



Effects of Irrigation Method on Pollination and Pollinators (Hymenoptera: Apoidea) in an Open-Field Tomato Crop

Authors: Barbosa, Fernando Mendes, Lima, Jonas Torres, Santos, Márcio Adriano, and Campos, Lucio Antonio de Oliveira

Source: Florida Entomologist, 102(1) : 130-133

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.102.0121>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Effects of irrigation method on pollination and pollinators (Hymenoptera: Apoidea) in an open-field tomato crop

Fernando Mendes Barbosa^{1,2,}, Jonas Torres Lima², Márcio Adriano Santos², and Lucio Antonio de Oliveira Campos³*

Abstract

Tomato is one of the highest water-demanding crops, and the use of different irrigation systems and different water management strategies may affect crop yield. Despite the fact that tomato is a self-fertilizing (autogamous) plant, research has shown that bees (“buzz pollination”) improve yield and fruit quality. Here, we assess the effect of the irrigation method on bee visitation and pollination on flowers of the tomato crop. The study was conducted from Jul to Oct 2017 in Minas Gerais State, Brazil, using 6 plots with 150 tomato plants per plot. Three plots received water by sprinkler irrigation and the other 3 by drip irrigation, in a randomized complete block design. Bees were sampled from plants watered with both irrigation systems to evaluate visitation rate. Fruit set and fruit weight were compared between irrigation systems. Bee visitation rate was not affected by the irrigation method, and the mechanical impact of the sprinkler did not provide the same level of bee pollination. As pollination and pollinators were not negatively affected, the best irrigation method should take into account agronomic aspects, such as financial viability and water use efficiency. The drip irrigation system seems to be the most effective, because it exhibits these characteristics, even though it may have a higher cost.

Key Words: Apidae; bees; drip irrigation; tomato flower; species richness; sprinkler irrigation

Resumen

El tomate es uno de los cultivos con mayor demanda de agua, y el uso de diferentes sistemas de riego y diferentes estrategias de manejo del agua pueden afectar el rendimiento del cultivo. A pesar de que el tomate es una planta auto-fertilizante (autógama), la investigación ha demostrado que las abejas (“polinización zumbante”) mejoran el rendimiento y la calidad de la fruta. Aquí, evaluamos el efecto del método de riego en las visitas de abejas y la polinización en las flores del cultivo de tomate. Se realizó el estudio de julio a octubre del 2017 en el estado de Minas Gerais, Brasil, utilizando 6 parcelas con 150 plantas de tomate por parcela. Tres parcelas recibieron agua por irrigación por aspersión y las otras 3 por riego por goteo, en un diseño de bloques completos al azar. Se tomaron muestras de abejas de plantas regadas con ambos sistemas de riego para evaluar la tasa de visitas. Se compararon el amarre y el peso del fruto entre los sistemas de riego. El método de riego no afectó la tasa de visitas de las abejas, y el impacto mecánico del rociador no proporcionó el mismo nivel de polinización de las abejas. Como la polinización y los polinizadores no se vieron afectados negativamente, el mejor método de riego debería tener en cuenta aspectos agronómicos como la viabilidad financiera y la eficiencia en el uso del agua. El sistema de riego por goteo parece ser el más eficaz porque exhibe estas características, aunque puede tener un costo mayor.

Palabras Clave: Apidae; abejas; riego por goteo; flor de tomate; riqueza de especies; riego por aspersión

Tomato is one of the world’s most important and widespread crops, with a global production in 2016 of about 177 million tons (FAOSTAT 2018). Tomato production depends on several factors including water management and environmental factors, such as crop variety, soil type, soil moisture, temperature, humidity, and rainfall. Considering that this crop has a high water requirement, especially in the blooming and fruit development stages, irrigation is necessary to achieve production quality (Cantore et al. 2016).

Tomato irrigation can be carried out using sprinkler, drip, or furrow irrigation systems. The sprinkler irrigation system is characterized by wetting the entire plant, and is performed with sprinklers or a center pivot. On the other hand, drip irrigation is characterized by delivering water directly to the plant root zone, which can be done with drip emitters. This latter method has high efficiency of water application (Gerçek

et al. 2017), and plays an important role in water conservation as well as allowing the application of fertilizers via an irrigation system (Lu et al. 2016). Efficient water use is one of the principal concerns today, especially in arid and semi-arid regions. Thus, different irrigation systems and management strategies have been introduced to the tomato crop to improve water use efficiency in irrigation (Al Ghobari et al. 2016; Gerçek et al. 2017). However, irrigation practice changes may influence other factors that affect crop yield, such as pollinators and pollination.

Seventy-five percent of global crops benefit from animal pollination to some degree (Klein et al. 2007). Wild bees are the most efficient pollinators of cultivated plants (Garibaldi et al. 2013), improving yield, quality, shelf life, and food commercial value (Bartomeus et al. 2014; Brittain et al. 2014). Among these crops, the tomato has been studied both in the open field and greenhouse. The tomato is an autogamous

¹Universidade Federal de Viçosa, Departamento de Entomologia, Viçosa, 36570-900, Minas Gerais, Brazil; E-mail: fernandosagarana@gmail.com (F. M. B.)

²Instituto Federal de Educação, Ciência e Tecnologia do Norte de Minas Gerais-Campus Januária, Departamento de Produção, Januária, 39480-000, Minas Gerais, Brazil; E-mail: jonas.torres@ifnmg.edu.br (J. T. L.), marcio.santos@ifnmg.edu.br (M. A. S.)

³Universidade Federal de Viçosa, Departamento de Biologia Geral, Viçosa, 36570-900, Minas Gerais, Brazil; E-mail: lucioaoc@gmail.com (L. A. O. C.)

*Corresponding author; E-mail: fernandosagarana@gmail.com

plant; however, its flower requires external stimulus for the release of pollen and fertilization, because its anthers are poricidal (the pollen is released via small apical pores or slits). Although the wind may promote self-pollination in tomato (Thorpe 2000), studies have shown that sonicating bees (buzz pollination syndrome) improve yield and fruit quality (Greenleaf & Kremen 2006; Bartelli & Nogueira-Ferreira 2014; Deprá et al. 2014).

Bees can be affected directly when the irrigation affects nesting, principally of underground and solitary bee species (Cane 2008), or indirectly, when the flower's attractiveness is affected by soil water availability (Gillespie et al. 2015; Sardinás et al. 2016). Here, we believe that the irrigation system may affect tomato pollination in 2 ways: when sprinkling is used, the impact of water droplets on the plant may lead to the release of pollen from the anthers sufficient for fertilization and formation of heavier fruits, or indirectly by affecting the presence of pollinators in the crops, mainly wild bees (Gallagher & Campbell 2017).

Considering that bees benefit the tomato and that the crop is carried out under different watering systems, including sprinkler irrigation and drip irrigation, this research seeks to determine if the irrigation method affects pollinator presence and pollination in the tomato crop. Two hypotheses were formulated: (a) the impact of water droplets from the sprinkling system is sufficient to allow the same level of pollination performed by bees, and (b) bee visitation rate in the dripping system is greater than that in the sprinkling system.

Materials and Methods

STUDY SITE

This study was conducted from Jul to Oct 2017 at the Instituto Federal do Norte de Minas Gerais - Campus Januária (15.487777°S, 44.361944°W), Minas Gerais State, Brazil, in a region characterized by transition areas between the Cerrado (Brazilian savannah) and the Caatinga (dry forest). The climatic type of the region is Aw, according to the classification of Köppen, with a dry winter and rainy summer.

TOMATO CROP

Six plots (8 × 10 m), each with 150 tomato plants per plot, were used. Tomato hybrid H9553® (Heinz Seeds, Uberlândia, Minas Gerais, Brazil) was grown in 1 m spacing between rows and 0.5 m between plants. Fertilization was carried out according to the soil analysis recommendations. Spraying of insecticides, fungicides, and leaf fertilizers was performed twice per wk during the tomato crop cycle, except for the blooming stage.

IRRIGATION SYSTEMS

Three plots were irrigated by sprinkling and the other 3 by drip-irrigation; the plot arrangement was a randomized complete block design. In the sprinkler treatment, we used Fabrimar Pingo Set 30® (Fabrimar, Rio de Janeiro, Rio de Janeiro, Brazil) sectoral sprinklers with a flow rate of 0.5 m³ per h (red nozzle), with an operating pressure of 0.196 MPa, and a 90° operating angle. In the drip treatment, Azud ASR R70® (Azud, Salvador, Bahia, Brazil) adjustable drippers were used, with a flow rate of 0.07 m³ per h and an operating pressure of 0.098 MPa. For this treatment, 1 dripper per plant was inserted in polyethylene tubing. The main pipes of the 2 irrigation systems were independent, and irrigations were performed daily after 2:00 PM following management recommendations in order to maintain equivalent soil moisture levels according to the crop water requirements and soil type.

BEE SAMPLING

Bees visiting tomato flowers were collected in Aug and Sep 2017. We walked transects along all rows of each plot, and each plot was sampled between 8:00 AM and 1:00 PM for 5 min per h, on dry and warm days (> 20 °C) with low wind speeds. Temperature and humidity were recorded every h with a TFA® Wireless weather station Diva Plus (TFA, Wertheim-Reicholzheim, Germany). All bees that contacted the tomato flowers were sampled with a sweep net (20 cm in diam) and were subsequently killed with ethyl acetate in a killing jar. Bee samples of each plot and sampling period were pooled, sorted, pinned, labeled, and subsequently identified to species level by Eduardo Andrade Botelho de Almeida (Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, São Paulo, Brazil). Voucher specimens were deposited at the Entomological Museum of the Universidade Federal de Viçosa, and in the bee collection of the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, São Paulo, Brazil.) The number of bees visiting tomato flowers per min was calculated (visitation rate).

POLLINATION TESTS

Three pollination treatments were installed in each plot to evaluate if the irrigation system influenced pollination: bagged (control), open pollination, and open + mechanical pollination. These treatments were carried out in the 6 central rows of each plot. In each row, 3 plants were randomly selected for each treatment, totaling 18 plants per treatment. The first flower cluster produced by each plant was selected for the application of treatments. In the bagged treatment, the flower cluster was completely wrapped with an organza bag (10 × 15 cm) before the first flower's anthesis and was removed after the senescence of the last flower. In the open pollination treatment, the flowers remained unbagged for visitation by bees. In the treatment of open + mechanical pollination, the flowers were vibrated daily for 5 s (Palma et al. 2008) with a vibrator made with an electric toothbrush, and they remained unbagged for visitation by bees. The vibration (open + mechanical pollination) was performed from 11:00 AM to 12:00 PM, from anthesis to flower senescence. In all treatments, the fruit set was evaluated in all clusters identified. The first 4 fruits located basally on each cluster were weighed at the time of harvest to evaluate individual fruit weight. The tomato yield was evaluated in the 10 center plants of the penultimate row of each plot.

STATISTICAL ANALYSES

Values of all the response variables were analyzed with Shapiro-Wilk and Bartlett tests to verify the normality and homogeneity of variances, respectively. The Mann-Whitney U test was used to determine if there were differences in visitation rate between the irrigation systems. Fruit set and fruit weight of the pollination treatments were analyzed by ANOVA ($\alpha = 0.05$) and, when significant, with the Tukey HSD test ($\alpha = 0.05$). An unpaired *t*-test ($\alpha = 0.05$) was used to test whether there were differences in fruit set and fruit weight between the 2 irrigation systems. In addition, the unpaired *t*-test ($\alpha = 0.05$) was used to evaluate whether there was a difference in mean productivity between the 2 irrigation systems. The analyses were conducted in R (R-Core-Team 2017).

Results

Two hundred seventy-three bees of 18 species were collected (Table 1). One hundred forty-two individuals of 12 species were collected in the sprinkling system, along with 134 individuals of 16 species in the

Table 1. Family, species, abundance, and richness of bees collected in the tomato crop in sprinkler and drip irrigation systems.

Family and species	Sprinkler	Drip	Total
Apidae			
<i>Apis mellifera</i> Linnaeus, 1758	3	—	3
<i>Bombus (Fervidobombus) brevivillus</i> Franklin, 1913	51	23	74
<i>Centris (Hemisiella) tarsata</i> Smith, 1874	5	6	11
<i>Centris (Hemisiella) trigonoides</i> Lepeletier, 1841	12	11	23
<i>Centris (Trachina) fuscata</i> Lepeletier, 1841	2	2	4
<i>Euglossa</i> sp.	1	—	1
<i>Exomalopsis (Exomalopsis) analis</i> Spinola, 1853	15	20	35
<i>Melipona (Melikerria) quinquefasciata</i> Lepeletier, 1836	—	1	1
<i>Trigona recurva</i> Smith, 1863	10	26	36
<i>Trigona spinipes</i> (Fabricius, 1793)	2	1	3
Halictidae			
<i>Augochlora (Oxystoglossella) sp.2</i>	—	1	1
<i>Augochloropsis aff. iris</i>	—	2	2
<i>Augochloropsis illustris</i> (Vachal, 1903)	15	10	25
<i>Augochloropsis melanochaeta</i> Moure, 1950	—	1	1
<i>Dialictus</i> sp.	—	1	1
<i>Pseudaugochlora graminea</i> (Fabricius, 1804)	—	1	1
<i>Pseudaugochlora pandora</i> (Smith, 1853)	11	13	24
Abundance	142	134	276
Richness	12	16	18

dripping system. The visitation rate (number of bees per min) did not differ between the irrigation systems ($W = 40$; $P > 0.05$).

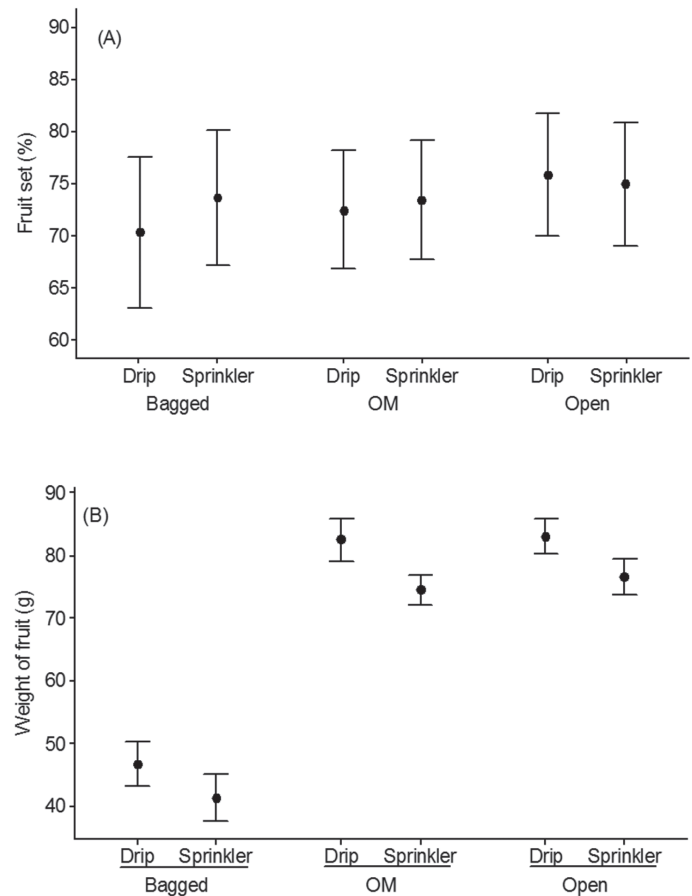
Fruit set did not vary with pollination types in the sprinkler treatment ($F = 0.09$; $df = 115$; $P > 0.05$) or in the drip treatment ($F = 0.84$; $df = 115$; $P > 0.05$). Fruit weight was lower in bagged pollination and did not differ between the open pollination and open + mechanical pollination in both irrigation systems ($F = 169.33$; $df = 313$; $P < 0.001$, and $F = 167.63$; $df = 313$; $P < 0.001$).

Fruit set did not vary with irrigation systems (Fig. 1A). On the other hand, fruit weight was higher in the drip irrigation system in the 3 types of pollination (Fig. 1B). The yield was higher in the drip irrigation system, with an average of 2.82 kg per plant vs. 2.15 kg in the sprinkler irrigation system ($t = -2.37$; $df = 58$; $P < 0.05$).

Discussion

The irrigation method did not affect the visitation rate of bees on the tomato flowers, and this may be related to the indirect effects on the bees. Irrigation may indirectly affect pollinators because it changes flower attractiveness (Gillespie et al. 2015; Burkle & Runyon 2016). Pollen production and other important characteristics, such as flower morphology and floral volatile emission, may be affected by soil water availability (Waser & Price 2016; Gallagher & Campbell 2017). The lack of significant difference in the visitation rate between the 2 irrigation systems leads us to believe that there were no variations in the floral characteristics of the 2 systems, or if there were variations, they did not influence bee visitation. In addition, the bees collected in our study are similar to bee fauna described in other studies on the tomato crop (Silva-Neto et al. 2013; Deprá et al. 2014; Santos et al. 2014), principally the dominant species or genera, which reinforces our conclusions about irrigation effect on the visitation rate.

The absence of effects due to pollination on fruit set indicates that the irrigation method does not affect this characteristic. It is possible that the mechanical stimulus caused by wind offset any interference with pollination due to irrigation. On the other hand, the lower fruit

**Fig. 1.** Fruit set (A) and weight of fruit (B) in relation to type of irrigation and type of pollination. OM = open + mechanical pollination.

weight in the bagged (control) treatment in the sprinkler irrigation treatment indicates that the external stimulus caused by the sprinkler water droplets was not sufficient to reach the pollination level performed by the bees. Open pollination, possibly performed by the bees sampled in the crop, did not differ from the open + mechanical pollination, and this result is an indicator that there was no pollination deficit in the crop.

The higher weight of fruits in the drip irrigation system may be related to the effect of irrigation on the physiology of the tomato. In drip irrigation there is better distribution of water, which can affect the development of the root, and consequently the absorption and assimilation of nutrients that directly influence the fruit mass (Nangare et al. 2016). Irrigation could affect fruit mass through pollination in 2 ways. First, irrigation could directly induce pollination due to the impact of the water droplets of the sprinkler on the flower, causing release of the pollen and, consequently, pollination. This hypothesis would be confirmed if the bagged (control) treatment of the sprinkler irrigation system had produced fruits with equal or greater weight to those that underwent the treatments of open pollination and open + mechanical pollination, but this did not occur. Second, irrigation could affect the presence of the pollinators and consequently the pollination, but the results showed that the visitation rate was not affected either.

Our results demonstrate the importance of bees to improve tomato yield. This is based on the observation that, contrary to our expectations, the mechanical impact of the sprinkler did not provide the same level of bee pollination. On the other hand, it is possible that high-flow sprinklers produce results contrary to our expectations because they

produce larger droplets and could have a greater mechanical impact on the tomato flowers. However, high-flow systems are not common in tomato production. Because pollination and pollinators were not affected, the choice of irrigation system should take into account agronomic criteria such as financial viability, and water use efficiency. The drip irrigation system seems to be the most effective because it demonstrates these characteristics even though it may be more expensive initially (Baiamonte et al. 2015; Lu et al. 2016).

Acknowledgments

We would like to thank Eduardo Andrade Botelho de Almeida (Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, São Paulo, Brazil) for the identification of the Halictidae bees that were collected; the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ), and the Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for their financial support; and the Eagle Seeds company for supplying H9553® hybrids. Laura Clark (MyProofreadingPro) revised and corrected the English language used in this manuscript. F. M. B. received support from the Program for Qualification of Public Servants - Campus Januária (223/2014; 066/2015; 086/2016; 173/2017).

References Cited

- Al-Ghobari HM, Mohammad FS, El Marazky MS. 2016. Evaluating two irrigation controllers under subsurface drip irrigated tomato crop. *Spanish Journal of Agricultural Research* 14: 1206–1218.
- Baiamonte G, Provenzano G, Rallo G. 2015. Analytical approach determining the optimal length of paired drip laterals in uniformly sloped fields. *Journal of Irrigation and Drainage Engineering* 141: 1–8.
- Bartelli BF, Nogueira-Ferreira FH. 2014. Pollination services provided by *Melipona quadrifasciata* Lepeletier (Hymenoptera: Meliponini) in greenhouses with *Solanum lycopersicum* L. (Solanaceae). *Sociobiology* 61: 510–516.
- Bartomeus I, Potts SG, Steffan-Dewenter I, Vaissiere BE, Woyciechowski M, Krewenka KM, Tscheulin T, Roberts SPM, Szentgyörgyi H, Westphal C, Bommarco R. 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ* 2: e328. doi.org/10.7717/peerj.328
- Brittain C, Kremen C, Garber A, Klein AM. 2014. Pollination and plant resources change the nutritional quality of almonds for human health. *PLoS One* 9: e90082. doi.org/10.1371/journal.pone.0090082
- Burkle LA, Runyon JB. 2016. Drought and leaf herbivory influence floral volatiles and pollinator attraction. *Global Change Biology* 22: 1644–1654.
- Cane JH. 2008. A native ground-nesting bee (*Nomia melanderi*) sustainably managed to pollinate alfalfa across an intensively agricultural landscape. *Apidologie* 39: 315–323.
- Cantore V, Lechkar O, Karabulut E, Sellami MH, Albrizio R, Boari F, Stellacci AM, Todorovic M. 2016. Combined effect of deficit irrigation and strobilurin application on yield, fruit quality and water use efficiency of “cherry” tomato (*Solanum lycopersicum* L.). *Agricultural Water Management* 167: 53–61.
- Deprá MS, Delaqua GG, Freitas L, Gaglianone MC. 2014. Pollination deficit in open-field tomato crops (*Solanum lycopersicum* L., Solanaceae) in Rio de Janeiro State, Southeast Brazil. *Journal of Pollination Ecology* 12: 1–8.
- FAOSTAT (Food and Agriculture Organization Corporate Statistical Database). 2018. Food and Agriculture Organization of the United Nations. <https://faostat.fao.org>
- Gallagher MK, Campbell DR. 2017. Shifts in water availability mediate plant-pollinator interactions. *New Phytologist* 215: 792–802.
- Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhöffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipólito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Rickerts TH, Rundlöf M, Seymour CL, Schüepp C, Szentgyörgyi H, Taki H, Tscharnkte T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, Klein AM. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339: 1608–1611.
- Gerçek S, Demirkaya M, İşik D. 2017. Water pillow irrigation versus drip irrigation with regard to growth and yield of tomato grown under greenhouse conditions in a semi-arid region. *Agricultural Water Management* 180: 172–177.
- Gillespie S, Long R, Williams N. 2015. Indirect effects of field management on pollination service and seed set in hybrid onion seed production. *Journal of Economic Entomology* 108: 2511–2517.
- Greenleaf SS, Kremen C. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation* 133: 81–87.
- Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B: Biological Sciences* 274: 303–313.
- Lu S, Zhang X, Liang P. 2016. Influence of drip irrigation by reclaimed water on the dynamic change of the nitrogen element in soil and tomato yield and quality. *Journal of Cleaner Production* 139: 561–566.
- Nangare DD, Singh Y, Kumar PS, Minhas PS. 2016. Growth, fruit yield and quality of tomato (*Lycopersicon esculentum* Mill.) as affected by deficit irrigation regulated on phenological basis. *Agricultural Water Management* 171: 73–79.
- Palma G, Quezada-Euán JJG, Reyes-Oregel V, Meléndez V, Moo-Valle H. 2008. Production of greenhouse tomatoes (*Lycopersicon esculentum*) using *Nannotrigona perilampoides*, *Bombus impatiens* and mechanical vibration (Hym.: Apoidea). *Journal of Applied Entomology* 132: 79–85.
- R-Core-Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Santos AOR, Bartelli BF, Nogueira-Ferreira FH. 2014. Potential pollinators of tomato, *Lycopersicon esculentum* (Solanaceae), in open crops and the effect of a solitary bee in fruit set and quality. *Journal of Economic Entomology* 107: 987–994.
- Sardiñas H, Yee C, Kremen C. 2016. Irrigation method does not affect wild bee pollinators of hybrid sunflower. *California Agriculture* 71: 35–40.
- Silva-Neto CM, Lima FG, Gonçalves BB, Bergamini LL, Bergamini BAR, Elias MA, Franceschinelli EV. 2013. Native bees pollinate tomato flowers and increase fruit production. *Journal of Pollination Ecology* 11: 41–45.
- Thorp RW. 2000. The collection of pollen by bees. *Plant Systematics and Evolution* 222: 211–223.
- Waser NM, Price MV. 2016. Drought, pollen and nectar availability, and pollination success. *Ecology* 97: 1400–1409.