







# Progresses of the international community to understand sunflower–pollinator interactions through multiscale approaches<sup>☆</sup>

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**Abstract** – The first web conference on sunflower–pollinator interactions gathered the international community around a major topic for sunflower productivity and ecosystemic biodiversity. Insect-mediated pollination is important for increasing sunflower seed yield, but is dependent on environmental factors. Climate change can impact sunflower–pollinator interactions by influencing both plant and pollinator behavior. Natural or artificially elevated ambient temperatures appear to accelerate floret development and advance the timing of pollen presentation to coincide with pollinator activities. Drought showed no major effect on morphological traits such as anther or corolla length, but dramatically reduced nectar and pollen productions. Flavonol-glycoside conjugates lower head transpiration thereby mitigating deleterious effects of abiotic stresses. Wild pollinators show fine scale preferences among sunflower varieties, likely due to the different resource focus of wild and managed honeybees. Agricultural practices such as planting flower strips to provide nesting sites for wild pollinators, or supplementing crop plots with hives, can have a positive effect on insect-mediated pollination efficiency and ensure optimal yields. All together, recent results on sunflower–pollinator interactions pave the way to develop varieties and corresponding cropping systems more favorable to pollinator biodiversity while maintaining high yields in the context of climate change.

**Keywords:** pollinators / sunflower / attractiveness / drought / landscape

**Résumé** – Progrès le communauté internationale pour la compréhension des interactions tournesol pollinisateurs par une approche multi-échelle. La première conférence en ligne sur les interactions entre les tournesols et les pollinisateurs a réuni la communauté internationale autour d'un sujet majeur pour la productivité des tournesols et la biodiversité écosystémique. La pollinisation par les insectes est importante pour augmenter le rendement en graines de tournesol, mais elle dépend de facteurs environnementaux. Le changement climatique peut avoir un impact sur les interactions entre les tournesols et les pollinisateurs en influençant le comportement des plantes et des pollinisateurs. Les températures élevées (canicule ou de façon artificielle) accélèrent le développement des fleurons et avancent la présentation du pollen devant coïncider avec l'activité des pollinisateurs. La sécheresse n'a montré aucun effet majeur sur les traits morphologiques tels que la longueur des anthères ou des corolles, mais a considérablement réduit la production de nectar et de pollen. Les conjugués de flavonol-glycosides réduisent la transpiration des capitules, pouvant ainsi atténuer les effets néfastes des stress abiotiques. Les pollinisateurs sauvages montrent des préférences à petite échelle parmi les variétés de tournesols, probablement en raison des

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différentes ressources auxquelles les abeilles sauvages et domestiques ont accès. Les pratiques agricoles telles que la plantation de bandes fleuries pour fournir des sites de nidification aux pollinisateurs sauvages, ou l'apport de ruches près des parcelles de culture, peuvent avoir un effet positif sur l'efficacité de la pollinisation par les insectes et garantir des rendements optimaux. Dans l'ensemble, les résultats récents sur les interactions entre les tournesols et les pollinisateurs ouvrent la voie au développement de variétés et de systèmes de culture plus favorables à la biodiversité des pollinisateurs tout en maintenant des rendements élevés dans le contexte du changement climatique.

**Mots clés** : pollinisateurs / tournesol / attractivité / sécheresse / paysage

### Highlights

- Landscape pattern, pollinator diversity and density impact sunflower pollination, yield, and seed production.
- Heat, drought, and floret morphology can limit pollen and nectar availability to pollinators.
- Molecular and genetic understanding of circadian clock floret development, and ligule color paves the way to breeding more pollinator-friendly sunflowers.

## 1 Introduction

Sunflower (*Helianthus annuus* L.) is originally self-incompatible and was domesticated 4500 years ago in eastern North America (Crites, 1993; Blackman *et al.*, 2011; Seiler *et al.*, 2017). In more recent times, sunflower productivity increased several times following the discovery of the Cytoplasmic Male Sterility (CMS) from *H. petiolaris* and the restorer line gene, which led to the development of the first hybrid cultivars in the 1980s (Leclercq, 1969, 1983). Despite the fact that sunflower can be largely self-fertile (Mallinger and Prasifka, 2017b), it remains pollinator dependent, and particularly dependent on the honeybee (*Apis mellifera*) to ensure pollen transfer from anthers to styles and seed production (Dag *et al.*, 2002; Perrot *et al.*, 2019). Nowadays, the sunflower, with 51 million metric tons produced in 2021 (World Agricultural Production Information 2021/2022), is the fourth largest oilseed crop in the world, and modern cultivars have essential agronomic qualities, including drought, cold, and heat tolerance. Sunflower also requires lower fertilizer and pesticide inputs compared to other crops, making it an attractive alternative for growers. It is cultivated worldwide, from tropical and sub-tropical (Chambó *et al.*, 2011; Castro and Leite, 2018) areas to continental, temperate, semi-arid (Ghanavati *et al.*, 1981) or Mediterranean climates (Bartual *et al.*, 2018). In each of these climates, the main pollinator for sunflower is the domesticated honeybee except in North America –from where sunflowers are originated– where native solitary and eusocial bees have co-evolved with sunflowers (Greenleaf and Kremen, 2006), and southeastern Asia where some other *Apis* species participate in sunflower pollination (Singh *et al.*, 2000; Said, 2018).

However, wild pollinators are facing adverse conditions worldwide, including mass extinction and the consequences of climate change (Thomann *et al.*, 2013), as well as destruction of natural or semi-natural habitats (Olynyk *et al.*, 2021). Managed honeybees are also experiencing declines

(Becher *et al.*, 2013) due to usage of pesticides in agricultural systems, management practices, and pests (Vanbergen and Initiative the IP, 2013; Panziera *et al.*, 2022; Simone-Finstrom *et al.*, 2022).

In this compelling context, both at the scientific and socio-economic levels, the research community joined for the *1st Sunflower–Pollinators Interaction Web-Conference*, on October 6th and 7th, 2021. Here, we present their main results and provide links to the talks on the International Sunflower Association's (ISA's) Youtube channel<sup>1</sup>. Sunflower–pollinator interaction with different perspectives, from the agronomical and environmental, the entomological, the global warming point of views, and from landscape to gene scales.

## 2 Agronomy and environment

Sunflower, with an abundant production of floral resources, is considered a Mass Flowering Crop (MFC), which has an important effect on pollinators' populations and diversity. International teams (INRAE, France; USDA and University of Florida, USA; FABI, South Africa; and LoginEKO, Serbia) adopt a range of approaches from ecology, biodiversity and agronomy to study this interaction from the plot to field scales.

### 2.1 Optimising spatial distribution of mass-flowering patches at the landscape scale to increase crop pollination

In Europe, the addition of wildflower strips is often recommended to promote crop pollination (Altieri *et al.*, 2015), but the addition of such wildflowers can have adverse effects on wild bees visitation rate on MFCs (Westphal *et al.*, 2003). Using landscape ecology, and modeling and simulation approach could help to increase crop pollination. Some hypotheses have been proposed to explain such puzzling results: (i) the number of pollinators is diluted (Holzschuh *et al.*, 2016) with the number of MFC plots; (ii) wild flower plots can concentrate pollinators and distract bees from the crop (Bartomeus and Winfree, 2011); (iii) the distance between wild and crop floral resources can provoke “spillover” effect if placed near each other (Ganser *et al.*, 2018). In his talk, Desaegeher addressed two questions: “What is the optimal distance between existing crop fields and new floral plots to enhance crop pollination?” and “How does the quantity of nesting sites in additional floral plots modify the optimal location of new floral plots?” (Desaegeher, 2021). Addition of floral patches increases food resources leading to an increased

<sup>1</sup> ISA Youtube Channel: [https://www.youtube.com/channel/UCWBTS9FBzA4wtUb1\\_H6xLUG](https://www.youtube.com/channel/UCWBTS9FBzA4wtUb1_H6xLUG).

pollinators' population around patches, but a decreased pollinators' availability within 800 m radius from a patch due to competition, and a facilitated availability beyond 1 km distance due to an increase of nesting sites, with an optimal distance of 1.2 km. This competition/facilitation balance has been mathematically modeled, but would benefit from empirical observations (Desaegher *et al.*, 2021).

## 2.2 Hoverflies (Diptera: Syrphidae) as pollinators of sunflowers in the Waterberg Region area of Limpopo Province, South Africa

To determine the potential role of hover flies as pollinators of sunflower in South Africa, Brits (2021) focused on two main objectives: (1) to establish the species richness and abundance of hoverflies in sunflower fields and surrounds throughout the growing season, and (2) to establish which flower species the hoverflies visited based on a pollen library of the region. In northern South Africa, sunflowers are actively visited by hoverflies, with 53 species from Syrphinae and Eristalinae subfamilies. Abundance of hoverflies was significantly greater at the edge of sunflower fields than sampling plots 50 m inside the field or 50 m outside the field. Hoverflies carried mainly *Asteraceae* pollen (~47%) but also included *Pedaliaceae* (~15%), *Solanaceae* (~13%), *Fabaceae*, *Lamiaceae* and *Commelinaceae*. Some hoverflies carried up to 10 different pollen types at the same time. Incorporating natural pollinators such as hoverflies, which may be hardier to local environments than managed bee species, into field management practices might have a positive effect on pollination and subsequent seed set.

## 2.3 Sunflower traits and crop pollination

In the USA, cultivated sunflower has a low to moderate dependence on pollinators, except for the seed producers where cytoplasmic male sterility (CMS) needs the involvement of pollinators to provide pollen from maintainer or restorer to the CMS lines (Prasifka, 2021). For the growers, bees are essential to sunflower profitability, where 100% of insect mediated pollination is required for hybrid seed production and approximately 25–45% increase in seed yield was observed in field trials of cultivated hybrids. Growers know that insect-mediated pollination is important for seed yield and pest management, however not all bees are equivalent in terms of pollination efficiency, with wild bees being more efficient than honeybees in most cases. Wild bees clearly show fine scale preferences among sunflower varieties and bee diversity was not affected by floret depth (Ferguson *et al.*, 2021), but community composition did vary. The absence of pollen led to a poorer bee abundance and diversity and sowing date affected community composition. Six major floral traits are involved in sunflower's attractivity: color/patterns, odor, pollen availability, nectar quantity and concentration, nectar composition (sucrose, fructose and glucose) and floret size. As floret size QTLs only partially colocalize with seed size QTLs (Reinert *et al.*, 2020), it is possible to breed large seed varieties with small florets. The recent public releases of several sunflower genomes allows Marker Assisted Breeding to improve yield stability, improve forage for bees while maintaining yield potential, oil content, disease resistance, and

use of genetics to map traits of interest for sunflower-pollinator interactions. Future research has to focus on assessing the benefits of bees for current hybrids and associate bee preference with crop traits for better pollination. Breeders have the tools now to breed plants that are better in terms of agronomy, but also better for bees by the selection of favorable floral traits to facilitate bees foraging.

## 2.4 Past and ongoing trials oriented at improving the pollination efficiency by evaluating pollinators, plants and environment

Research on sunflower pollination at the Institute of Field and Vegetable Crops in Novi Sad (IFVCNS) began in 1979 exploring various aspects of the complex interaction between sunflower and pollinators (Terzić *et al.*, 2017; Terzić, 2021). Yield of sunflower honey in Serbia was 10 kg/hive in 1949 with old varieties, 20 kg/hive with the introduction of 1961 Russian varieties. It reached 66 kg/hive in the 1980s with the first hybrids, and then decreased to 20 kg/hive by 2000 due to inadequate agricultural practices, soil degradation and climate change. Today, sunflower fields produce 12–96 kg nectar/ha and up to 80 kg pollen/ha. NPK fertilization significantly increases nectar production in optimal water conditions, but is non-significant in limiting water conditions. For a given variety, nectar production can vary 5-fold depending on the environmental conditions. Sowing density does not have a significant effect on nectar production at floret or head scale, but has a significant effect at plot scale, with maximum production at 70 000 plants/ha. Seed treatment with insecticides did not show any difference in honeybee preference. In isolation cage experiments with hybrids and parents, bumblebees showed a high preference for A maintainer lines and hybrids carrying the PET1 cytoplasm (Leclercq, 1969), and avoided restorer lines. These PET1 genotypes produced more nectar than restorer or B maintainer lines. In open pollination conditions, pollinators tend to prefer hybrids on parental lines. Bumblebees seem to collect more nectar and honeybees more pollen. In addition, bumblebees can serve as bioagent vectors to control *Sclerotinia* head rot to lower disease incidence and increase seed yield under *Sclerotinia* pressure.

## 2.5 Insect pollination is necessary to maximize seed yield and oil content in sunflower, but a low bee density is enough

Maximum seed yield and oil content is reached from 0.2 pollinators/head, while this natural density very rarely falls below this threshold (Chabert, 2021; Chabert *et al.*, 2022). On experiments conducted in 2015 and 2017 on four cultivars in southwestern France, plots were supplemented with 2 hives/ha on one side of each plot in order to have a gradient of honeybees on plants. In such conditions, sunflowers were visited by 94% of honeybees, 4.5% bumblebees, 1% others wild bees and 0.5% hoverflies. Visitation rate actually decreased with distance to hives. Plants were sampled at 30, 140 and 250 m from the border of the field and the hive location (*i.e.*, pollinator front). Sampled plants were isolated under mesh bags to prevent insect pollination to assess the minimal seed set, were left for open pollination to measure the

actual seed-set depending on the pollinator gradient, or were hand-pollinated to ensure maximum pollination efficiency and measure the yield potential. Depending on genotype, sunflower has an average of 46% of self-fertility for seed set, and 57% for seed weight with a partial size compensation showing the high importance of pollinators' presence. Interestingly, open pollination appeared to improve oil content by ~6%.

### 3 Global warming: Heat and drought stress

Global warming has a dramatic effect on sunflower's attractiveness with the variation of floret anatomical and physiological traits. The two main abiotic stresses caused by global warming are (1) heat waves which effects were studied in FABI (South Africa), and (2) drought stress in Central Washington University, (USA) and INRAE (France).

#### 3.1 The physiological effects of heat stress conditions during anthesis and pollination in domesticated sunflowers

Increasing temperatures and heat waves have an impact on the timing of floral organ development, pollinator visits attractiveness and pollination success. On either heated or unheated sunflower heads, Memela (2021) measured insect visits using time-lapse cameras, stigma receptivity and style elongation. Artificially heated heads have significantly quicker style elongations than unheated ones. This style elongation drives pollen presentation and the same phenomenon was observed with a quicker pollen presentation in warmer heads. Warmer sunflower heads also attracted pollinators earlier and in a greater amount. On the other hand, in natural conditions, differences between sunny days and heat wave periods were not significant. The effect of heat on stigma receptivity is unclear as the results obtained with artificially heated are contrasted with those of natural heat waves.

#### 3.2 Trait architecture and drought tolerance in cultivated sunflower: Focus on floral traits

Floral trait architecture is affected by drought stress. Stem height, stem diameter, apical inflorescence mass and seed set significantly decrease with drought, while days to flower are longer. On a large panel constituted by 40 USDA lines (Segarra, 2020; Dechaine and Segarra, 2021) measured several morphological and physiological traits. Based on these traits they calculated a drought tolerance index. On floral traits, drought stress resulted in a strongly reduced head diameter, weaker but consistent and significant reduction of traits like shorter corolla and styles, and decreased nectar volume, while nectar concentration and anther length remain unchanged. They finally found that there is no obvious correlation between small floret traits and tolerance index except for anther length, which seems to be positively correlated with tolerance.

#### 3.3 Impact of drought stress on sunflower attractiveness to pollinators

Attractiveness is driven by a combination of anatomical and physiological traits (Mallinger and Prasifka, 2017a; Portlas *et al.*, 2018). In a study on three sequenced lines that have differential yield plasticity in response to stress, grown in randomly distributed pots on a high-throughput platform Catrice (2021) showed a similar small corolla depth reduction and a nectar volume decrease than Dechaine and Segarra (2021). Pollen quantity was also reduced, but its lipid and protein composition remained unchanged in response to drought stress. While Dechaine and Segarra (2021) did not observe a variation in nectar concentration, Catrice (2021) observed a 15 to 40% decrease in response to drought, resulting in a decrease of sugar production from 25 to 60%. Sugar composition varied between genotypes, with a high sucrose concentration in the most water deprivation tolerant line while the two others had only traces suggesting the involvement of a cell wall invertase as Prasifka *et al.* (2018) suggested. Physiology experiments with dye diffusion suggest that water in nectar is actively transported rather than passively diffused by osmotic pressure. Nectar global composition shows high genotypic effect in metabolic signature, with exotic glucosides produced by fungi in one line, antimicrobial molecules in another. This signature suggests differential microbial community.

#### 4 Late floral development – Microclimate, circadian clock control and gene mapping

Plants have evolved multiple reproductive strategies to promote outcrossing. However, our understanding of the mechanisms driving such strategies appears inadequate. In sunflowers, the late-stage floral developments of coordinated male and female organs promote outcrossing by temporally separating male (staminate) and female (pistillate) stages. The floret buds open to release pollen on the first, followed by the stigma elongation and receptive stage promoting outcrossing. The corolla breaks open with anther filaments elongating and releasing the pollens inside the corolla tube at dawn, followed by style elongation pushing the pollens through the tube. The staminate and pistillate stages are propagated from outer to inner parastichies (spiral rows of florets) on the capitulum. Notably, these stages co-occur in florets of the parastichy, and the separation of developmental stages over consecutive days is coordinated with the time of day. Sunflower is an excellent model for studying how the growth and development of plant organs are coordinated with environmental factors. Three presentations by Nicky Creux (FABI, Pretoria, South Africa), Carine Marshall (University of California, Berkeley, CA, USA), and Srinidhi Holalu were delivered on topics related to microclimate of eastward orientation of capitulum, pollinator visitations, circadian biology of floret maturation and genomic approaches to identify the genetic architecture underlying the timing of floral maturation traits.

#### 4.1 Sunflower anthesis: The delicate balancing act of climate control

It is striking that solar tracking ceases at anthesis, and developing heads face east direction until maturity. Creux (2021) experiments compared the development of late floral stages and pollination visitations between east and west-facing head orientations. The east-facing heads warmed up earlier and acquired more pollinator visitations than west-facing heads. It was also noted that artificial heating of west-facing heads improved the pollination visitations (Atamian *et al.*, 2016). The east-facing heads also sired more offspring and produced heavier seeds at their experiment site in Davis, CA (Creux *et al.*, 2021). The east-facing heads were also developmentally advanced compared to west facing heads, where style elongation was markedly rapid on east-facing heads. However, the anther filament elongation was not affected by the head orientation. Overall, east-facing head orientation was found to benefit through temperature-dependent changes in the timing of floral development and the promotion of insect visits. Creux *et al.* (2021) are now investigating the effect of heat stress on floral development and pollinator visitations.

#### 4.2 Daily rhythms of sunflower anthesis are coordinated by circadian clock

Floret maturation is well coordinated within pseudowhorls, and that the elongation of the ovary, style and stigma occur at daily rhythm (24 h). To establish the role of circadian in floret maturation, Marshall (2021) conducted time-lapse studies measuring the ovary, style and stamen elongation in capitula exposed to cycling light-dark conditions or constant light or temperature conditions. The capitula grown under cycling light-dark conditions were transferred to constant light conditions to test if the circadian clock regulates the rhythmic anthesis. The data indicated that under constant light and temperature conditions, the normal anthesis rhythm was absent, and the developmental gradient among the pseudowhorl was also abolished. This suggests the role of the circadian clock that integrates environmental signals with elongation growth. Under constant-dark conditions, the ovary and stamen elongation proceeded normally. However, style elongation was slowed down. The anthesis was also temperature compensated, meaning that circadian clocks maintain a relatively constant period at different temperatures. The experiments were also performed to assess clock gating by giving pulses of dark treatments during different times of the subjective day. The dark cue during the subjective day delayed the ovary and stamen elongation, indicating time of day sensitivity response, which again suggests the role of clock gating. To summarize, Marshall's work implicated the circadian clock in coordination of floral maturation stages occurring every 24 h in addition to the role of age of the pseudowhorl. Marshall's work demonstrated that circadian clock and environmental inputs determine the transition from age-gradient in floret development to separate clusters of maturing florets on the capitulum.

#### 4.3 Mapping floral maturation traits in cultivated and wild sunflowers

To follow floret development (bud break, pollen, and style maturation timing) in nearly 260 field-grown sunflower genotypes (Sunflower Association Mapping (SAM) population), Holalu (2021) used time-lapse image series at 5-minute intervals over 72 h. At anthesis, plants facing East were filmed for three days and then rotated 180 degrees to face West, and filmed again for the next three days. The resulting time-lapse images were analyzed to record the time of the day for 50% bud break, pollen-star emergence, and style emergence occurred. The experimental design also provided insights into the sensitivity of floral development to the orientation of the capitulum. Variation in corolla length, width and stigma color was also recorded. Holalu's work used a set of 600 000 SNPs generated by the International Consortium on Sunflower Genomics, and based on the XRQ.v1 reference genome assembly to identify genomic association with the different traits using Bayesian sparse linear mixed model (BSLMM). Time-lapse data indicated that pollen-star (staminate stage) and style elongation (pistillate) stages were delayed in west-facing capitula. Holalu found various SNPs associated with all the three floral maturation traits. Annotated genes within 50 kb windows surrounding significant associations were considered as potential candidates. For bud-break, an association with a gene encoding a Cytochrome b561/auxin-responsive family protein was identified. Pollen-star timing was associated with multiple SNPs on chromosomes 1, 5, 10, 11, 13 and 14. These regions included a gene involved in the gibberellic acid (GA) signaling pathway, on chromosome 10. This association is particularly suggestive, since previous research in *Arabidopsis* (Plackett *et al.*, 2011) and sunflower (Cecconi *et al.*, 2002) has implicated GA in floral development and pollen extrusion. Additionally, photoperiod-dependent anther filament elongation in response to GA application was also noted in sunflowers (Lobello *et al.*, 2000). Style maturation timing was associated with SNPs on chromosomes 10 and 14; notably these regions included a member of a shaggy kinase domain-containing family that has been shown to regulate perianth and gynoecium development in *Arabidopsis* (Dornelas *et al.*, 2001). Holalu's ongoing work includes mapping experiments for the same traits in the F4 and F5 progeny of an intercross between wild *H. annuus* individuals from natural populations growing at different latitudes. Holalu also touched on the use of artificial intelligence and machine learning tools to aid in counting pollinator visits.

#### 4.4 UV patterns in wild sunflowers: One gene and two functions

UV-absorbing pigments accumulate at the base of ray flowers in sunflowers, forming a circular UV bullseye patterns through the inflorescence. These patterns are known to increase attractiveness to pollinators in many flowers (Rae and Vamosi, 2013; Horth *et al.*, 2014). Todesco (2021) and colleagues observed extensive variation both between and

within wild sunflower species for the size of UV bullseyes. Their study focused on two main questions: what are the genetic basis of variation for UV bullseyes in wild sunflowers, and what are the factors driving this variation across natural populations. In wild *H. annuus*, UV bullseyes vary in size from a very small UV-absorbing ring close to the inflorescence disk, to the whole ray flower being UV-absorbing. A GWAS conducted on several hundred wild *H. annuus* individuals identified a single MYB transcription factor (*HaMYB111*) controlling about two-thirds of variation for the size of UV bullseyes in *H. annuus*. Using a combination of genetic mapping, heterologous complementation, expression analyses and metabolite profiling, Todesco showed that *HaMYB111* affects the size of UV bullseyes by regulating the accumulation of UV-absorbing flavonol glycosides. Variation in the promoter region of *HaMYB111* was consistently associated with larger or smaller UV bullseyes, suggesting that *cis*-regulatory variation is responsible for differences in the activity of *HaMYB111* alleles. Interestingly, cultivated sunflowers were found to be almost completely fixed for the “large UV bullseyes” allele of *HaMYB111*; consistent with this, cultivated sunflowers exhibit almost uniformly large UV bullseyes. The authors examined possible factors driving the diversity in UV patterns found between natural populations of wild *H. annuus*. Intermediate-to-large UV bullseyes (50–80% of the ray flower being UV-absorbing) were found to increase pollinator visits, while very small UV bullseyes had lower visitation rates. However, the size of UV bullseyes was also found to be very strongly correlated with relative humidity across the range of wild *H. annuus* throughout most of North America, with larger UV-bullseyes found in drier environments. Flower are known to be major sources of water loss in flowering plants (Galen, 2000), and flavonol glycosides have been previously shown to be involved in increasing drought resistance by reducing water losses (Nakabayashi *et al.*, 2014). Todesco found that ray flowers with larger UV bullseyes (*i.e.*, accumulating larger amounts of flavonol glycosides) lost water at a significantly lower rate than UV-reflecting ray flowers (*i.e.*, containing limited/no flavonol glycosides). This suggests that UV bullseyes affect more than pollinator preferences in sunflowers, and should be a factor to consider improving the resilience of cultivated sunflower to drier environments.

## 5 Discussion

Sunflower, a major oilseed crop worldwide, has positive effects on pollinators’ populations, due to the large amounts of nectar and pollen produced during its summer bloom. However, despite the importance of pollinators for sunflower production, and of sunflowers for pollinator populations, studies on the interactions between the two are rare, and the community working on these interactions is largely disconnected. This research area is often secondary in teams working on other aspects of sunflower genetics and physiology. Several aspects of sunflower-pollinator interactions were addressed, with the focus of inquiries ranging from the level of genes and individuals tissues, to the level of entire landscapes.

### 5.1 Female function

Catrice showed that nectary sits at the top of the ovary and remains at the top of the hull after the floret withered and fell. It suggests that it is part of the female apparatus, thus nectar production must be associated with the female reproductive function. Terzić showed that CMS lines produce more nectar than male fertile counterparts, which seems to confirm this hypothesis, and attracted more honeybees and bumblebees. Anthers and ovary are sink organs and there must be a competition for the carbon resource between pollen production and nectar secretion. The counterpart is that, as Prasifka showed, the absence of pollen due to PET-1 cytoplasm results in poorer abundance in pollinators’ diversity.

### 5.2 Sucrose in nectar

In the literature, we find that many lines show sucrose traces (~0.5%) in nectar (Vear *et al.*, 1990), but Prasifka (Mallinger and Prasifka, 2017a) and Catrice showed independently that some rare lines have a high amount of sucrose (~50%). These results orient towards the activity of a cell wall invertase, CWINV4, located on chromosome 1 (HanXRQr2Chr01g0013971). Cell wall invertases hydrolyse sucrose to fructose + glucose, and are known in *Brassicaceae* to be involved in nectar elaboration (Ruhlmann *et al.*, 2009; Minami *et al.*, 2021). Sucrose had been reported to be the preferred carbon source for bees and bumblebees (Waller, 1972; Fonta *et al.*, 1985; Terzić *et al.*, 2017) and the lack of CWINV4 activity may play a role in attractivity.

### 5.3 Effect of temperature, light signaling and circadian clock on floret development

Marshall *et al.* (2023) showed that illumination initiates anthesis after a, setting the circadian clock involved in floret development. In nature, there is a coordination of both plant and insect clocks (Bloch *et al.*, 2017) that affect pollinators’ activity. Sunflower circadian clock could therefore have an effect on pollinators’ attractivity. Creux showed that east-facing capitula are exposed to sun earlier than those with other orientations, conferring a competitive advantage as the early warming favors anthesis, anther maturation and pollen presentation, style elongation and stigma receptivity, thus attracting pollinators earlier than west facing capitula and siring more offspring. Creux and Memela also showed that artificial heating of the capitula could mimic the early warming indicating that heat is a major factor influencing attractivity. Holalu performed GWAS on floret developmental traits and found SNPs associated with three floral maturation traits.

### 5.4 Heat, drought stress and water loss

Heat increases water loss at both vegetative (Crawford *et al.*, 2012) and reproductive organs (Galen, 2000) level. In a recent study, Prasifka *et al.* (2023) showed that warm conditions increase nectar volume production but not concentration. On the other hand, extreme temperatures strong evaporation at the head level and could lead to reduced nectar

production. In dry environments, UV patterns tended to be larger, and flavonol glycosides involved in floral UV-patterns also decreased flower water loss (Todesco *et al.*, 2022). This reduced water loss could result in a higher nectar secretion; then the foraging insects could memorize that, in dry environments, larger UV bullseyes could be associated to higher rewards. Drought stress is also associated with a decrease in nectar production, reduction in floret size and an increase in days to flower (Dechaine and Segarra, Segarra, 2020).

## 5.5 Floral traits mapping

Holalu, Prasifka and Todesco independently mapped floral trait genes on the genome. Prasifka showed that Floret size QTLs only partially co-localize with seed size QTLs (Reinert *et al.*, 2020). By a GWAS approach, Holalu mapped several genes involved in floret development such as Auxin response protein or Gibberellic acid signaling pathway.

## 5.6 Pollinators density

It is well known by growers that pollinators are important to sunflower profitability but the minimal density to obtain maximal yields remained unknown. Chabert (2021) showed that 0.2 pollinators/head is enough to ensure a maximum yield. This density is close to natural density of honeybees and wild pollinators; sunflower fields are naturally near to saturation. On another hand Desaegeher showed that adding non-crop flowering patches can have contradictory effects on pollination. A short distance, below 700 m, between wildflower patches and crop plots has an adverse effect on sunflower yield by competition or density dilution between crop and wild floral resources, which can be more attractive; while it has a facilitation effect on longer distance above 700 m by increasing nesting sites. Wild bees' scale of effect relies on the bee species and vary from 10 m from the nesting site, up to 2550 m (Desaegeher *et al.*, 2022).

## 6 Future perspectives

The 1st web conference on sunflower-pollinators interactions was born from the necessity of giving this area of research its due relevance, and of developing connections between researchers working on this topic. The conference gathered 200 attendees from 39 countries, and twelve speakers presented their work. It was a first step in order to provide structure to the sunflower-pollinator interactions community, and will hopefully be the foundation of international research collaborations on the topic.

This conference raised several methodological challenges—first and foremost, the limitations and biases of manual insect counting, and the importance of developing automated detection and sampling approaches. Manual counting is time-consuming, and needs several people to obtain sufficient statistical power. Moreover, counting is affected by the hour of the day, ideally requiring to follow the kinetics of the visiting population throughout the day. (Semi-) automatic imaging done with cameras as presented by Holalu, Memela *et al.* diminishes biases, as several operators can analyze on a single image and validate each others' counts;

they also allow a single operator to rapidly analyze many images long after they have been acquired. Detection of pollinator visits from digital images can also be improved with the development of automatic insect-identification software that take advantage of artificial intelligence and machine learning approaches. Finally, these methods need to be broadly available for the whole community, in order to standardize measurements and allow comparisons between different studies. Automated detection would also have applications in following floret development, and automated nectar sampling could help improve measurement precision by reducing operator variability

Sunflower provides large amounts of food to pollinators: nectar and pollen. This ecosystem service is limited by the relatively short period of flowering (seven to ten days for a given plot) and a slight extension of this period could result in great benefits for pollinators and beekeeper alike, as bees would have more time to forage on a given plot. Sunflower pollen and nectar are not only a source of carbohydrates, lipids and proteins, but also supply pollinators with molecules that are known to have beneficial effects on bee health, such as flavonols contained in pollen (Giacomini *et al.*, 2018; LoCascio *et al.*, 2019). Moreover, sunflower cultivation has many virtues, as it is heat and drought tolerant and does not require irrigation, but it is also resistant to many pests and diseases and needs few to no phytopharmaceutical compounds that can remain in soils for years. Pollinators have an impact on seed set and seed quality, the optimisation of the interaction is of importance for the breeder to produce hybrid seeds, for the grower at the farm level by increasing yields and profitability, for the industrial extracting oil and proteins, and finally for the consumer. Breeders have tools to improve varieties towards these ecosystemic service goals as genetic control of the attractiveness traits is being deciphered and to adapt to new agricultural practices in a One Health vision from soil to final consumer.

In this context and accordingly to the audience's will, a second conference should be organized by 2025, hopefully live.

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## Conflicts of interest

The authors declare that there is no conflict of interest in relation to this article.

## Author's contributions

Olivier Catrice, Srinidhi Holalu, Sreten Terzić and Marco Todesco wrote the original draft. Nicole Creux and Nicolas B. Langlade reviewed and edited the article.

## References

Altieri MA, Nicholls CI, Gillespie M, *et al.* 2015. Crops, weeds and pollinators understanding ecological interaction for better

- management. Food and Agriculture Organization of the United Nations. <https://www.fao.org/3/i3821e/I3821E.pdf>.
- Atamian HS, Creux NM, Brown EA, Garner AG, Blackman BK, Harmer SL. 2016. Circadian regulation of sunflower heliotropism, floral orientation, and pollinator visits. *Science* 353(6299): 587–590. <https://doi.org/10.1126/science.aaf9793>.
- Bartomeus I, Winfree R. 2011. The circe principle: Are pollinators waylaid by attractive habitats? *Curr Biol* 21(17): R652–R654. <https://doi.org/10.1016/j.cub.2011.07.010>.
- Bartual A, Bocci G, Marini S, Moonen AC. 2018. Local and landscape factors affect sunflower pollination in a Mediterranean agroecosystem. *PLOS ONE* 13(9): e0203990. <https://doi.org/10.1371/journal.pone.0203990>.
- Becher MA, Osborne JL, Thorbek P, Kennedy PJ, Grimm V. 2013. Towards a systems approach for understanding honeybee decline: A stocktaking and synthesis of existing models. *J Appl Ecol* 50: 868–880. <https://doi.org/10.1111/1365-2664.12112>.
- Blackman BK, Scascitelli M, Kane NC, *et al.* 2011. Sunflower domestication alleles support single domestication center in eastern North America. *Proc Nat Acad Sci* 108(34): 14360–14365. <https://doi.org/10.1073/pnas.1104853108>.
- Bloch G, Bar-Shai N, Cytter Y, Green R. 2017. Time is honey: Circadian clocks of bees and flowers and how their interactions may influence ecological communities. *Philos Trans Royal Soc B: Biol Sci* 372(1734): 20160256. <https://doi.org/10.1098/rstb.2016.0256>.
- Brits X. (2021). Hoverflies (Diptera: Syrphidae) as pollinators of sunflowers in the Waterberg Region area of Limpopo Province, South Africa. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/NuGyp1101vk>.
- Castro C, Leite RMVBC. 2018. Main aspects of sunflower production in Brazil. *OCL* 25(1): D104. <https://doi.org/10.1051/ocl/2017056>.
- Catrice O. 2021. Heliopollen: Impact of drought stress on sunflower attractiveness to pollinators. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. [https://youtu.be/5oUA\\_hQRo\\_k](https://youtu.be/5oUA_hQRo_k).
- Cecconi F, Gaetani M, Lenzi C, Durante M. 2002. The sunflower dwarf mutant dw1: Effects of gibberellic acid treatment. *Helia* 25(36): 161–166. <https://doi.org/10.2298/HEL0236161C>.
- Chabert S. 2021. Insect pollination is necessary to maximize seed yield and oil content in sunflower, but a low bee density is enough. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. [https://youtu.be/oMQvGY\\_Z\\_7s](https://youtu.be/oMQvGY_Z_7s).
- Chabert S, Mallinger RE, Sénéchal C, *et al.* 2022. Importance of maternal resources in pollen limitation studies with pollinator gradients: A case study with sunflower. *Agric Ecosyst Environ* 330. <https://doi.org/10.1016/j.agee.2022.107887>.
- Chambó ED, Garcia RC, Oliveira NTE de, Duarte-Júnior JB. 2011. Honey bee visitation to sunflower: Effects on pollination and plant genotype. *Sci Agric* 68(6): 647–651. <https://doi.org/10.1590/S0103-90162011000600007>.
- Crawford AJ, McLachlan DH, Hetherington AM, Franklin KA. 2012. High temperature exposure increases plant-cooling capacity. *Curr Biol* 22(10): R396–R397. <https://doi.org/10.1016/j.cub.2012.03.044>.
- Creux N. 2021a. Sunflower anthesis: The delicate balancing act of climate control. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/RrBn71YVG10>.
- Creux NM, Brown EA, Garner AG, *et al.* 2021b. Flower orientation influences floral temperature, pollinator visits and plant fitness. *New Phytol* 232(2): 868–879. <https://doi.org/10.1111/nph.17627>.
- Crites GD. 1993. Domesticated sunflower in fifth millennium B.P. temporal context: New evidence from Middle Tennessee. *Am Antiq* 58(1): 146–148. <https://doi.org/10.2307/281459>.
- Dag A, Lior E, Afik O. 2002. Pollination of confection sunflowers (*Heliantus annuus* L.) by honey bees (*Apis mellifera* L.). *Am Bee J* 142(6): 443–445.
- Dechaine J, Segarra L. 2021. Trait architecture and drought tolerance in cultivated sunflower: Focus on floral traits. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/v5k2GKpjhgg>.
- Desaegher J. 2021. Optimising spatial distribution of mass-flowering patches at the landscape scale to increase crop pollination. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. [https://youtu.be/HFpS6EPJ\\_Z8](https://youtu.be/HFpS6EPJ_Z8).
- Desaegher J, Sheeren D, Ouin A. 2021. Optimising spatial distribution of mass-flowering patches at the landscape scale to increase crop pollination. *J Appl Ecol* 58: 1876–1887. <https://doi.org/10.1111/1365-2664.13949>.
- Desaegher J, Ouin A, Sheeren D. 2022. How far is enough? Prediction of the scale of effect for wild bees. *Ecography* 2022(5). <https://doi.org/10.1111/ecog.05758>.
- Dornelas MC, van Lammeren AAM, Kreis M. 2001. Arabidopsis thaliana SHAGGY-related protein kinases (AtSK11 and 12) function in perianth and gynoecium development. *Plant J* 21(5): 419–429. <https://doi.org/10.1046/j.1365-3113x.2000.00691.x>.
- Ferguson B, Mallinger RE, Prasiifka JR. 2021. Bee community composition, but not diversity, is influenced by floret size in cultivated sunflowers. *Apidologie* 52: 1210–1222. <https://doi.org/10.1007/s13592-021-00897-z>.
- Fonta C, Pham-Delègue M-H, Marilleau R, Masson C. 1985. Rôle des nectars de tournesol dans le comportement des insectes pollinisateurs et analyse qualitative et quantitative des éléments glucidiques de ces sécrétions. *Acta Oecol Oecol Applic* 6: 165–175.
- Galen C. 2000. High and dry: Drought stress, sex-allocation trade-offs, and selection on flower size in the Alpine wildflower *Polemonium viscosum* (Polemoniaceae). *Am Nat* 156(1): 72–83. <https://doi.org/10.1086/303373>.
- Ganser D, Mayr B, Albrecht M, Knop E. 2018. Wildflower strips enhance pollination in adjacent strawberry crops at the small scale. *Ecol Evol* 8(23): 11775–11784. <https://doi.org/10.1002/ece3.4631>.
- Ghanavati NA, Nahavandi E, Ghaderi A. 1981. Breeding sunflower for semi-arid regions. *J Agric Sci* 96(2): 447–450. <https://doi.org/10.1017/S0021859600066211>.
- Giacomini JJ, Leslie J, Tarpy DR, Palmer-Young EC, Irwin RE, Adler LS. 2018. Medicinal value of sunflower pollen against bee pathogens. *Sci Rep* 8(1): 14394. <https://doi.org/10.1038/s41598-018-32681-y>.
- Greenleaf SS, Kremen C. 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc Nat Acad Sci* 103(37): 13890–13895. <https://doi.org/10.1073/pnas.0600929103>.
- Holalu S. 2021. Mapping floral maturation traits in cultivated and wild sunflowers. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/YuLwo5xaoLY>.
- Holzschuh A, Dainese M, González-Varo JP, *et al.* 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol Lett* 19(10): 1228–1236. <https://doi.org/10.1111/ele.12657>.
- Horth L, Campbell L, Bray R. 2014 Wild bees preferentially visit Rudbeckia flower heads with exaggerated ultraviolet absorbing floral guides. *Biol Open* 3(3): 221–230 <https://doi.org/10.1242/bio.20146445>.
- Leclercq P. 1969. Une stérilité mâle cytoplasmique chez le tournesol. *Annales de l'Amélioration des Plantes*, 99–106. <https://hal.archives-ouvertes.fr/hal-02731548>.



- Leclercq P. 1983. Étude de divers cas de stérilité mâle cytoplasmique chez le tournesol. *Agronomie* 3(2): 185–187. <https://doi.org/10.1051/agro:19830211>.
- Lobello G, Fambrini M, Baraldi R, Lercari B, Pugliesi C. 2000. Hormonal influence on photocontrol of the protandry in the genus *Helianthus*. *J Exp Bot* 51(349): 1403–1412.
- LoCascio GM, Aguirre L, Irwin RE, Adler LS. 2019. Pollen from multiple sunflower cultivars and species reduces a common bumblebee gut pathogen. *Royal Soc Open Sci* 6(4): 190279. <https://doi.org/10.1098/rsos.190279>.
- Mallinger RE, Prasifka JR. 2017a. Bee visitation rates to cultivated sunflowers increase with the amount and accessibility of nectar sugars. *J Appl Entomol* 141(7): 561–573. <https://doi.org/10.1111/jen.12375>.
- Mallinger RE, Prasifka JR. 2017b. Benefits of insect pollination to confection sunflowers differ across plant genotypes. *Crop Sci* 57(6): 3264–3272. <https://doi.org/10.2135/cropsci2017.03.0148>.
- Marshall C. 2021. Daily rhythms of sunflower anthesis are coordinated by circadian clock. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/vRHF6dO5tZs>.
- Marshall CM, Thompson VL, Creux NM, Harmer SL. 2023. The circadian clock controls temporal and spatial patterns of floral development in sunflower. *Elife* 12: e80984. <https://doi.org/10.7554/eLife.80984>.
- Memela U. 2021. The physiological effects of heat stress conditions during anthesis and pollination in domesticated sunflowers. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/HOzNQXWenZU>.
- Minami A, Kang X, Carter CJ. 2021. A cell wall invertase controls nectar volume and sugar composition. *Plant J* 107(4): 1016–1028. <https://doi.org/10.1111/tpj.15357>.
- Nakabayashi R, Yonekura-Sakakibara K, Urano K, *et al.* 2014. Enhancement of oxidative and drought tolerance in Arabidopsis by overaccumulation of antioxidant flavonoids. *Plant J* 77(3): 367–379. <https://doi.org/10.1111/tpj.12388>.
- Olynyk M, Westwood AR, Koper N. 2021. Effects of natural habitat loss and edge effects on wild bees and pollination services in remnant prairies. *Environ Entomol* 50(3): 732–743. <https://doi.org/10.1093/ee/nvaa186.p>>
- Panziera D, Requier F, Chantawannakul P, Pirk CWW, Blacquièrre T. 2022. The diversity decline in wild and managed honey bee populations urges for an integrated conservation approach. *Front Ecol Evol* 10: 767950. <https://doi.org/10.3389/fevo.2022.767950>.
- Perrot T, Gaba S, Roncoroni M, Gautier J-L, Saintilan A, Bretagnolle V. 2019. Experimental quantification of insect pollination on sunflower yield, reconciling plant and field scale estimates. *Basic Appl Ecol* 34: 75–84. <https://doi.org/10.1016/j.baee.2018.09.005>.
- Plackett ARG, Thomas SG, Wilson ZA, Hedden P. 2011. Gibberellin control of stamen development: A fertile field. *Trends Plant Sci* 16(10): 568–578. <https://doi.org/10.1016/j.tplants.2011.06.007>.
- Portlas ZM, Tetlie JR, Prischmann-Voldseth D, Hulke BS, Prasifka JR. 2018. Variation in floret size explains differences in wild bee visitation to cultivated sunflowers. *Plant Genet Resour* 16(6): 498–503. <https://doi.org/10.1017/S1479262118000072>.
- Prasifka J. 2021. Sunflower traits and crop pollination. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/5ueEk8sSTKg>.
- Prasifka JR, Mallinger RE, Portlas ZM, *et al.* 2018. Using nectar-related traits to enhance crop-pollinator interactions. *Front Plant Sci* 9: 812. <https://doi.org/10.3389/fpls.2018.00812>.
- Prasifka J, Ferguson B, Fugate KK. 2023. Genotype and environment effects on sunflower nectar and their relationships to crop pollination. *J Pollinat Ecol* 32: 54–63. [https://doi.org/10.26786/1920-7603\(2023\)719](https://doi.org/10.26786/1920-7603(2023)719).
- Rae JM, Vamosi JC. 2013. Ultraviolet reflectance mediates pollinator visitation in *Mimulus guttatus*. *Plant Species Biol* 28: 177–184. <https://doi.org/10.1111/j.1442-1984.2012.00375.x>.
- Reinert S, Gao Q, Ferguson B, *et al.* 2020. Seed and floret size parameters of sunflower are determined by partially overlapping sets of quantitative trait loci with epistatic interactions. *Mol Genet Genom* 295: 143–154. <https://doi.org/10.1007/s00438-019-01610-7>.
- Ruhlmann JM, Kram BW, Carter CJ. 2009. Cell wall invertase 4 is required for nectar production in Arabidopsis. *J Exp Bot* 61(2): 395–404. <https://doi.org/10.1093/jxb/erp309>.
- Said F. 2018. Foraging behavior of the giant honey bee, *Apis dorsata* F. (Hymenoptera: Apidae) in sunflower (*Helianthus annuus* L.) at Peshawar District of Pakistan. *Pure Appl Biol* 7(3). <https://doi.org/10.19045/bspab.2018.700130>.
- Segarra L. 2020. Floral trait architecture in crop sunflower (*Helianthus annuus*) under drought conditions. <https://digitalcommons.cwu.edu/etd/1344/>.
- Seiler GJ, Qi LL, Marek LF. 2017. Utilization of sunflower crop wild relatives for cultivated sunflower improvement. *Crop Sci* 57(3): 1083–1101. <https://doi.org/10.2135/cropsci2016.10.0856>.
- Simone-Finstrom M, Strand MK, Tarpay DR, Rueppell O. 2022. Impact of honey bee migratory management on pathogen loads and immune gene expression is affected by complex interactions with environment, worker life history, and season. *J Insect Sci* 22(1). <https://doi.org/10.1093/jisesa/ieab096>.
- Singh M, Singh K, Devi C. 2000. Foraging behaviour of *Apis cerana* Himalaya for sunflower and rapeseed. In: *Asian bees and beekeeping, progress of research and development, Kathmandu, ICIMOD*, pp. 199–202.
- Terzić S. 2021. Past and ongoing trials oriented at improving the pollination efficiency by evaluating pollinators, plants and environment. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/FqbEV6juHDO>.
- Terzić S, Miklič V, Čanak P. 2017. Review of 40 years of research carried out in Serbia on sunflower pollination. *OCL* 24(6): D608. <https://doi.org/10.1051/ocl/2017049>.
- Thomann M, Imbert E, Devaux C, Cheptou P-O. 2013. Flowering plants under global pollinator decline. *Trends Plant Sci* 18(7): 353–359. <https://doi.org/10.1016/j.tplants.2013.04.002>.
- Todesco M. 2021. UV patterns in wild sunflowers: One gene and two functions. In: *1st Web-Conference on Sunflower–Pollinators Interactions*. <https://youtu.be/QevxVjuw7xY>.
- Todesco M, Bercovich N, Kim A, *et al.* 2022. Genetic basis and dual adaptive role of floral pigmentation in sunflowers. *Elife* 11: e72072. <https://doi.org/10.7554/eLife.72072>.
- Vanbergen AJ, Initiative the IP. 2013. Threats to an ecosystem service: Pressures on pollinators. *Front Ecol Environ* 11(5): 251–259. <https://doi.org/10.1890/120126>.
- Vear F, Pham-Delegue M, Tourvieille de Labrouhe D, *et al.* 1990. Genetical studies of nectar and pollen production in sunflower. *Agronomie* 10(3): 219–231. <https://doi.org/10.1051/agro:19900305>.
- Waller GD. 1972. Evaluating responses of honey bees<sup>1</sup> to sugar solutions using an artificial-flower feeder<sup>2</sup>. *Ann Entomol Soc Am* 65(4): 857–862. <https://doi.org/10.1093/aesa/65.4.857>.

Westphal C, Steffan-Dewenter I, Tschamtko T. 2003. Mass flowering crops enhance pollinator densities at a landscape scale: Flowering crops enhance pollinator densities. *Ecol Lett* 6(11): 961–965. <https://doi.org/10.1046/j.1461-0248.2003.00523.x>.

World Agricultural Production Information 2021/2022. Barley, corn, palm oil, rapeseed, rice, sorghum, soybean, sunflower and wheat. (n.d.). Available from <http://www.worldagriculturalproduction.com/default.aspx> (last consult.: September 23, 2022).

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