

## Predominance of parthenogenetic reproduction in *Aphis gossypii* populations on summer crops and weeds in Greece

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### Abstract

The photoperiodic response of 56 parthenogenetic lineages of *Aphis gossypii* Glover was examined by rearing the aphids for three generations under short day conditions (SD, L10:D14) and 17 °C. The lineages were derived from aphid samples collected in central and northern Greece from various crops and uncultivated plants of the families Asteraceae [chrysanthemum *Chrysanthemum* sp., smooth sow-thistle *Sonchus oleraceus* L. and dahlia *Dahlia variabilis* (Willd.)], Cucurbitaceae [watermelon *Citrullus lanatus* (Thunb.) and zucchini *Cucurbita pepo* L.] and Malvaceae [cotton *Gossypium hirsutum* L., okra *Abelmoschus esculentus* (L.), and rose of Sharon *Hibiscus syriacus* L.]. The results showed that the predominant life cycle category in both central and northern Greece (despite possible differences in winter severity among regions) was obligate parthenogenetic (anholocyclic) as 55 out of the 56 lineages belonged to this category. These lineages produced mostly wingless parthenogenetic females at percentages 59-83% and 48-86% in the first and late born progeny of the second generation under SD, respectively. The remaining percentages refer to winged parthenogenetic females. The only lineage capable of sexual reproduction was an 'intermediate' one which was sampled on cotton in northern Greece. Most of its progeny in the second generation under SD were wingless parthenogenetic females (65%). The percentage of winged parthenogenetic females, males and 'intermediate' females (produce wingless parthenogenetic and a few sexual females) were 8, 22, and 5%, respectively. The results reported here are considered as the first for southern European populations and support the general belief that *A. gossypii* is mostly anholocyclic in Europe.

**Key words:** cotton aphid, life cycles, cyclical parthenogenesis, obligate parthenogenesis, Greece.

### Introduction

*Aphis gossypii* Glover (Homoptera Aphididae), known as cotton or melon aphid, is a remarkable species in terms of geographical and host plant range. It is extremely polyphagous infesting over 900 plant species (Blackman and Eastop, 2000). The aphid has become a serious pest of field and glasshouse crops, especially cotton *Gossypium hirsutum* L. (Malvaceae), Cucurbitaceae and ornamental plants such as *Chrysanthemum*. Besides the direct damage on the crops the aphid causes indirect damages by transmitting more than 50 plant viruses (Blackman and Eastop, 2000).

In Europe, *A. gossypii* is considered as a subspecies of the *Aphis frangulae* Kaltenbach complex (Homoptera Aphididae), a group of closely-related indigenous European species (Stroyan, 1984; Heie, 1986). Heie (1986) has described four members in this group which are almost morphologically indistinguishable. Two subspecies are holocyclic (= cyclical parthenogens) with host alternation between *Rhamnus frangula* L. (Rhamnaceae), the primary host where the sexual phase take place, and various plant species serving as secondary hosts where several parthenogenetic, all-female, generations are observed. Another subspecies is also holocyclic, but probably lives on *Rhamnus* only. *A. gossypii* is considered as the only subspecies that does not have a sexual phase on *Rhamnus* and reproduces parthenogenetically (= obligate parthenogen) all-year-round on a wide range of herbaceous plants. However, it has been found that populations from chrysanthemum *Dendranthema grandiflora* Tzvelev (Asteraceae) (Guldmond *et*

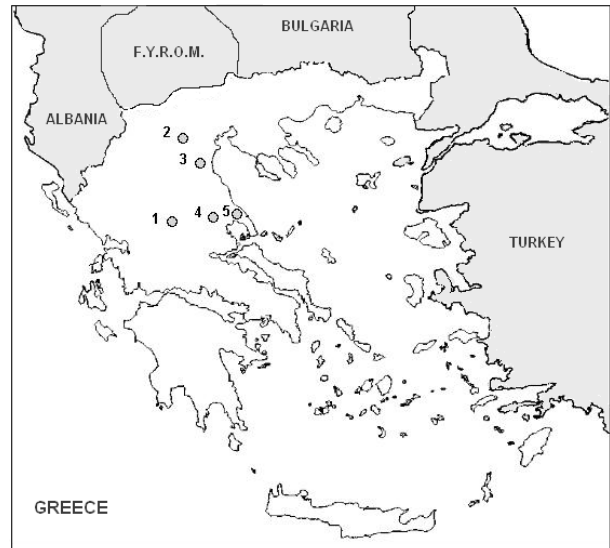
*al.*, 1994) and cucumber (Fuller *et al.*, 1999) in western European glasshouses can produce sexual morphs under certain conditions. Previously Thomas (1968) and Böhm (1964) reported sexual reproduction of this aphid in Europe. The former author got oviparous females in a culture on shepherd's purse *Capsella bursa-pastoris* (L.) (Brassicaceae) derived from aphids from *Cucumis sativa* L. (Cucurbitaceae) in Berlin-Dahlem, but males were not observed. Böhm (1964) reported that *A. gossypii* populations in Austria complete a holocyclic life cycle between *Frangula* or *Rhamnus* and Cucurbitaceae or *Verbena*.

Sexual reproduction has been also reported in other parts of the world. Kring (1959) found that *A. gossypii* populations complete a holocyclic life cycle and utilize southern catalpa *Catalpa bignonioides* Walter (Bignoniaceae) and rose of Sharon *Hibiscus syriacus* L. (Malvaceae) as primary hosts in Connecticut, USA. In Far East (China and Japan), populations of *A. gossypii* can also reproduce sexually and various unrelated primary hosts including *Rhamnus* spp., flatspine prickly ash *Zanthoxylum simulans* Hance (Rutaceae), pomegranate *Punica granatum* L. (Punicaceae), oriental bittersweet *Celastrus orbiculatus* Thunb. (Celastraceae), and *H. syriacus* have been recorded (Inaizumi, 1980; Zhang and Zhong, 1990). A monoecious holocyclic life cycle of *A. gossypii* on Indian madder *Rubia cordifolia* L. (Rubiaceae) and *H. syriacus* has also been reported by Inaizumi (1980) and Zhang and Zhong (1990), respectively. Apart from genetic factors (loss of sexuality) sexual reproduction in aphids, including *A. gossypii*, is driven from environmental conditions such as photoper-

riod and temperature. In temperate regions, sexual morphs of most aphid species usually appeared in autumn as daylight becomes shorter and temperature also drops. In several species sexual females and males are induced mostly by less than 15.0 hours light per day and by temperatures lower than 25 °C (see Kawada, 1987 and references therein).

Although *A. gossypii* is considered as an extremely polyphagous species, host-adapted races have been identified. In European glasshouses, aphids from chrysanthemum *Chrysanthemum* or *D. grandiflora* did not colonize cucumber *Cucumis sativus* L. (Cucurbitaceae) and vice-versa (Furk and Hines, 1993; Guldmond *et al.*, 1994). Vanlerberghe-Masutti and Chavigny (1998) reported RAPD variation among populations from various parts of the world and showed that *A. gossypii* forms with particular host associations are distributed over a wide area. It is considered that two forms of *A. gossypii* have become widely distributed, both with rare sexual reproduction, being one colonizing Cucurbitaceae and Malvaceae and the other Asteraceae (Blackman and Eastop, 2007). Recent evidence of the existence of a distinct, widely distributed form of *A. gossypii* feeding on Asteraceae has been provided by a multivariate morphometric study by Margaritopoulos *et al.* (2006).

*A. gossypii* is an economically important aphid pest in southern Europe. In Greece it is a serious pest of cotton as well as of several vegetable and ornamental crops. In 2003 season 6.5 tonnes of active ingredient of different insecticides were used against *A. gossypii* in cotton (Bayer CropScience Hellas, pers. Comm.). A survey of aphid vectors of non-persistent virus in zucchini, *Cucurbita pepo* L. (Cucurbitaceae), crops in northern Greece using Moericke traps revealed *A. gossypii* as one of the most abundant vector (Katis *et al.*, 2006). In addition, *A. gossypii* was the most frequent captured species (ranked first or second according to the region and year) in the Greek network of suction traps consisted of five traps in different regions, i.e., Mikra, Thessaloniki; Velestino, Magnesia; Kopais, Voiotia; Pyrgos, Peloponnese; Lasithi Plateau, Crete (Tsitsipis *et al.*, 1998; Katis *et al.*, 2006). However, there is not any study about the life cycle variation in this aphid species in Greece and therefore about its overwintering strategy. There are some indications from the early detection of the aphid in the Greek network of suction traps about possible parthenogenetic overwintering. The temperate climate of Greece is suitable for aphids to reproduce sexual, given the availability of a primary host, and this has been demonstrated in another host-alternating species, i.e., *Myzus persicae* (Sulzer) (Homoptera Aphididae) (Margaritopoulos *et al.*, 2002). In addition, aphids can also overwinter parthenogenetically on protected crops or in the field on winter crops and weeds in mild winters. Knowledge on the life cycle of aphid populations could aid crop protection strategies as the source of aphids can be determined and their migration can be elucidated. Such information could also complement studies on aphids' population genetics and those focusing on the development of resistance to insecticides. The present study aims at exploring the life cycle category of cotton aphid lineages originating from various hosts in mainland Greece.



**Figure 1.** Sampling sites of *A. gossypii* parthenogenetic lineages. 1: Karditsa (39°22'N, 21°53'E), 2: Meliki (40°32'N, 22°25'E), 3: Katerini (40°16'N, 22°30'E), 4: Velestino (39°23'N, 22°45'E), 5: Volos (39°22'N, 22°56'E). All sites are approximately at sea level.

## Materials and methods

The life cycle category of 56 *A. gossypii* parthenogenetic lineages from various hosts and regions of Greece was examined during the years 2003-2004 (figure 1, table 1). The lineages were derived from samples collected from various crops and uncultivated plants belonging to the families Asteraceae [chrysanthemum *Chrysanthemum* sp., smooth sow-thistle *Sonchus oleraceus* L. and dahlia *Dahlia variabilis* (Willd.)], Cucurbitaceae [watermelon *Citrullus lanatus* (Thunb.) and zucchini] and Malvaceae [cotton, okra *Abelmoschus esculentus* (L.), and rose of Sharon]. Each sample was placed in a self-sealing plastic bag containing a piece of paper towel to absorb excessive moisture. Bags were put in insulated plastic containers, containing frozen ice packs, and transferred to the laboratory. In the laboratory, the samples were inspected for parasitoids and aphid species was identified using the key of Blackman and Eastop (2000). The parthenogenetic lineages were established from one adult wingless female per sample and they were kept for more than 5 generations in a climatic chamber at long day conditions (LD, L16:D8) and 17 °C until the examination of the life cycle category. Aphids were reared mainly on pepper *Capsicum annum* L. (Solanaceae) [potato *Solanum tuberosum* (L.) (Solanaceae), and zucchini were also used occasionally] excised leaves in Blackman boxes (Blackman, 1971). The rearing unit (Blackman box) is a clear perspex box with a lid (Azpack Limited, Leicestershire, UK). Two holes were opened, one in the box and the other in the lid (3 and 2 cm, respectively), both near to the one end, covered with aphid-proof muslin to allow ventilation. A perspex partition with a ~5 mm hole in the center was cemented across the box ~1.5 cm from the other end. A piece of

**Table 1.** Life cycle category (LC) of *A. gossypii* parthenogenetic lineages.

Region of origin	Host	Collection year	LC*	
			An	Int
Karditsa, central Greece	Cotton	2004	5	0
"	Smooth sow-thistle	2004	3	0
Meliki, northern Greece	Cotton	2004	5	0
Katerini, northern Greece	Cotton	2003-04	8	1
"	Water melon	2003	1	0
"	Smooth sow-thistle	2004	3	0
Velestino, central Greece	Cotton	2004	1	0
"	Okra	2004	6	0
"	Smooth sow-thistle	2003	4	0
Volos, central Greece	Cotton	2004	2	0
"	Rose of Sharon	2003	2	0
"	Zucchini	2004	5	0
"	Chrysanthemum	2003	9	0
"	Dahlia	2003	1	0

\*An = anholocyclic; Int = intermediate.

water-saturated sponge was placed in the small compartment, and a vertical split was made in the sponge corresponding to the hole in the partition. The petiole of the excised leaves was inserted through the hole in the partition into the sponge. Boxes were placed in trays containing water 3 to 5 mm deep. The leaves were replaced by fresh ones when it was deemed necessary. In addition, extra care was taken to minimize risk of clone contamination. Enough space was left among boxes to avoid cross-box contamination and fresh leaves were inspected for aphid infection.

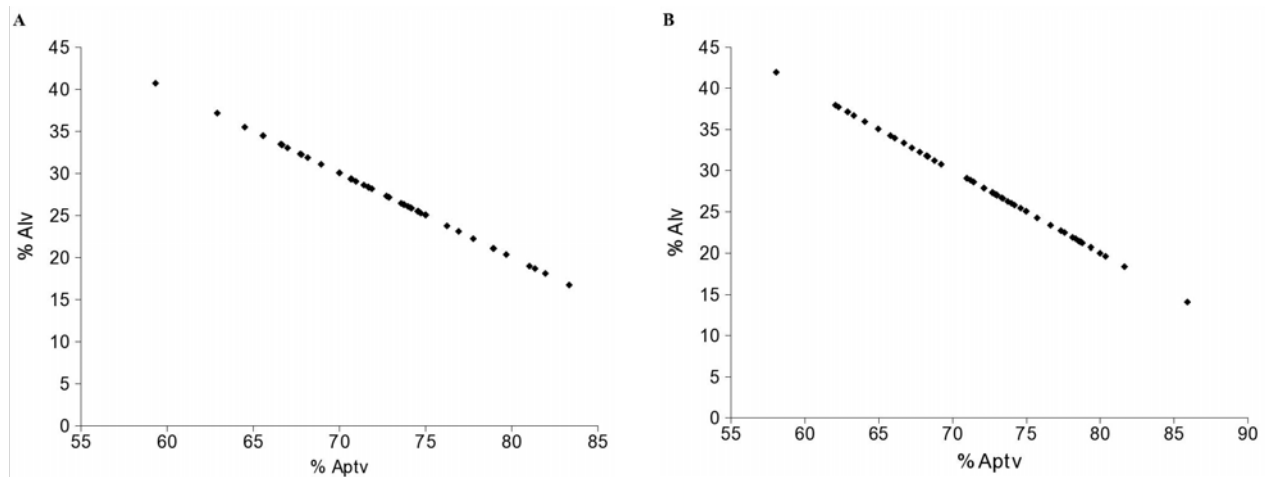
The life cycle category of the aphid lineages was determined after rearing them for three consecutive generations under short day conditions (SD, L10:D14) and 17 °C. The 10-hour photoperiod was chosen as in many aphid species the critical photoperiod for sexual morph production is less than 15 hours (Kawada, 1987), and longer periods of dark increase sexual morph production (e.g., Tsitsipis and Mittler, 1977; Mittler and Wilhoit, 1990). For each lineage a single young wingless adult female, from the colony kept in LD, was transferred to SD in a Blackman box. Five to six apterous wingless females from the first batch of individuals of the first generation (F1, produced during the first 1-2 days) under SD were selected and the first 53-66 progeny (= first born second generation, F2, progeny) were morphed on reaching adulthood as well as 50-66 progeny which were produced after the 13<sup>th</sup> - 15<sup>th</sup> day of reproduction (= late born second generation progeny). Wingless parthenogenetic females, oviparae (sexual females) and males can be easily identified (for description of the morphs see Miyazaki, 1987; Blackman and Eastop, 2000). In general, three morphological similar winged females can be produced, which can be identified according to the morph of their progeny. These three types are: parthenogenetic females that produce wingless and none or a few winged parthenogenetic females, gynoparae (sexual female, oviparae, producers) and 'intermediate' females that produce wingless parthenogenetic females and a few sexual females. Therefore, the type of the winged females (F2 generation) produced by each line-

age (9-26) were identified by rearing the females separately in Blackman boxes and recording the morph of all of their progeny (F3 generation) with particular emphasis on the appearance or not of sexual females.

## Results and discussion

All the four life cycle categories, i.e., cyclical parthenogenetic (holocyclic, one sexual generation alternates with many parthenogenetic, all female, generations), obligate parthenogenetic (anholocyclic) and functional parthenogenetic (mostly parthenogenetic females are produced along with some males in androcyclic genotypes and/or a few sexual females in 'intermediate' genotypes), described in other host-alternating aphid species such as *M. persicae* (Blackman *et al.*, 1972) and *Rhopalosiphum padi* (L.) (Simon *et al.*, 1991) have been reported in *A. gossypii*. However, all these categories were found only in populations from the Far East (Takada, 1988; Komazaki and Osakabe, 1998). The results of the present study showed that the predominant life cycle category on the summer crops surveyed in both central and northern Greece was anholocyclic as 55 of the 56 *A. gossypii* lineages examined were anholocyclic (table 1). These lineages produced wingless parthenogenetic females at percentages 59-83% and 48-86% in the first and late born progeny of the second generation (F2) under SD, respectively (figure 2). The remaining percentages refer to winged parthenogenetic females (they produce exclusively wingless parthenogenetic females or along with a few winged parthenogenetic females).

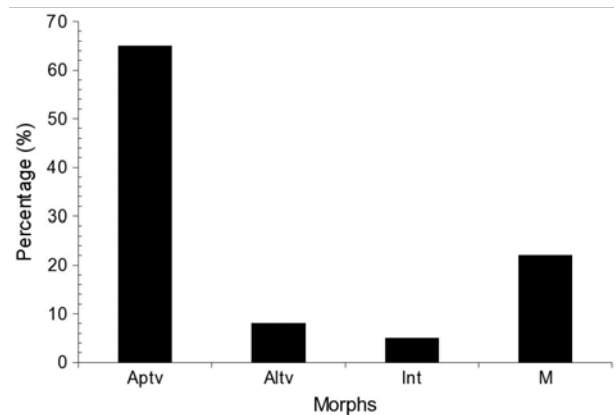
Holocyclic (cyclical parthenogenetic) lineages were not found. In general, these lineages produce mostly winged gynoparae along with winged males and sometimes a few parthenogenetic females in the second generation under SD. The only lineage capable of sexual reproduction was found on cotton in northern Greece. It was an 'intermediate' (functional parthenogenetic) lineage, i.e., it produced mainly wingless females and a number of winged parthenogenetic females, males and



**Figure 2.** Percentage of wingless parthenogenetic females (Aptv, apterous virginoparae) and winged parthenogenetic females (AltV, alate virginoparae) among the first born (A) and late born (B) progeny of 55 parthenogenetic lineages of *A. gossypii* in the second generation under short day conditions (L10:D14) and 17 °C. In each batch of progeny 50-66 individuals were examined in each aphid lineage.

'intermediate' females. In order to investigate in detail the sexual morph production by the intermediate lineage the morph of all the progeny of 10 first generation wingless females under SD were examined. The females were kept in separate Blackman boxes and transferred every four days in new boxes until they died. Their progeny were morphed at reaching adulthood and the type of the winged females produced was identified as described previously. Most of the progeny of the 'intermediate' lineage in the second generation under SD were wingless parthenogenetic females (65%, mean number = 18.4, mean total number of progeny = 28.4). The percentage of winged parthenogenetic females, males and 'intermediate' females were 8, 22, and 5%, respectively (the respective mean numbers were 2.2, 6.3, 1.5) (figure 3).

In general, the photoperiodic response (types and percentages of the different morphs produced) of the 'intermediate' lineage examined here is in agreement with that reported previously for similar genotypes of *A. gossypii* from the Far East (Takada, 1988; Komazaki and Osakaabe, 1998) and of other host-alternating species such as *M. persicae* (Blackman, 1971; Poupoulidou *et al.*, 2006) and *R. padi* (Tatchell and Parker, 1990; Simon *et al.*, 1991). However, one of the two 'intermediate' lineages from Japan examined by Takada (1988) showed differences compared to our as it produced more winged females (pooled data for parthenogenetic and 'intermediate' females) and fewer wingless parthenogenetic females and males. These differences could be attributed mostly to factors related to the aphid genotypes examined in the two studies as Takada (1988) used similar temperature to ours (18 vs. 17 °C) and the same photoperiod. In general, interclonal variation in morph production within life cycle category is common in aphids (e.g., Blackman, 1971; 1972; Simon *et al.*, 1991; Poupoulidou *et al.*, 2006). As it was expected our 'intermediate' lineage produced fewer males and winged females and much more wingless parthenogenetic females than the holocyclic lineages from Japan examined by Takada (1988).



**Figure 3.** Percentage of wingless parthenogenetic females (Aptv), winged parthenogenetic females (AltV), 'intermediate' females (Int) and males among the progeny of an intermediate *A. gossypii* lineage in the second generation under short day conditions (L10:D14) and 17 °C.

Our study contributes considerably to the belief that *A. gossypii* is mostly anholocyclic in Europe (Stroyan, 1984; Heie, 1986) as this is the first time that detailed results on the life cycle variation of this species have been provided for southern European populations. In Greece most of tree species that have been reported as primary hosts of the aphid can be found, although some of them not so frequently. The discovery of the intermediate genotype suggests that sexual phase could be gained by the Greek populations of *A. gossypii* taking into account that climatic conditions allow the production of sexual morphs. Nevertheless, no holocyclic genotypes on herbaceous crops were detected. There are several possible explanations for this lack. For instance, the species is considered anholocyclic in most parts of the world, including Europe (Stroyan, 1984; Heie, 1986; Blackman and Eastop, 2000), and therefore Greek populations may originate from such anholocyclic pools of genotypes.

Furthermore, winters in central Greece are often mild and sometimes in the northern regions surveyed in the present study allowing aphids to overwinter parthenogenetically not only on protected crops but also outdoors on crops and weeds. Under the Risper Model (Risper and Pierre, 1998; Risper *et al.*, 1998) parthenogenetic lineages due to their superior population growth out-compete sexual genotypes when freezing conditions during winters are infrequent. On the contrary, sexual reproduction in aphids has a short-term advantage during cold winters because of the overwintering, freezing resistant, sexually produced egg. Rarity of primary hosts, necessary for holocyclic genotypes to complete the annual life cycle, in the sampling regions might also be involved.

This predominance of parthenogenetic lineages might also be consistent with the General Purpose Genotype hypothesis (Lynch, 1984). This hypothesis seeks to explain the phenomenon of geographical parthenogenesis and makes also two predictions, i.e., clonal selection favours generalists that are able to survive environmental fluctuations compared to specialist and, most interesting, sexual genotypes are out-competed in parts of the range of parthenogens. Clonal selection, environmental factors (e.g., mild winters permitting all-year-round parthenogenetic reproduction) and rarity of primary hosts are among the factors responsible for the predominance of parthenogens of other aphid species in certain regions [Sitobion aphids: Simon *et al.* (1999), Wilson *et al.* (1999); *R. padi*: Martinez-Torres *et al.* (1997); *M. persicae*: Margaritopoulos *et al.* (2002), Guillemaud *et al.* (2003)].

Information on the life cycle and, therefore, the overwintering strategy of *A. gossypii* populations could support crop protection schemes. This information is useful in terms of aphid-borne virus epidemiology as the source of aphids can be determined. Individuals that overwinter on secondary hosts can transmit viruses to summer crops as weeds can also serve as virus reservoirs. By contrast, spring migrants of holocyclic clones are not vector of virus on leaving the woody primary hosts. Therefore, the predominance of anholocyclic lineages in the regions surveyed might suggest that there is a high risk of virus infections on summer crops through the immigration of viruliferous *A. gossypii* winged aphids.

Knowledge on life cycle variation of *A. gossypii* might also be useful for the interpretation of data from studies of the aphids' population genetics and those dealing with the development of resistance to insecticides. The anholocyclic way of life of *A. gossypii* in Greece is an indication of reduced genetic variation in terms of the number of distinct genotypes that comprise the species populations on herbaceous crops. A previous morphometric study on populations from Malvaceae, Cucurbitaceae and Asteraceae clearly differentiated the aphids collected on plant species from the latter family and clustered the individuals into two groups Asteraceae and Malvaceae-Cucurbitaceae (Margaritopoulos *et al.*, 2006). There was not found any distinct clustering within the two major groups which might suggest the existence of two or a few clones with different host-associated properties. Recent studies involving microsatellite DNA markers on populations from glasshouse cucurbit crops in France (Fuller *et al.*, 1999) and from

cotton in Cameroon (Brévault *et al.*, 2008) showed that the populations consisted mostly of 1-3 different genotypes (clones). This may be also the case for the Greek populations although further research is needed involving the examination of lineages of known life cycle category with DNA tools, such as microsatellite DNA markers that are able to track clones in space and time, and to evaluate the aforementioned hypotheses about the predominance of parthenogens on summer crops. Lastly, further surveys are needed especially from northern regions of Greece or from higher altitudes as well as from primary hosts in order to obtain a complete picture about the ability of *A. gossypii* to reproduce sexually and to produce holocyclic lineages in Greece that are fitted and able to persist.

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