Emirates Journal of Food and Agriculture. 2022. 34(2): 170-175
doi: 10.9755/ejfa.2022.v34.i2.2817
http://www.ejfa.me/

REGULAR ARTICLE

Effect of drought stress on the foraging behavior of insect pollinators and the reproductive success of canola (*Brassica napus* L.)

Muqaddas Younas[1], Mudssar Ali[1]*, Amar Matloob[2], Asif Sajjad[3], Hafiza Tahira Gul[1], Shafqat Saeed[1]

[1]Institute of Plant Protection, MNS University of Agriculture Multan, Pakistan, [2]Department of Agronomy, MNS University of Agriculture Multan, Pakistan, [3]Department of Entomology, Faculty of Agriculture and Environment, The Islamia University of Bahawalpur, Pakistan.

ABSTRACT

To appraise the effect of drought stress on the foraging behavior (visitation frequency and visitation rate) of insect pollinators and its ultimate impact on reproductive success of canola (*Brassica napus* L.), an experiment was carried out at the Research Farm of MNS-University of Agriculture, Multan, Pakistan. Previously, only a few studies have evaluated drought stress as a predictor of plant-pollinator interactions. Normal irrigated and drought stress plots of canola were separated by a distance of fifteen meters. Normal irrigated plots received recommended number of irrigations (three times) i.e., 1st irrigation at 30 days after germination (DAG), 2nd at flowering, and 3rd at pod setting. However, irrigation was applied only once to drought-stressed plots i.e., 1st irrigation at 30 DAG. Twelve insect species in two orders and five families visited the canola flowers. These floral visitor species were grouped into three categories, i.e., *Apis* bees (honey bees), non-*Apis* bees, and flies. The abundance of *Apis* and non-*Apis* bees was significantly higher in irrigated plots than in drought plots, while the abundance of flies did not differ significantly in both plots. Stay time of all the floral visitors was significantly higher in drought plots, while the visitation rate was significantly higher in irrigated plots. The interaction between pollination modes (open pollination and self-pollination) and water regimes (normal irrigation and drought stress) was significant for all the reproductive success parameters of canola (silique length and weight, number of seeds per silique, seed weight per silique, number of siliques per plant and fatty acid contents (%) of canola seeds) under normal irrigation regime for free insect visits treatment. Moreover, a variation of 83% to 207% was observed for these parameters between irrigated and drought plots receiving insect pollination (free insect visits) due to higher pollinator abundance and visitation rate in the former ones. However, all the reproductive success parameters did not vary between irrigated and drought plots with no insect pollination (no insect visits, caged treatment). In conclusion, drought stress negatively affected insect pollinators' foraging behavior, leading to low reproductive success in canola. In the climate change scenario and limited water availability, future studies should consider drought stress for other cross-pollinated crops under varying environments and pollinator fauna.

Keywords: *Apis* bees; climate change; non-*Apis* bees; pollination modes; stay time; visitation rate; water regimes

INTRODUCTION

Climate change seriously affects the phenology, distribution, and physiology of various groups of invertebrates (Prather et al., 2013). As pollinators play a vital role in crop pollination and maintenance of plant diversity, it is important to study their vulnerability towards climate change (Gallai et al., 2009; Ollerton et al., 2011). Some previous studies have reported a negative impact of environmental warming on overall pollination (Settele et al., 2016; Forrest, 2017) due to resultant phenological and spatial mismatches between flowering plants and pollinators (Scaven and Rafferty, 2013; Miller-Struttmann et al., 2015).

Drought stress as an outcome of climate change is increasing worldwide (IPCC 2014). A perusal of global rainfall variability suggests a 5-8% increase in drought-prone areas in the regions receiving monsoon rainfall (Giannini et al., 2008; Rodenburg et al., 2011). Besides its direct impact on plant structural and functional homeostasis, drought stress also affects plant-pollinator interactions by influencing the availability of floral resources (Brown et al., 2016; Thomson 2016). The drought stress can decrease the number and size of flowers (Halpern et al., 2010; Burkle and Runyon, 2016) with fewer pollen grains of low viability (Al-Ghzawi et al., 2009; Waser and Price, 2016). The resultant alteration in shape and size of flower

***Corresponding author:**
Mudssar Ali, Institute of Plant Protection, MNS University of Agriculture Multan, Pakistan. **E-mail:** mudssar.ali@mnsuam.edu.pk

Received: 26 August 2021; **Accepted:** 13 January 2022

corolla leads to fewer insect visits (Thompson 2001) and decreased pollination efficiency (Campbell et al., 1991). Drought also modulates the floral volatiles that attracts the pollinators (Burkle and Runyon, 2016).

Drought stress has also been reported to alter the nectar volume of flowers (Halpern et al., 2010; Gallagher and Campbell, 2017) along with occasional variation in sugar concentration (Nicolson et al., 2007; Waser and Price, 2016). Such changes in nectar volume and sugar concentration affect the foraging behavior of pollinators (Cnaani et al., 2006; Borrell, 2007; Schweiger et al., 2010). Moreover, quantitative and qualitative changes in floral resources have been known to influence the pollinators at the population level (Wallisdevries et al., 2012; Baude et al., 2016; Carvell et al., 2017). It is unequivocal that drought stress reduces the number of the honey bee and bumble bee visits to flowers leading to a severe reduction in yield (Al-Ghzawi et al., 2009; Zhao and Conner, 2016; Gallagher and Campbell, 2017).

Understanding the impact of climate change, especially drought, on the biology of plants and pollinators is crucial. Drought stress may affect the photosynthetic activity of plants which leads to decreased investment in their reproduction in temrs of quanitiy and quality of nectar and pollen (Pinheiro and Chaves, 2011; Lemoine et al., 2013). This degradation in floral traits significantly impacts pollinator visitation and their effectiveness (Cane, 2016; Byers, 2017).

The entomophilous flowers of canola –the experimental plant in this study- are capable of both self and cross-pollination while out-crossing ranges 12 to 47 percent depending upon the cultivar (Becker et al., 1992). The open flowers of canola with copious nectar and pollen attract a wide array of insect pollinators i.e., flies, bees and butterflies (Kunin, 1993; Stanley et al., 2013). The adhesive and aggregated pollen grains of oilseed rape facilitate insects in its cross-pollination (Cresswell et al., 2004).

Although the overall pollination process is being disturbed by climate change (Phillips et al., 2018), only a few studies have evaluated drought stress as a predictor of plant-pollinator interactions. For instance, Elferjani and Soolanayakanahally (2018) studied the effect of drought stress -both alone or in combination with heat stress- on photosynthetic capacity, seed yield, and oil contents of canola. Previously, no study reported the impact of drought stress on insect pollinators across the Arid region (Multan) in Punjab, Pakistan. Therefore, the current study was planned to evaluate the effect of drought stress on the foraging behavior and reproductive success of canola under the arid climatic condition of Punjab, Pakistan.

MATERIALS AND METHODS

Study site description

This study was carried out at the research farm of the Muhammad Nawaz Shareef University of Agriculture, Multan, Pakistan (30.152˚N and 71.447˚E) from November to March 2017-18. The climate of the area is arid with cold winters and hot summers; the average temperature remains in the range of 25˚C-30˚C having 35˚C-40˚C maximum and 10˚C-20˚C minimum temperature. The yearly all rainfall ranges from 5-10 inches and 2-4 knots wind speed. The soil in this region is sandy, while alluvium land is present close to the Indus, Sutlej, and Chenab rivers (Khan, 2019).

Drought and normal irrigation treatments

Canola (Hyaola-401) was grown on an area of 4000 m^2 that was divided into two main plots. Each of these plots was designated as a normal irrigated plot, and the other was a drought stress plot, and a distance of fifteen meter was maintained between these two main plots. Normal irrigated plots received recommended number of irrigations, i.e., three times, 1st irrigation at 30 days after germination (DAG), 2nd at flowering, and 3rd at pod setting (Directorate of Agriculture Information, 2021). However, irrigation was applied only once to drought-stressed plots i.e., 1st irrigation at 30 DAG.

Abundance and diversity of insect pollinators

The abundance and diversity of insect pollinators in normal irrigated and drought-stressed plots was recorded throughout the flowering season. Weekly observations were recorded twice a day, i.e., 10:00 am and 12:00 pm, with an interval of two days. A wooden quadrate of 1m2 was randomly placed in each census at five different places, and flower-visiting insects were recorded in each quadrate for five minutes. The bee species were identified by using the keys of Michener (2000), while syrphid fly species were identified by an expert (acknowledgment). The voucher specimens were submitted to the Ecology Lab at the MNS University of Agriculture, Multan.

Foraging behavior of insect pollinators

The foraging behavior of insect pollinators was recorded in terms of stay time (time spent on a flower) and visitation rate (number of flowers visited per one minute). Weekly observations were made twice a day, i.e., 10:00 am and 12:00 pm, in the normal irrigated and drought-stressed plots.

Reproductive success of canola

For measuring reproductive success, open-pollinated (free insect visits) and self-pollinated (caged with nylon mesh bags) plants were also maintained for comparison. To compare the reproductive success between open-pollinated and self-pollinated treatments in the irrigated and drought stressed plots, the following parameters were recorded i.e. silique length, silique weight, number of seeds per silique, seed weight per silique, and number of siliques per plant.

Statistical analyses

The means of visitation frequency, stay time, and visitation rate of floral visitors was compared between drought and irrigated plots using an independent sample t-test. Moreover, the interactive effect of water regimes (regular irrigation and drought stress), pollination modes (open pollination and self-pollination) on reproductive success parameters (silique length, silique weight, number of seeds per silique, seeds weight per silique, and number of siliques per plant) were analyzed using two-way analysis of variance (ANOVA). All the statistical analyses were performed on computer software Minitab (16).

RESULTS

Abundance and Diversity of insect pollinators on Brassica flowers

The pollinator community visiting canola flowers was comprised of four bee species (Hymenoptera) and eight true fly species (Diptera). The bee species belonged to three families i.e., Apidae (*Apis mellifera*, *Apis dorsata*), Halictidae (*Lasioglossum* sp.), and Andrenidae (*Andrena* sp.). Among the bees, *A. dorsata* were the highest in abundance followed by *Andrena* sp. The eight true fly species belonged to two families i.e., Syrphidae and Calliphoridae. The abundance of *Ischiodon scutellaris* was the highest, followed by *Eristalinus aeneus* and *Melanostoma* sp. (Table 1)

Two sample proportion test showed significant differences in visitation frequency of *Apis* (p=0.000) and non-*Apis* bees (p=0.047) in irrigated and drought-stressed plots (Fig. 1). However, there was no significant difference in the abundance of flies (i.e. p=0.195) in both irrigated and drought plots (Fig. 1).

Visitation rate and stay time

The results of t-test revealed significant differences in the visitation rate of *Apis* bees (p=0.001), non-*Apis* bees (p=0.001), and flies (p=0.000) in irrigated vs. drought subjected plots. The visitation rate for all three groups was higher in irrigated plots than the drought plots (Table 2).

The results of the t-test showed that the stay time of *Apis* bees, non-*Apis* bees and flies was significantly greater (p=0.000, 0.029 and 0.015, respectively) in drought stressed plots than that of irrigated plots. (Table 3).

Reproductive success

The interaction between pollination modes (open pollination and self-pollination) and water regimes (normal irrigation and drought stress) was significant for all the reproductive success parameters (silique length and weight, number of seeds per silique, seed weight per silique, number of siliques per plant and fatty acid contents %) under normal irrigation regime for free insect visits treatment (Table 4). It was found that silique length was 83% higher in open-pollinated plots as compared to self-pollinated plots, while silique weight and the number of seeds per silique were 150% and 191% more numerous. Seed weight per silique, number of siliques per plant, and fatty acid content (%) of canola were 200%, 103%, and 207% higher, respectively, for open-pollinated plots as compared to self-pollinated plots under a normal irrigation regime. However, all the reproductive success parameters did not vary between drought and irrigated plots under no insect visit modes of pollination (Table 4).

DISCUSSION

In the present study, canola flowers were visited by twelve insect pollinators belonging to four distinct families and two different orders. The canola flower with a landing platform of yellow petals and floral rewards (pollen and

Table 1: List of insect pollinators foraging on canola flowers in drought and irrigated plots

Pollinator Groups	Order	Family	Scientific Name
Apis bees	Hymenoptera	Apidae	*Apis dorsata*
			A. mellifera
Non-*Apis* bees		Halictidae	*Lassioglosum* sp.
		Andrenidae	*Andrena* sp.
Flies	Diptera	Syrphidae	*Eristalinus laetus*
			E. aeneus
		Calliphoridae	*Episyrphus balteatus*
			Melanostoma sp.
			Ischiodon scutellaris
			Eupeodes corollae
			Euphumosia sp.
			Calliphora vomitoria

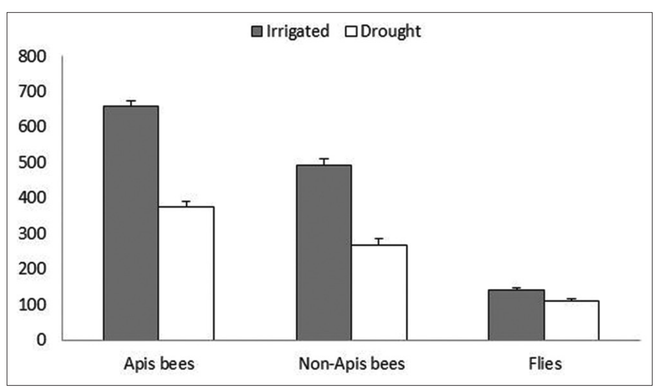

Fig 1. Total Abundance of different insect pollinator groups in irrigated and drought plots. Capped bars above total abundance bars denote standard errors of ten replicates.

Table 2: Visitation rate of insect pollinators observed on canola flowers

	Honey bees		Non- Apis Bees		Syrphid flies	
	Drought	Irrigated	Drought	Irrigated	Drought	Irrigated
Mean ± S.E	10.25±0.40	12.16±0.45	3.82±0.43	5.9±0.27	1.41±0.06	2.5±0.17
df	79		79		79	
P-value	< 0.0001		< 0.0001		< 0.0001	

Table 3: Stay time of insect pollinators observed on canola flowers

	Honey bees		Non- *Apis* Bees		Syrphid flies	
	Drought	Irrigated	Drought	Irrigated	Drought	Irrigated
Mean±S.E	5.01±0.25	3.75±0.17	8.86±1.15	5.97±0.43	19.21±0.94	16.35±1.12
df	79		79		79	
P-value	< 0.0001		< 0.0001		< 0.0001	

Table 4: Two-way ANOVA showing the interaction of water regimes and pollination modes with reproductive success parameters of canola.

Water regimes	Pollination modes		Mean
	Open	Caged	
Silique length (cm)			
Irrigated	9.17 a	5.00 c	7.08
Drought	6.67 b	4.77 c	5.71
Mean	7.91	4.88	
LSD $p \leq 0.05$	1.26		
Silique weight (g)			
Irrigated	0.15 a	0.06 c	0.10
Drought	0.09 b	0.05 c	0.06
Mean	0.11	0.05	
LSD $p \leq 0.05$	1.76		
Seeds per silique			
Irrigated	36.00 a	12.33 c	24.16
Drought	24.67 b	8.67 c	16.66
Mean	30.33	10.5	
LSD $p \leq 0.05$	4.88		
Seed weight per silique (g)			
Irrigated	0.09 a	0.03 c	0.06
Drought	0.06 b	0.02 c	0.04
Mean	0.07	0.02	
LSD $p \leq 0.05$	0.01		
Silique per plant			
Irrigated	206.67 a	101.33 c	154
Drought	137.00 b	96.67 c	116.83
Mean	171.83	99	
LSD $p \leq 0.05$	28.07		
Fatty acid (%)			
Irrigated	17.14 a	5.58 c	11.36
Drought	11.45 b	4.57 c	8.01
Mean	14.29	5.07	
LSD $p \leq 0.05$	2.68		

Means followed by the same letters in a column are not statistically different according to Tukey at 5% level of significance.

nectar) attracts a wide array of insect pollinators such as honeybees, wild bees, and flies (Ali et al., 2011). The abundance of honey bees was found highest, followed by non-*Apis* bees and syrphid flies. Some previous studies have reported honey bees as more abundant pollinators of canola flowers (Bommarco et al., 2012). Because of their short-tongue, syrphid flies prefer to forage from plants that have short corolla and easy access to pollen and nectar such as canola flowers (Colley and Luna, 2000)

The abundance of *Apis,* non-*Apis* bees, and flies varied between irrigated and drought conditions. The abundance of these pollinators groups was higher under irrigated regime than drought. The low pollinator abundance in drought may be due to the two type of variations in flowering plants that make these plants less attractive for insect pollinators: first, drought negatively affect the floral signals of the plants (shape, colour, scent of flowers) for the reward status, second, it also affect the rewards i.e., nectar (sugar source for insect pollinators) and pollen (source of protein and amino acids for pollinators) (Byers, 2017). Moreover, it has been suggested that such indirect effect of drought on insect pollinators is more drastic than the direct effect on insect pollinators (Ogilvie et al., 2017; Ropars et al., 2020). A previous study on pollination of *Trigonella moabitica* (Fabaceae) has also reported a significant lower abundance of honey bees in moderately watered and drought stress conditions than fully watered plants (attracted nearly 70% of all bees' visits). This low visitation is because flowers of water-stressed plants are less attractive to pollinators, especially bees (Al-Ghazawi et al., 2009) and food-based cues affect the foraging behavior of honey bees (Pernal and Currie, 2002).

The stay time and visitation rate of all the pollinator groups (*Apis*, non- *Apis* bees, and flies) varied significantly under irrigated and drought conditions. Stay time was comparatively higher on flowers of canola crop subjected to drought than the irrigated condition. Contrarily, visitation rate of all pollinator groups was higher for irrigated plots than the drought plots. Bees and other pollinators alter their foraging behavior (stay time and visitation rate) in response to floral rewards and preferably visit those flowers that produce greater nectar rewards (Dreisig, 2012).This frequent visitation results in higher pollen deposition on the stigmatic surface of *Brassica* species leading to the higher yield (Cresswell, 2000).

The visitation and foraging rate of insect pollinators are governed by factors such as length of proboscis, natural foraging behavior, nectar sugar concentration (Abrol, 2007), floral rewards, and prevailing abiotic factors including wind speed, relative humidity, light intensity, and temperature (Vicens and Bosch, 2000). Pollination success relies on both components, such as the amount of conspecific pollen that is compatible delivered in a visit and number of visits (visitation rate) a flower received; and that both factors are related to nectar and pollen rewards which in turn are affected by biotic and abiotic factors, i.e., soil moisture (Waser and Price, 2016).

Yield and quality attributes of canola (silique length, silique weight, numbers of seeds per silique, seed weight per silique, numbers of siliques per plant, and fatty acid percentage) did not vary under no insect pollination (cage treatment) in drought and irrigated plots. Nevertheless, in the case of open-pollination, the difference among the two water regimes for reproductive success parameters was more pronounced, suggesting that pollinators play a crucial role in enhancing seed set and yield of canola crop (Sanas et al., 2014).

Besides low pollinator visitation in drought-stressed plots of canola in our study, reduction in reproductive success of this crop can be further attributed to increase in pollen sterility and ovary abortion as these are the major drivers affecting seed setting (Melser and Klinkhamer, 2001; Boyer and Westgate, 2004). The same mechanism has been reported for low yield under drought-stressed conditions in maize, *Trigonella coerulea* (Akhalkatsi and Rainer, 2005) and wheat (Sinclair and Jamieson, 2006) due to reduction in seed number. Moreover, drought stress during the flowering stage may reduce the harvest index by 60% due to the decline in seed setting (Garrity and O'Toole, 1994).

In conclusion, drought stress reduced the abundance and visitation rate of insect pollinators leading to the lower reproductive success of canola. Considering the current climate change scenarios and limited water availability, future studies should consider this aspect in other cross pollinated crops under varying environments and insect fauna.

Authors' contributions

All authors contributed to the conceptualization and design of the experiment. Muqadas Younas did material preparation and data collection while Mudssar Ali and Amar Matloob performed data analysis. Muqadas Younas wrote the first draft of the manuscript and all the authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

ACKNOWLEDGMENTS

We are all highly thankful to the Muhammad Nawaz Shareef University of Agriculture Multan for providing the facility to perform the current research work.

REFERENCES

Abrol, D. P. 2007. Honeybees and rapeseed: A pollinator-plant interaction. Adv. Bot. Res. 45: 337-367.

Akhalkatsi, M. and L. Rainer. 2005. Water limitation effect on seed development and germination in *Trigonella coerulea* (Fabaceae). Flora. 200: 493-501.

Al-Ghzawi, A. A., S. Zaitoun, H. Gosheh and A. Alqudah 2009. Impacts of drought on pollination of *Trigonella moabitica* (Fabaceae) via bee visitations. Arch. *Agron. Soil Sci.* 55: 683-692.

Ali, M., S. Saeed, A. Sajjad and A. Whittington. 2011. In search of the best pollinators (*Brassica napus* L.) production in Pakistan. Appl. Entomol. Zool. 46: 353-361.

Baude, M., W. E. Kunin, N. D. Boatman, S. Conyers, N. Davies, M. A. Gillespie and J. Memmott. 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. Nature. 530: 85-88.

Bommarco, R., L. Marini and B. E. Vaissière. 2012. Insect pollination enhances seed yield, quality and market value in oilseed rape. Oecologia. 169: 1025-1032.

Borrell, B. J. 2007. Scaling of nectar foraging in orchid bees. Am. Nat. 169: 569-580.

Boyer, J. and M. Westgate. 2004. Grain yields with limited water. J. Exp. Bot. 55: 2385-2394.

Brown, M. J., L. V. Dicks, R. J. Paxton, K. C. Baldock, A. B. Barron, M. P. Chauzat and J. Li. 2016. A horizon scans of future threats and opportunities for pollinators and pollination. Peer. J. 4: 2249.

Burkle, L. A. and J. B. Runyon. 2016. Drought and leaf herbivory influence floral volatiles and pollinator attraction. Glob. Change. Biol. 22: 1644-1654.

Byers, D. L. 2017. Studying plant-pollinator interactions in a changing climate: A review of approaches. Appl. Plant Sci. 5: 1700012.

Cane, J. H. 2016. Adult pollen diet essential for egg maturation by a solitary Osmia bee. J. Insect Physiol. 95: 105-109.

Carvell, C., A. F. Bourke, S. Dreier, S. N. Freeman, S. Hulmes, W. C. Jordan and M. S. Heard. 2017. Bumblebee family lineage survival is enhanced in high-quality landscapes. Nature. 543: 547-549.

Campbell, D. R., N. W. Waser, M. V. Price, E. A. Lynch and R. J. Mitchell. 1991. Components of phenotypic selection: Pollen export and flower corolla width in *Ipomopsis aggregata*. Evolution. 45: 1458-1467.

Cnaani, J., J. D. Thomson and D. R. Papaj. 2006. Flower choice and learning in foraging bumblebees: Effects of variation in nectar volume and concentration. Ethology. 112: 278-285.

Colley, M. R. and J. M. Luna. 2000. Relative attractiveness of potential linsectary plants to aphidophagous hoverflies (*Diptera: Syrphidae*). Environ. Entomol. 29: 1054-1059.

Cresswell, J. E. 2000. Manipulation of female architecture in flowers reveals a narrow optimum for pollen deposition. Ecology. 81: 3244-3249.

Dreisig, H. 2012. How long to stay on a plant: The response of bumblebees to encountered nectar levels. Arthropod. Plant Int. 6: 315-325.

Elferajani, R. and R. Soolanayakanahally. 2018. Canola responses to drought, heat, and combined stress: Shared and specific effects on carbon assimilation, seed yield, and oil composition. Front. Plant Sci. 9: 1224.

Forrest, J. R. K. 2017. Insect pollinators and climate change. In: S. N. Johnson and T. H. Jones (Eds.), Global Climate Change and Terrestrial Invertebrates. Wiley-Blackwell, Hoboken, NJ, pp. 71-91.

Gallagher, K. M. and D. R. Campbell. 2017. Shifts in water availability mediate plant-pollinator interactions. New Phytol. 215: 792-802.

Gallai, N., J. M. Salles, J. Settele and B. E. Vaissiere. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. 68: 810-821.

Garrity, D. P. and J. C. O'Toole. 1994. Screening rice for drought resistance at the reproductive phase. Field Crops Res. 39: 99-110.

Giannini, A., M. Biasutti, I. M. Held and A. H. Sobel. 2008. A global perspective on African climate. Climatic Change. 90: 359-383.

Halpern, S. L., L. S. Adler and M. Wink. 2010. Leaf herbivory and drought stress affect floral attractive and defensive traits in *Nicotiana quadrivalvis*. Oecologia. 163: 961-971.

IPCC. 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. In: R. K. Pachauri, L. A. Meyer and Core Writing Team (Eds.), Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Khan, S. 2019. Climate classification of Pakistan. Int. J. Econ. Environ. Geol. 10: 60-71.

Lemoine, R., S. L. Camera and R. Atanassova. 2013. Source-to-sink transport of sugar and regulation by environmental factors. Front. Plant Sci. 4: 272.

Melser, C. and P. G. L. Klinkhamer. 2001. Selective seed abortion increases offspring survival in *Cynoglossum officinale* (Boraginaceae). Ann. Bot. 88: 1033-1040.

Miller-Struttmann, N. E., J. C. Geib, J. D. Franklin, P. G. Kevan, R. M. Holdo and D. Ebert-May. 2015. Functional mismatch in a bumble bee pollination mutualism under climate change. Science. 78: 75-78.

Nicolson, S. W. and R. W. Thornburg. 2007. Nectar chemistry. In S. W. Nicolson, M. Nepi, E. Pacini (Eds.), Nectaries and Nectar. Dordrecht, The Netherlands, Springer, pp. 215-264.

Ogilvie, J. E., S. R. Griffin, Z. J. Gezon, B. D. Inouye, N. Underwood, D.W. Inouye and R. E. Irwin. 2017. Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. Ecol. Letter. 20: 1507-1515.

Ollerton, J., R. Winfree and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos. 120: 321-326.

Pernal, S. F. and R. W. Currie. 2002. Discrimination and preferences for pollen-based cues by foraging honeybees, *Apis mellifera* L. Anim. Behav. 63: 369-390.

Phillips, B. B., R. F. Shaw, M. J. Holland, E. L. Fry, R. D. Bardgett, J. M. Bullock, and J. L. Osborne. 2018. Drought reduces floral resources for pollinators. Glob. Chang. Biol. 24: 3226-3235.

Pinheiro, C. and M. M. Chaves. 2011. Photosynthesis and drought: Can we make metabolic connections from available data? J. Exp. Bot. 62: 869-882.

Prather, C. M., S. L. Pelini, A. Laws, E. Rivest, M. Woltz, C. P. Bloch and S. Parsons 2013. Invertebrates, ecosystem services and climate change. Biol. Rev. 88: 327-348.

Rodenburg, J., H. Meinke and D. E. Johnson. 2011. Challenges for weed management in African rice systems in a changing climate. J. Agric. Sci. 149: 427-435.

Ropars, L., L. Affre, L. Schurr, F. Flacher, D. Genoud, C. Mutillod and B. Geslin. 2020. Land cover composition, local plant community composition and honeybee colony density affect wild bee species assemblages in a Mediterranean biodiversity hot-spot. Acta Oecol. 104: 103546.

Sanas, A. P., A. L. Narangalkar, S. K. Godase and V. V. Dalvi. 2014. Effect of honeybee pollination on quantitative yield parameters of mustard (*B. juncea*) under Konkan condition of Maharastra. Green Farm. 5: 241-243.

Scaven, V. L. and N. E. Rafferty. 2013. Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. Curr. Zool. 59: 418-426.

Schweiger, O., J. C. Biesmeijer, R. Bommarco, T. Hickler, P. E. Hulme, S. Klotz and T. Petanidou. 2010. Multiple stressors on biotic interactions: How climate change and alien species interact to affect pollination. Biol. Rev. 85: 777-795.

Settele, J., J. Bishop and S. G. Potts. 2016. Climate change impacts on pollination. Nat. Plants. 2: 16092.

Sinclair, T. R. and P. D. Jamieson. 2006. Grain number, wheat yield, and bottling beer: An analysis. Field Crops Res. 98: 60-67.

Thompson, J. D. 2001. How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? Oecol. 126: 386-394.

Thomson, D. M. 2016. Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. Ecol. Lett. 19: 1247-1255.

Vicens, N. and J. Bosch. 2000. Pollination efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on "Red Delicious" apple. Environ. Entomol. 29: 235-240.

Wallisdevries, M.F., C.A.M. Van Swaay, and C.L. Plate. 2012. Changes in nectar supply: A possible cause of widespread butterfly decline. Curr. Zool. 58: 384-391.

Waser, N. M. and M. V. Price. 2016. Drought, pollen and nectar availability and pollination success. Ecology. 97: 1400-1409.

Zhao, Z., N. Lu and J. K. Conner. 2016. Adaptive pattern of nectar volume within inflorescences: Bumblebee foraging behavior and pollinator mediated natural selection. Sci. Rep. 6: 34499.