану історію з перевідкриттям олійності його насіння і репатріацією у формі крупнокошикових олійних сортів у Північній Америці. Суцвіття соняшника складається з одностатевих безплідних несправжньоязичкових квіток з показними великими пелюстками, що приваблюють запилювачів і двостатевих плідних трубчастих квіток, що продукують насіння. Його цвітіння розвивається поступовим відкриттям квіток з переходом із чоловічої тичинкової стадії в жіночу приймочкову стадію. В природі соняшник є перехреснозапильною рослиною, що запилюється комахами. Кількість і якість урожаю насіння соняшника й досі сильно залежать від запилення медоносними бджолами навіть у випадку сучасних автофертильних гібридів та достовірно зростає за наявності цієї екосистемної послуги. Трубчасті квітки продукують нектар і пилок, що відіграють роль винагороди для запилювачів. Нектарники соняшника розміщені при основі стовпчика прямо над квітковою зав'яззю. Вони виділяють нектар, який бджоли використовують в якості сировини для виробництва меду. Пиляки соняшника виробляють велику кількість пилку. На додачу до репродуктивної функції він використовується бджолами в якості корму. Цей пилок має високу енергетичну цінність через наявність жирних кислот (головним чином лауринової, пальмітинової та α-ліноленової), але дефіцит білків та незамінних амінокислот (метіоніну й триптофану) знижує його поживну цінність. Ультрафіолетовий цільовий візерунок соняшникових суцвіть проводить бджіл від краю до середини кошикового диска. Вони відкладають пилок, який зібрали при відвідуванні інших кошиків під час руху міжряддями приймочок квіток у жіночій стадії, а потім досягають квіток у чоловічій стадії для збору нектару й пилку. На додачу, постійно виводять багато нових автофертильних гібридів соняшника, що вимагає оцінки їх потенційної медодайності, а також її порівняння зі старими перехреснозапильними сортами. *Ключові слова:* соняшник, медоносна бджола, запилення.

Problem statement. A synthetic review of sunflower evolutionary adaptations for cross bee pollination in context of ecological coaction is necessary for conscious effective management of this ecosystem service (pollination of sunflower crops by honey bees).

Topicality of the research. Sunflower (*Helianthus annuus* L.) is one of the most important plants among oilseed crops in the world. Its oil is very popular due to light taste, the stability at high cooking temperatures, the absence of cholesterol, high contents of unsaturated fatty acids and vitamin E [1; 2, p. 85; 3; 4]. This crop is pollinator-dependent and needs insects for cross-pollination. Honey bee (*Apis mellifera* L., 1758) is the most numerous and effective among its pollinators (fig. 1).

Sunflower honey is tasty, good looking and widespread due to big areas of sunflower crops and long period their flowering [5-10]. It is interesting that Ukraine is one of the biggest exporters of sunflower oil [11; 12] and honey [13] in the world simultaneously. Also beekeepers are interested in melliferous potential of modern autofertile sunflower hybrids [14].

Connection of the author's research with important scientific and practical tasks. The research is performed in frame of research project No. 0122U001217 "Monitoring and optimization of ecosystem services

Fig. 1. Honey bees which are visiting inflorescence of sunflower. Photo taken by Dr. Yaroslav Shpak

under conditions of destructive agroindustrial impacts based on the concept of socioecological system".

Analysis of recent researches and publications. In papers [7; 9; 10] is emphasized current meaning of pollination by honey bee for sunflower seed yield. Study [11] highlights significance of sunflower cultivation and its oil production for Ukraine. Article [13] tells about history, modern level, problems and Ukrainian potential of honey production. Work [4] is devoted to sunflower adaptations for attraction of pollinators. Researches [5; 6] describe particularities of sunflower nectar productivity.

The specification of previously unresolved parts of the general problem, the article is devoted to. Majority of previous papers that devoted to pollination of sunflower by honey bee are analytical and describe this topic outside of ecological and evolutionary contexts.

Novelty. Synthetic literature review of sunflower adaptations for bee pollination in ecological context is performed.

Methodological and scientific significance. Studying of sunflower floral anatomy and flowering physiology is needed for performing of practical nectar productivity estimation. Syntetical review of sunflower adaptations for bee pollination is important for modern agroecology.

Presentation of the main material. Sunflower belongs to Compositae (Asteraceae) family [15]. The word "helianthus" is derived from the Greek words "helios", meaning sun, and "anthus", meaning flower. The sunflower plant origins from eastern North America [16]. Archaeologists state that Native Americans began to cultivate sunflower more than four millenniums ago. Locals even squeezed oil from its seeds long time prior to European colonization. Sunflower was taken to Europe by Spanish explorers in 1500s and was utilized widespread for ornamental and medicinal purposes [2]. The first European record of using sunflower seed as a source of oil is an English patent No. 408, in 1716, granted to Arthur Bunyan. Sunflower seeds came into Russian Empire from the Netherlands in the 18th century. The first suggestion of extracting oil from the seed was recorded in the proceedings of the Russian Academy in 1779. Inadvertently the Orthodox Church of Russian Empire may have encouraged sunflower as an oilseed because Strict Lenten regulations prohibited many oil foods, but they omitted specific mention of sunflower. Consequently sunflower oil became popular as a food [17]. In the mid-twentieth century after great breeding efforts to increase the oil content in Soviet Union, sunflower turned into one of the most important oil crops in the world [2; 9; 16]. Sunflower inflorescence is located at the head (also known as "capitulum") which is surrounded by three rows of involucral bracts for protecting during development. There are two florets (individual inflorescence flowers, also known as "flowers" too) types of sunflower: showy zygomorphic *ray florets* (also known as "ligulate" or "pistillate" florets/flowers) at the head edge and actinomorphic *disc florets* (also known as "perfect" or "hermaphrodite" florets/flowers) wich are located on the remainder head place (fig. 2).

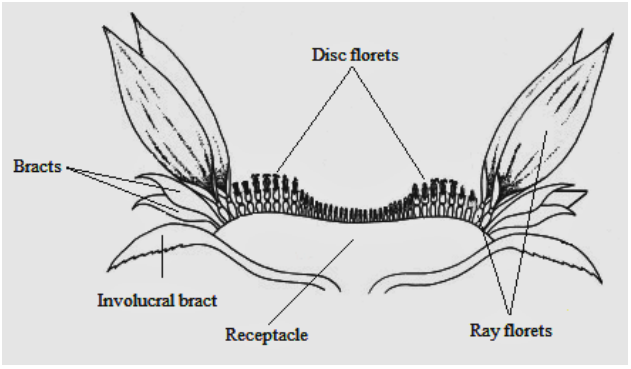

Fig. 2. Longitudinal section of sunflower head.
Adapted from [15, p. 3].

Unisexual ray flowers are *sterile*, although they have a *pistil*. Their big petals are usually golden yellow and also may be pale yellow, orange-yellow, reddish or even white. The sunflower disc at flowering has florets transition from pistillate to staminate stage (fig. 3).

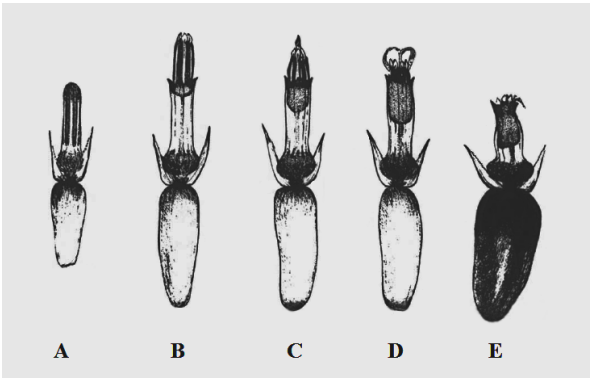

Fig. 3. Stages of sunflower floret maturation: A – unopened bud; B – staminate; C – transitional; D – pistillate; E – wilted
Adapted from [18].

Bisexual disc florets with pistil and *stamen* are *fertile* (fig. 4)

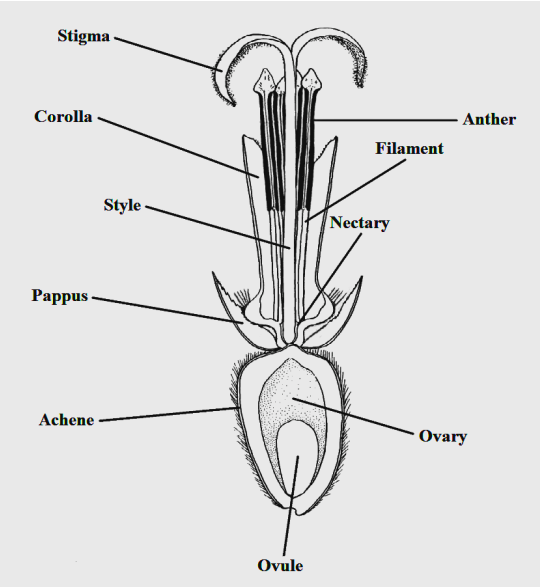

Fig. 4. Longitudinal section of sunflower disc floret in pistillate stage

Adapted from [19].

Their *corolla* (except at the tip) consists of five fused petals. Five fused *anthers* in the corolla tube form the second tube with separate *filaments* which attached to the base. The *style* is enclosed in the anther tube and terminated distally in the bilobed *stigma* which is curled outward above the anther tube [16, p. 21; 17, p. 85; 20-22]. In different papers the disk of the sunflower inflorescence conventionally is divided into 3 regions (also known as "zones"/"circles"/whorls), where each occupies 1/3 its radius. In fact, it contains florets rows that form spiral pattern wich closely is connected to the Fibonacci sequence (fig. 5, 6).

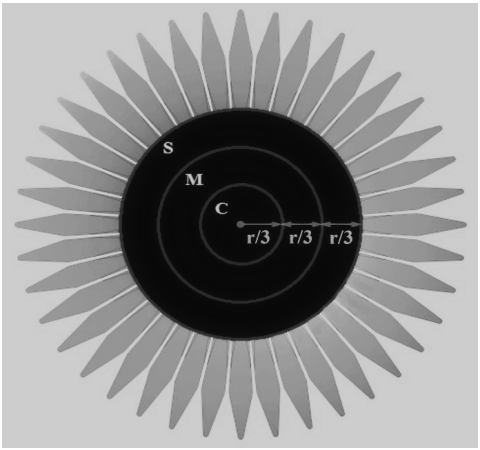

Fig. 5. Regions of sunflower head: S – side; M – middle; C – central

Adapted from [3].

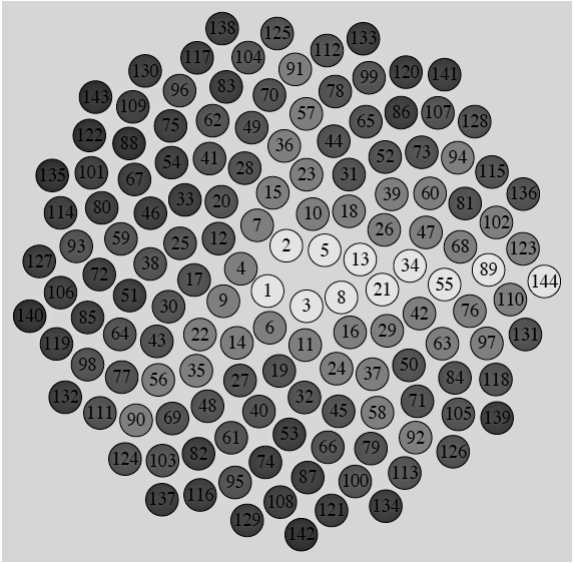

Fig. 6. Nodes of the sunflower spiral according to the Fibonacci metric

Adapted from [23].

The flowering (with staminate to pistillate stage transition) starts in side (also known as "outmost whorl", "outer circle", "periphery"), continues in middle (also known as "middle whorl", "middle circle", "middle") and finishes in central region (also known as "inner whorl", "inner circle", "center") of sunflower disc. Typical sunflower head has next florets rows toward from side to center: wilted → staminate stage → pistillate stage → unopened. The flowering takes 5 to 10 days for single disc. Usually its florets are open for 2 days. On the 1 day, in the anther tube is released own anthers pollen, on the 2 day, any pollen mass remaining is pushed up through the stigmas, then their lobes open outward. They are receptive for another florets pollen, but unattainable for own pollen. The sunflower florets wilt soon after the pollination. Their fertility can holds even 2 weeks at pollinators absence, but durative waiting of pollination reduces seed quantity and quality [1; 3; 19, p. 345-346; 21; 23; 24]. Naturally sunflower is an insect pollinated plant, and the lack of pollinators causes development of unfertilized seeds which have hulls without kernels [5; 25]. It is self-incompatible and needs coming of pollen from another plants because fertilization between florets of same head worsens size, oil content and germination of seed. No exact quantity of honey bees for maximum seed productivity is known. For estimatin of pollination activity count bees quantity per: sunflower head/ crops area or quantity their colonies per crops area unit [19, p. 346-348]. The sunflower has different adaptations for attraction of pollinators. Particulary, its inflorescence has *UV (ultraviolet) target pattern* which are visible for compound eyes of bees (fig. 7).

It guides them toward from side to center of inflorescence. Bees move through rows of pistillate stage florets, thus deposite the pollen collected at previous

Fig. 7. Sunflower inflorescence photographed in visible light (left) and under UV-lighting (right)
Adapted from [26, p. 93].

visitations of another inflorescences, before reaching pollen of staminate stage florets which are located in head central region [21; 22; 26, p. 93]. *Ffloral nectar* (also known as "flower nectar") of sunflower is secreted from the *nectaries* at style base directly above the ovary, mainly at staminate stage but to pistillate stage while the stigmas are still receptive. Timely nectar reward to bees facilitates incoming of pollen to receptive stigmas. Nectaries parameters vary among genotypes and impact on the florets attraction for pollinators. Nectar quality and quantity depend on size, shape and location density of nectaries stomates. Florets of highly attractive genotypes have large nectaries with more stomata than florets of less attractive ones. Sunflower nectar has high energy value due to presence of sugars, particularly fructose, glucose, raffinose and sucrose [5; 18; 21; 22]. *Extrafloral nectar (EFN)* is secreted by nectar-producing glands (also known as "extrafloral nectaries") apart from the flowers. Bees periodically collect it from the glands in bracts and on upper leaves of sunflower, particularly during the afternoon. They rarely collect floral nectar simultaneously with extrafloral nectar and never do it at the same visit of individual plant [27; 28].

Pollen of the sunflower is released from the anthers when open the staminate stage florets [19, p. 345-346]. It contains eight fatty acids which make up the half mass its lipids. The most abundant among them are lauric, palmitic and α-linolenic acids. Instead, amino acids and protein contents of sunflower pollen are relatively low compare to other important forage plants of bees. Particulary, contents of essential amino acids such as methionine and tryptophan in it, are likely below then minimum requirements for honey bees. This composition disbalance adversely affects on their development in case when the almost exclusive source of pollen are the sunflower crops [29]. The anthers tops of sunflower are covered by glandular and non-glandular trichomes which may are dehisced, dislodged or collected by insects at the foraging. Suggested that trichomes contain chemical agents that play role of "repelents" or "attractiants" [21]. Honey bees collect pollen mainly early in the morning and late afternoon, probably in the association with its availability. They actively scrape pollen from the anthers, others collect it incidentally during the collecting of nectar and either put it into their corbicula or discarded it. Often bees are dusting by pollen when collect nectar (fig. 8).

A few of them scrabble over the florets in the staminate stage for pollen without collecting nectar at same visits, but collect nectar at others. It is interesting that nectar-collecters with pollen visit more florets per head than nectar-collecters without pollen [27]. A lot of modern sunflower hybrids are the autofertile, because their self-incompatibility is decreased because of selection against this trait. Although they are less dependent on cross-pollination, honey bee service is still needed for improving quantity and quality their seed yield [8; 9; 30]. There is hypothesis that self-fertile hybrids have less melliferous potential then traditional cross-pollinated cultivars, but it still needs autoritetical affirmation [5; 6].

The main conclusions. Sunflower gradual row flowering and the male to female disk florets transition are

Fig. 8. A honey bee wich is dusted by sunflower pollen. Photo taken by Dr. Yaroslav Shpak

adaptations for cross-pollination. Big bright petals of ray florets, the ultraviolet target pattern and nectaries promote the atraction of insect pollinators. Sunflower gives nectar which honey bees use for production of quality honey. Instead, its pollen has relatively low total nutrient value that is caused by composition disbalance. Sunflower crops need honey bee pollination service for the obtaining of high seed yield.

Prospects for using the research results. In the future, theoretical information of this review is planned will use for the research of nectar productivity and melliferous potential of modern autofertile sunflower hybrids.

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