RESEARCH ARTICLE

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Flower morphology and sexual phenotype of *Capparis ovata* Desf.

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Abstract

It was aimed to investigate the flower morphology and sexual phenotypes of *Capparis ovata* Desf. A *C. ovata* population inhabits in Çorum Osmancık Kumbaba locality. A total of 68 flower samples were collected from the population and their morphological characteristics and sexual phenotypes were investigated. According to the morphometric data, the coefficient of variation (CV) was calculated for the examined traits. Petal width (CV:3.11-20.26%) and sepal width (CV: 3.17-20.57%) showed the highest variation range. In terms of flower phenotype, 25 out of 68 flowers (36.76%) showed perfect flower and 43 (63.24%) showed male flower phenotype. The perfect flowers are hypogeynous flowers and have campylotropous type ovules. *C. ovata* has zygomorphic flower. *C. ovata* Desf. plants were defined as andromonoecious due to both the male flower and the perfect flower are present on the same plant. In conclusion, according to morphological analysis, a remarkably high variation was observed in flower morphological structures and the ratio of male flowers were found to be more common than perfect flowers in the *C. ovata* Desf. population. During evolutionary history, the protandry feature, in which male and female reproductive organs begin to develop at different times in perfect flowers, emerged in plants to prevent the depression of self-pollination, and inbreeding.

Keywords: *Capparis* L., *Capparis ovata* Desf., flower morphology, morphological variation, andromonoecious

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INTRODUCTION

Capparis ovata Desf., defined in the *Capparis* L. section of the *Capparis* L. genus of the *Capparaceae* L. family, includes more than 250 species (Jacobs, 1965; Mabberley, 1987: Willis, 1988; Fici, 1993; Inocencio et al., 2006) growing in tropical and subtropical regions of the New and Old World. Five main species are distributed in the Mediterranean region. These were defined as *Capparis spinosa* L., *Capparis sicula* Veill., *Capparis aegyptia* (Lam.) Boiss., *Capparis orientalis* Veill., and *Capparis ovata* Desf. (Inocencio et al., 2006). There are two species (*Capparis spinosa* L. and *Capparis ovata* Desf.) and three varieties of each species; *C. spinosa* L. var. *spinosa* L, *C. spinosa* L. var. *inermis* Turra., *C. spinosa* L. var. *aegyptia* (Lam) Boiss, and *C. ovata* Desf. var. *palaestina* Zoh., *C ovata* Desf. var. *herbacea* (wild) Zoh., and *C. ovata* Desf. var. *canescens* (Coss.) Heywood. growing in Türkiye (Zohary, 1960; Davis, 1965). While it is widespread in countries such as Spain, Italy, and Sicily in the Mediterranean region, it is also widespread in Far Eastern countries such as India and China,

It grows naturally in the provinces Hakkari, Karabük, Ankara, Artvin, Denizli, Tokat (TÜBİVES), Adıyaman, Antalya, Aydın, Balıkesir, Batman, Çorum, Denizli, Diyarbakır and Şanlıurfa (Özbek & Kara 2013) in Türkiye. The caper plant has various names used by local people around the world, some of which are "kapari, gebere otu, kapara, devedikeni, gebre, gebere, geber otu, gevil, bubu, kebere, yumuk, kemeri, menginik, keper, kepere, kedi tırnağı, şeballah" (Kara, 2012). In Türkiye, it is generally referred to as "kapari", "kebere" or "gebre otu" (Bilgin, 2004; Baytop, 1995).

C. ovata Desf. is a shrub that is shorter in height, grows procumbent and pendulous in habit (Figure 1), and can grow at higher altitudes such as 1500-2000 m (Davis, 1982). Its leaves are elliptical or broadly elliptical, rarely nearly round-shaped, with a distinct mucronate apex, and are often more or less hairy (Figures 2a, b and c). The flowers are strongly zygomorphic and andromonoecious, which is the presence of a male and a perfect flower on the same plant (Figure 3 and Figure 4). Stipules are strongly or weakly curved downwards or straight (Özcan, 1996; Kara, 2012; Özbek & Kara, 2013). The bery-like fruits, (called karpuzcuk in Turkish), rupture when they ripen and the seeds are scattered around (Figure 5 and Figure 6).

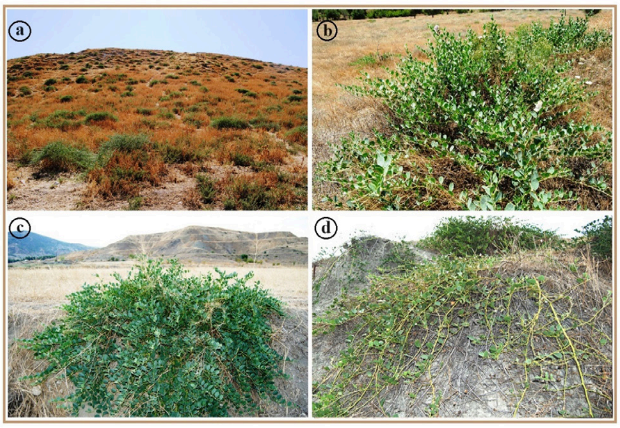

Figure 1. Types of habits in *C. ovata* Desf. a) procumbent, Diyarbakır Bismil-Üçtepe, b-c) procumbent, Çorum Osmancık, d) pendulous, Çorum Osmancık (Photo: Özlem Özbek)

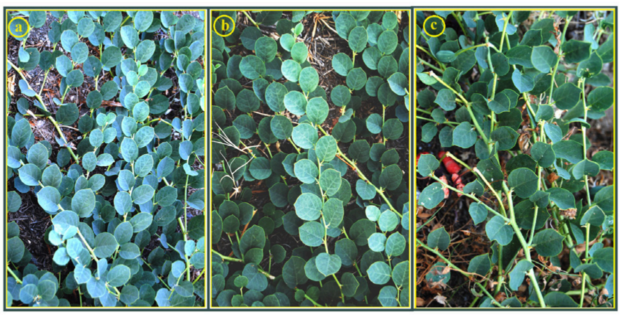

Figure 2. Leaf shapes seen on the *C. ovata* Desf. plants, in Çorum Osmancık, a-b) The leaves show an alternating arrangement, c) the mucronate structure on the apex of the leaves, and the backward and yellowish color stipules at the base of the leaves (Photo: Özlem Özbek)

Figure 3. A male flower on a *C. ovata* Desf. plant in Çorum Osmancık (Photo: Özlem Özbek)

Figure 4. A perfect (hermaphrodite) flower on a *C. ovata* Desf. plant in Çorum Osmancık (Photo: Özlem Özbek)

Figure 5. The ruptured berry-like fruit on a *C. ovata* Desf. plant in Çorum Osmancık (Photo: Özlem Özbek)

Figure 6. When the red-fleshy fruit completes its ripening, ruptured and opened to be dispersed its seeds (*C. ovata* Desf.) in Çorum Osmancık (Photo: Özlem Özbek)

Pollination is an important function in plants to ensure fertilization and development of seeds and to guarantee the continuation of generations. The adaptation of plants to different pollination factors in their evolutionary history is also observed in the capparis flower. During the evolutionary process, plants have gained plasticity in their reproductive organs to adapt to their environment. This flexibility is related not only to the flower symmetry, but also to features such as color, number of stamens, petal shape, long stamen filament, odor, time and rate of nectar production. Pollination agents have also diversified along with the evolution of plants in their evolutionary history. Pollination agents such as bees, humming birds, hawk moths and bats help pollination in capers. The existence of hermaphrodite species in which the male gamete matures before the female gamete and self-pollination is also frequently observed in hermaphrodite species in order to be protected from the depression of selfing (Kers, 2003).

Due to the very high level of dormancy observed in capparis seeds, there are not many studies on cytogenetics and karyotype of capparis. Although there is no study conducted in Türkiye, the chromosome number of *Capparis spinosa* was determined as 2n = 38 according to several previous studies (Murin & Chaudhri, 1970; Magulaev, 1979 according to Goldblatt, 1984; Al-Turki et al., 2000). According to researchers, it has been reported that caper is a polyploid and aneuploid plant, the number of chromosomes varies and the average number of chromosomes can be expressed as x = 10 (Kers, 2003).

Zhang and Tan (2009) investigated the pollen donor and pollinator attractor hypotheses of male flowers of andromonoecious plants in *C. spinosa* L. (Capparaceae). They showed that male flowers produced larger anthers, larger pollen grains, and smaller ovaries than perfect flowers, indicating that pollinators did not discriminate between flower morphs and transferred pollen grains a similar distance. They concluded that female reproductive success is likely not limited to pollen, with male flowers of *C. spinosa* L. conserving resources for female function and serving primarily to attract pollinators as pollen donors. Yang et al. (2014) examined the reproductive characteristics of *C. spinosa* L. (Capparaceae), they detected two different flowering periods in months. They stated that there were significant differences in the morphology of male flowers and perfect flowers in these two periods. The researchers concluded that variation in male to perfect flower ratio in *C. spinosa* L. plays a positive role in ensuring a constant pollen supply and controlling fruit investment. Shakarishvili and Osishvili (2013) studied the sexual phenotypes of *Capparis herbacea* Willd. They explained that *C. herbacea* Willd. also has androecium flower morphology, a hermaphrodite sexual system that produces both male and perfect flowers on the same plant. They stated that functionally male flowers have larger anthers and develop more stamens than perfect ones, while the male/perfect flower ratio varies between 0.5 and 2.6 during the flowering season. Additionally, they concluded that pollinating agents did not show any preference for flower morphs during their visit, and these results confirmed the pollen donation hypothesis regarding the role of male flowers in andromonoecious plants.

Most of the studies conducted on *Capparis* L. plants in Türkiye include on the propagation of the plant by vegetative methods and breaking seed dormancy. There are no comprehensive studies on the reproductive biology of the *Capparis* L. in Türkiye. For this reason, it was aimed to conduct a study on the investigation of flower morphology and sexual phenotypes regarding reproductive biology in *C. ovata* Desf.

MATERIALS AND METHODS

Materials

A total of 68 flower samples, including 8 plants, were collected from a *C. ovata* Desf. population located in Çorum Osmancık Kumbaba locality in June 2015.

Methods

The flowers were examined according to morphological characteristics of petal width (PW), petal length (PL), sepal width (SW), sepal length (SL), flower peduncle length (FPL), number of stamens (NS) and sexual phenotypes (male and perfect flowers). The mean and standard deviation values of morphological characters in flower structure were estimated (Table 1). Morphometrical characters for each flower were measured in cm with a ruler. Coefficients of variation (CV) were calculated based on the average morphometric values. The classical coefficient of variation (CV) is the ratio of the standard deviation calculated in a data set to the mean and can be used to compare normally distributed data based on their variability (Ospina & Marmolejo-Ramos 2019). The coefficient of variation is very useful as a statistical tool because it allows variables to be compared independently of scale effects and is dimensionless, meaning it has no units. It allows comparison of data sets with various different units of measurement (Ospina & Marmolejo-Ramos 2019). If the CV value is equal to 1 or 100%, the standard deviation is equal to the mean. Values less than one mean the standard deviation is smaller than the mean (typical), values greater than one mean the standard deviation is larger than the mean. A CV exceeding about 30 percent is usually an indication that there are problems with the data or that the experiment is out of control. Variables with a mean less than one will also provide inaccurate results and the coefficient of variation will be very large and often insignificant. This measurement is widely used in many fields such as social science, engineering, and life science (Brown, C.E. 1998). It is calculated according to the formula below.

$$CV = \frac{Standard\ Deviation}{Mean}$$

The structures of male and female organs in the flower structure during bud development were examined and visualized under a microscope.

RESULTS AND DISCUSSION

It was determined that the *C. ovata* Desf. plants examined in this study had an andromonoecious type reproductive system. Andromonoecy is a reproductive system in flowering plants where individuals produce both perfect flowers and male flowers. It is widely distributed in thirty-three families and approximately 4000 Angiosperm species (Yampolsky & Yampolsky, 1922; Bawa & Beach, 1981; Cruden & Lloyd, 1995; Miller & Diggle, 2003; Vallejo-Mar'in & Rausher, 2007; Zhang & Tan, 2009). It has been suggested that andromonoecy evolved from hermaphroditism with the loss of female reproductive structure, which was the first step in the evolution of the plant reproductive system towards monoecy, androdioecy and dioecy (Primack & Lloyd, 1980; Bertin, 1982; Zhang & Tan, 2009). It was determined that the capparis plants examined in this study had both male and perfect flowers on the same plant. The average values of metric measurements made for the morphological characteristics of the flowers were given in Table 1. When the number of flowers collected from eight plants was considered in the study, an average of 8.5 flowers per plant were examined, with a minimum of three and a maximum of 10 flowers. Of the 68 flowers examined, 25 showed perfect flower phenotype, while 43 showed male flower phenotype. The ratio of the number of male flowers to the number of female perfect flowers was calculated as 1.72. It was found that the number of male flowers is almost as high as twice the number of perfect flowers. When the data [APW (14.37), APL (30.87), ASW (10.32) and ASL (22.92)] were examined, it was seen that the rates were greater in male flowers than perfect flowers. It was observed that the mean values for ANS (67.33) was highger in plants with male flowers.

Table 1. Mean and standard deviation values of morphological characters measured in flower structure structures of *C. ovata* plants

PN	1	2	3	4	5	6	7	8
NFS	3	10	10	10	10	5	10	10
MF/PF	2/1	6/4	6/4	4/6	4/6	3/2	10/0	8/2
SNR	65-70	50-71	46-68	46-66	50-68	55-69	54-78	51-80
APW	14.37	8.98	11.58	11.9	13.1	10.96	13.07	8.51
St.Dev.	*0.45*	*1.3*	*1.77*	*2.41*	*1.81*	*1.38*	*1.46*	*1*
APL	30.87	18.1	24.96	22.84	20.81	28.27	24.45	21.01
St.Dev.	*0.48*	*1.85*	*4.19*	*3.33*	*1.83*	*3.77*	*2.87*	*1.89*
ASW	9.92	8.13	9.51	8.69	9.67	9.15	10.32	7.28
St.Dev.	*0.31*	*0.67*	*1.31*	*1.17*	*0.71*	*1.25*	*2.12*	*0.67*
ASL	22.92	17.21	19.71	19.13	17.54	21.02	22.32	18.02
St.Dev.	*2.17*	*1.48*	*1.13*	*0.76*	*0.86*	*1.42*	*1.41*	*1.61*
AFPL	47.24	45.85	49.16	42.39	36.64	51.29	57.23	51.12
St.Dev.	*8.07*	*3.66*	*5.71*	*3.92*	*4.39*	*2.48*	*4.06*	*5.43*
ANS	67.33	60.1	56.8	57.9	59.5	63.8	61.8	58.6
St.Dev.	*2.52*	*6.4*	*7.48*	*5.7*	*7.38*	*5.26*	*6.99*	*8.75*
ANMF	66	61.17	57.67	55.75	58.75	61.67	61.8	58.13
St.Dev.	*1.41*	*2.24*	*7.74*	*2.5*	*7.46*	*5.86*	*6.99*	*9.4*
ANPF	2.5	58.5	55.5	59.33	60	67	0	60.5
St.Dev.	*1.96*	*3.61*	*8.02*	*6.98*	*8*	*2.83*	*0*	*7.78*

Abbreviations: PN: Plant Number, NFS: Number of Flower Sample, MF/PF Male:Flower / Perfect Flower Number Ratio, SNR: Stamen Number Range, APW: Average Petal Width, APL: Average Petal Length, ASW: Average Sepal Width, ASL: Average Sepal Length, AFPL: Average Flower Peduncle Length, ANS: Average Number of Stamens, ANMF: Average Number of Male Flowers, ANPF: Average Number of Perfect Flowers, St. sp.: Standard Deviation

Flowering in the capparis plants continues from May to October in nature.

According to the results of the study, it was determined that the male flower ratio of 1.72 (43 male/25 perfect flowers) was more common in flower phenotypes in plants belonging to the *C. ovata* Desf. population. This result is consistent with Yang et al. (2014), it also appears to have a higher rate, although it is consistent with their 5-month observations. Researchers stated in their studies that in the first period of flowering, the number of male flowers is more than female flowers, and in the second period, while there is no difference in the number of male flowers, there is an increase in the number of female flowers. This ensures the pollen supply of male flowers while ensuring the perfect flower's adaptation to environmental conditions to produce reproductively functional fruits and seeds. Protandry is the condition in which male and female reproductive organs develop at different times in hermaphrodite flowers in order to limit the depression of inbreeding in plants, and it is estimated that this feature might be found in *C. ovata* Desf. plants, but further studies should be performed. The results of this study seem to be consistent with previous studies on the reproductive system of *Capparis* L. (Kers, 2003; Zhang & Tan, 2009; Shakarishvili & Osishvili, 2013; Yang et al., 2014).

When the peduncles of the buds were examined under the microscope, they were observed to be covered with very dense, white, and soft velvety hairs. It was observed that there was hairiness on the parts of the sepals surrounding the flower towards the receptacle, but the density decreased towards the tips (Figure 7a). When the sepals were opened, it was seen that the petals tightly covering the reproductive organs were white and their outer surfaces were hairy (Figure 7b). When the petals were stripped off, it was seen that numerous stamens with yellowish-white stems and violet-colored anthers tightly surrounded the pistil (Figure 7c). *C. ovata* Desf. had hypogynous flower, in which the floral parts sepals and petals attached to the receptacle were beneath the ovary including many campylotropous type ovule was observed in the perfect flowers (containing female and male organs) (Figures 8 a and b). While the flower shape was observed to be zygomorphic (bilaterally symmetrical) (Figures 3 and 4), the placentation pattern in the ovary was observed to be parietal placentation (Figures 7 f and g). The color of the ovary was from yellowish to light green, and the stigma was dark, almost black. It was determined that the color of the anthers of the stamens was violet in the early development stage and had a lobed appearance. It was observed that the anthers had a swollen and lobed dorsal area and a flattened and lobed shape on the lower surface in the advancing development phase, and the reproductive organs of the flower, especially around the anthers, were covered with crystal-shaped and dense white color nectar (Figures 6 h-j). Although the pollen shapes appeared to be oval-shaped, it was observed that there were also variations. The observed pollen grains had tricloplorate aperture (they had 3 pores and 3 colpus). The shape of amb was elliptic in generally but their equatorial view was circular. Ornamentation was not observed in LM (Light Microscope) (Figure 9).

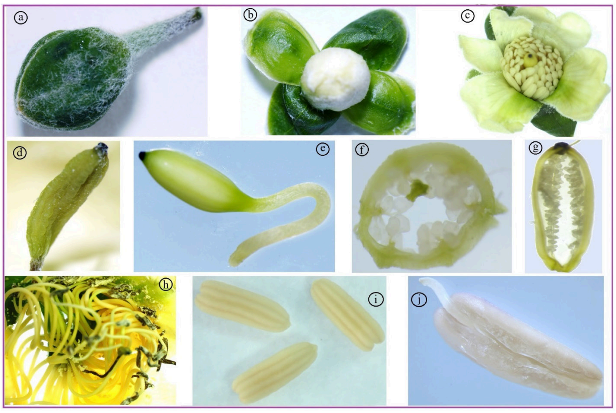

Figure 7. Flower morphology of *C. ovata* Desf. plants in Çorum Osmancık; a) flower bud, b) the flower bud with its sepals stripped off, c) the stamens surrounding the ovary in the bud, d and e) ovary, f) cross-section of an ovary, g) longitudinal section of an ovary, h) the scattered appearance of an ovarium and stamens, i-j) the unmatured anthers in Çorum Osmancık (Photo: Özlem Özbek)

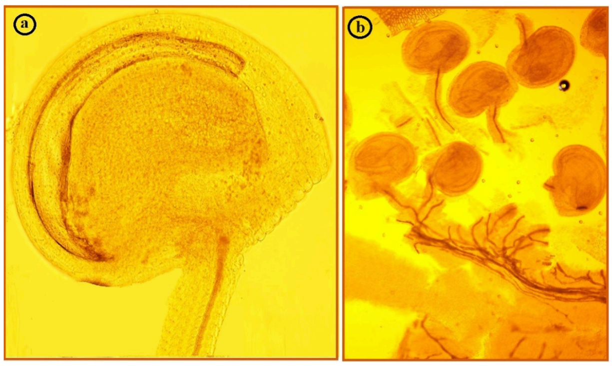

Figure 8. Morphology of the ovules in the ovary of the *C. ovata* Desf. plant in Çorum Osmancık; a) ovule, b) some ovules attached to the placenta and some was broken off (Photo: Özlem Özbek)

According to the data obtained as a result of morphometric measurements, mean, standard deviation and coefficient of variation values calculated (Table 2). PW (CV: 3.11-20.26%) and SW (CV: 3.17-20.57%) showed the highest variation range. The results showed that there is considerable variation in the morphological structures of flowers belonging to the *C. ovata* Desf. Considering the samples with high coefficient of variation, it was determined that the number of male and perfect flowers was higher in plants that were close to each other. This is because the petal and sepal sizes in male flowers are larger than in perfect flowers, causing variation. On the other hand, variation is seen less in samples with a high number of male flowers. The fact that male flowers are larger and showy makes them appear more attractive to pollinators. This increases pollination and ensures fertilization. In addition, the pollens produced in male flowers are larger, and the vegetative cell quickly forms the pollen tube in the stylus, ensuring the completion of the fertilization process (Skogsmyr & Lankinen, 2002; Shakarishvili & Osishvili, 2013).

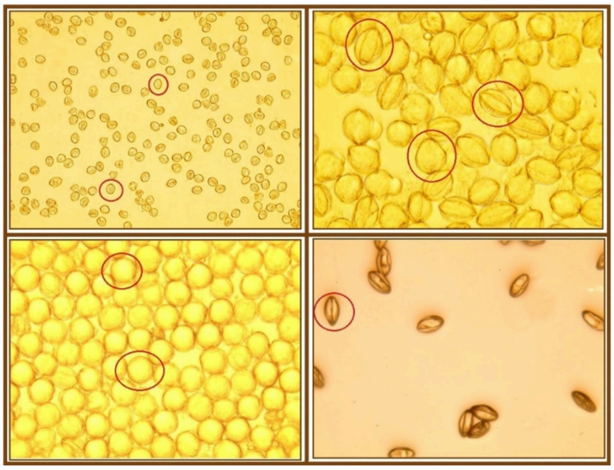

Figure 9. Images of the pollens produced in the anthers of the *C. ovata* Desf. plants in Çorum Osmancık (Photo: Özlem Özbek)

Although the formation of functional male or perfect flower sexual phenotypes on the same flower in plants expression of male genes in the late stages of bud development in *C. herbacea* is not yet known. Song et al. (2012) revealed that the flower development in poplar is regulated epigenetically. Organogenesis studies have suggested that the development of a male or perfect flower in a fully developed bud may result from late epigenetic regulation of gene expression responsible for their formation (Shakarishvili ve Osishvili, 2013).

Caper plants are wild forms that grow naturally, local people collect the caper buds and make pickles, and the number of flowers in the plants that are damaged by herbivorous animals grazing is generally low. In fact, this is an important issue that could be risky for the future of natural plant populations. Personal studies and observations on capers in the study field have been continuing for about 15 years. The number of individual plants in the caper populations in the region decreased greatly in this period and the plants in the current population remained very weak and could not produce sufficient flowers and fruits. Local people unconsciously collect almost all of the plant buds, and the remaining ones cannot produce sufficient flowers, fruits and seeds due to environmental conditions and herbivores damage. In addition, a small-scale farm-like area was established in the region where there was a *C. ovata* population, and the owner of the farm stated that the caper plants were still growing even though they were removed from his yard. In order to preserve valuable genetic resources and genetic diversity, educating local people on the importance of surviving natural populations and preserving genetic diversity, and how to collect flower buds and fruits, in regions where naturally growing and economically valuable plants such as capers are grown, will make a significant contribution.

Table 2. Coefficients of variation (CV%) of morphological characters measured in the flowers of *C. ovata* Desf. plants.

PN	NFS	MF/PF	PW-CV (%)	PL-CV (%)	SW-CV (%)	SL-CV (%)	FPL-CV (%)	NS-CV (%)	STL-CV (%)	NMF-CV (%)	NPF-CV (%)
1	3	2/1	3.11	1.57	3.17	9.49	17.09	3.74	-	2	0
2	10	6/4	14.44	10.20	8.23	8.59	7.97	10.65	22.47	4	6
3	10	6/4	15.33	16.79	13.74	5.72	11.61	13.17	10.51	13	14
4	10	4/6	20.26	14.60	13.48	3.98	9.25	9.85	12.69	4	12
5	10	4/6	13.85	8.80	7.36	4.91	11.98	12.41	9.00	13	13
6	5	3/2	12.60	13.34	13.70	6.75	4.83	8.25	4.44	10	4
7	10	10/0	11.17	11.75	20.57	6.31	7.10	11.31	-	11	0
8	10	8/2	11.76	8.98	9.25	8.95	10.62	14.92	11.41	16	13

Abbreviations: Abbreviations: PN: Plant Number, NFS: Number of Flower Sample, MF/PF: Male Flower / Perfect Flower Number Ratio, PW: Petal Width, PL: Petal Length, SW: Sepal Width, SL

is genetically determined, it may also depend on the availability of resources and other environmental conditions to ensure successful reproduction (Cao ve Kudo, 2008, Peruzzi ve diğerleri, 2012; Shakarishvili ve Osishvili, 2013). Andromonoecious, defined as the genetic mechanism responsible for the selective

CONCLUSION

This study is the first attempt to reveal the andromonoecious reproductive system of *C. ovata* Desf from Türkiye. *C. ovata* Desf. has zygomorphic flowers, and hermaphrodites have hypogynous flower type depending on the ovary position. It has campylotropous type ovules located on the parietal placenta in the ovary. The data obtained displayed that this species represents a variable sexual phenotype ratio (male flower/perfect flower = 1.72). Since the samples were collected from the natural environment, some environmental factors cannot be controlled; regular observations cannot be made on the plants throughout the flowering period from May to October. It was concluded that the studies on the reproductive biology of andromonoecious plants, especially in controlled environments such as botanical gardens, on more samples, would produce more efficient results about the reproductive biology of these species.

COMPLIANCE WITH ETHICAL STANDARDS

This research study complies with research and publishing ethics. The scientific and legal responsibility for manuscripts published in JAEFS belongs to the author(s).

Peer-review

Externally peer-reviewed.

Conflict of interest

The author declared that for this research article, she has no actual, potential or perceived conflict of interest.

Author contribution

The author verified that the Text, Figures, and Tables are original and that they have not been published before.

Ethical approval

Ethics committee approval is not required.

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Data availability

Not applicable.

Consent for publication

Single authorship, therefore consent for publication is not applicable.

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