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THE ROLE OF THRIPS IN POLLINATION OF *ARCTOSTAPHYLLOS UVA-URSI*

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Because of the low availability of insects other than thrips as potential pollinators in arctic environments, early botanists of the twentieth century proposed that thrips pollination would be important in many plants, especially those of the Ericaceae family. However, this was an object of controversy that continues today. In this article, we combined experimental evidence and a broad regional survey to analyze the role of thrips in flower pollination of the Ericaceae *Arctostaphyllos uva-ursi*. We conducted exclusion experiments, nectar measures, and observation of thrips in plants during 2 yr at four populations in southwestern Europe. We found that flower pollination by thrips seems to be a common element in the studied populations of *A. uva-ursi* that accounts for ~20% of the total pollination. We found seven species of thrips visiting the flowers of ~50% of the individuals of *A. uva-ursi*. The most abundant species were *Ceratothrips ericae*, previously cited as a potential pollinator of many Ericaceae in northern Europe, and *Haplothrips setiger*, a widely distributed Mediterranean Phlaeothripidae commonly cited in flowers of Asteraceae. We also discuss the role of spontaneous self-pollination in the reproductive success of *A. uva-ursi* and nectar consumption by thrips.

Keywords: Ceratothrips ericae, East Spain, Ericaceae, *Haplothrips setiger*, self-pollination, thrips pollination.

Introduction

Reproduction in *Arctostaphyllos uva-ursi* (L.) Spreng. (Ericaceae), as in many other Ericaceae plants from northern latitudes in Europe, has long been considered to depend mainly on self-fertilization, because this species flowers early in spring, even in cold places, when few or no insects are present (Warming 1908; Hagerup and Hagerup 1953; Haslerud 1974). Likewise, flower architecture seems to facilitate self-pollination in these plants because when the corolla begins to wither, it presses the stamens against the style (Hagerup 1954). However, several other flower characteristics that are also present in other Ericaceae, such as brightly colored corollas, nectar secretion, and anther appendages facilitating pollen discharge when visited by insects, have been viewed as adaptations to insect pollination. In addition, insect visits have been reported, mainly bumblebees and thrips (Warming 1908).

Although thrips are best known as agricultural pests that feed on leaf and flower tissues, pollen feeding by thrips has been considered as particularly relevant to pollination ecology (Kirk 1985; Ananthakrishnan 1993; Williams et al. 2001). Nevertheless, several authors claim that thrips may only play a minor role in flower pollination because they usually feed on pollen and rarely move out of the flowers and because most of the studies reporting thrips as pollinators are based on observations of thrips visiting flowers but no additional experiments (see Terry 2001 for a recent review). However, thrips movement between flowers and between plants are frequent (Bournier 1983), and thrips have been shown carrying pollen grains on their bodies, even in flight (Ananthakrishnan 1993; Mound and Terry 2001; Cornara et al. 2005). In addition, there are several well-established examples of thrips pollination (Baker and Cruden 1991; Momose et al. 1998; Zamora 1999; Sakai 2001; Moog et al. 2002; Zerega et al. 2004).

Hagerup (1954) and Hagerup and Hagerup (1953) proposed that pollination by thrips might be one of the most important means of pollination in Ericaceae shrubs in northern latitudes and that this had not previously been considered by earlier botanists because of observation limitations. Hagerup's (1950) description of *Calluna vulgaris* pollination by *Ceratothrips ericae* has been widely used as an example of pollination by thrips. He said that thrips become covered in pollen while moving around to feed on nectar. However, observations by Kirk (1985) revealed that larvae and adults of *C. ericae* feed largely on pollen grains of *C. vulgaris*, and because thrips search for pollen on which to feed, contact of thrips with pollen and its subsequent transportation to the stigma might be much more likely. However, Haslerud (1974) cautioned about overestimation of the importance of thrips as pollinators because he did not find thrips in flowers of several species in a survey on arctic Ericaceae in Norway (see also Mahy et al. 1998 for another unproductive search for thrips in *C. vulgaris* flowers in Belgium).

In this article, we present strong evidence supporting the importance of thrips in the pollination of *A. uva-ursi* in the southernmost limit of its distribution range. We conducted observations on the spatial and temporal variation of the presence of thrips in flowers of *A. uva-ursi* in eastern Spain and experimentally checked for the effectiveness of thrips pollination and the occurrence of spontaneous self-pollination. We bagged

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inflorescences (1) to permit flower access to thrips and (2) to prevent flower access by any potential pollinator including thrips. Then, we compared these results with those of inflorescences open to all potential pollinators. We also measured nectar consumption by thrips in flowers of *A. uva-ursi*.

Material and Methods

Study Area

A climatic gradient along the southern extreme of the Iberian mountain range in eastern Spain was used. We selected four sites, from continental mountains (Sierra Alta and San Ginés sites) to mountains near to the coastal plains (Mas del Peraire and La Palmereta sites). Experiments took place at Mas del Peraire and San Ginés sites, and observations were performed at all four sites.

The Sierra Alta site (SA; 40°29′N, 01°49′W; 1800 m asl) was located in a *Pinus sylvestris* L. forest on shallow acid soils with a near to continuous layer of *Arctostaphyllos uva-ursi*. Mean annual temperature and precipitation are 8.6°C and 1000 mm, respectively, and summer precipitation (July–September) totaled 160 mm. The San Ginés site (SG; 40°37′N, 01°28′W; 1500 m asl) was located in an open *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. in Bol. and *Quercus faginea* Lam. mixed forest on shallow acid soils with a discontinuous layer of *A. uva-ursi* as a consequence of the intense exploitation for medicinal use of their leaves from the 1940s to 1970s. Mean annual temperature and precipitation are 9°C and 500 mm, respectively, and summer precipitation is 100 mm. The Mas del Peraire site (MP; 40°43′N, 00°12′W; 1200 m asl) is located in the biological reserve owned by the Foundation Enrique Montoliu (http://www.fundem.org/). It is an open *Pinus nigra* Arnold subsp. *salzmannii* (Duanl) Franco forest with sparse *Q. ilex* subsp. *ballota*, *Amelanchier ovalis* Medik., and *Juniperus communis* L. shrubs and scattered *A. uva-ursi* plants on medium to deep calcareous soils. Mean annual temperature and precipitation are 9.7°C and 680 mm, respectively, and summer precipitation is 107 mm. The La Palmereta site (LP; 40°40′N, 00°09′W 900 m asl) was located in an open *P. nigra* subsp. *salzmannii* forest with dispersed *Q. ilex* subsp. *ballota*, *Juniperus phoenicea* L., *Juniperus oxycedrus* L., *Rosmarinus officinalis* L., *Thymelaea tinctorea* (L.) Endl., *Erica multiflora* L., and *Ulex parviflorus* Pourret shrubs and scattered *A. uva-ursi* plants on medium to deep calcareous soils. Mean annual temperature and precipitation are 11°C and 560 mm, respectively, and summer precipitation totaled 90 mm. The sources for the meteorological data were the 1961–1990 climatic series for the meteorological stations of Guadalaviar (SA), Ródenas (SG), Fredes (MP), and Morella (LP; DGA: http://portal.aragob.es/index.html) and Pérez-Cueva (1994).

Presence of Thrips in Plants

In the flowering seasons of 2004 and 2005, we checked for the presence of thrips in flowers of 20 inflorescences of 15 individuals in each of the four study sites. Each of the four populations was checked between 1000 and 1400 hours GMT on a single sunny day. We cut the flowers and inspected them for larvae and adult thrips with an optical glass binocular magnifier (×5). The number of inflorescences with thrips per plant was used as an indicator of the presence of thrips at each of the four sites. A hierarchical general linear model with quasi-Poisson distribution of errors was performed, considering population and individual (nested within population) as the main factors and percentage of inflorescences with presence of thrips as the response variable. Deviance quotients provided the percentage of relative variance accounted for by each hierarchical scale. Furthermore, we considered error deviance to represent the variance within the individual level. We used the "glm" option in the MASS library on the R statistical package to perform the analysis.

Additionally, in the flowering season of 2007, adult thrips and larvae were collected at all sites for taxonomic determination. Thrips were gathered with a small brush into vials containing 75% ethanol, macerated with 2% NaOH overnight, and transferred to water for 2 h. The samples were mounted on slides in Hoyer's solution and put into an oven for 5 h. All the slides were ringed twice with glycol to avoid rehydration.

Bag Experiments

In February 2004, we marked four individuals of *A. uva-ursi* at Mas del Peraire and four individuals at San Ginés. We selected 40 closed inflorescences of each plant and bagged 10 of them with 250-μm-mesh tulle bags to prevent the access of thrips and any other potential pollinator; so these inflorescences could produce fruits and seeds only by spontaneous self-pollination (thrips exclusion treatment). We also bagged 10 inflorescences with 1-mm-mesh nylon bags to permit ingress by thrips but to prevent access by any other potential pollinators to the flowers (only thrips treatment). The remaining inflorescences (20) were left open to every potential pollinator (control treatment). At the end of the flowering period, the inflorescences of the control treatment were also bagged to prevent fruits from falling off. At the end of the fruiting season (August–September), we collected the bags, counted the fruits, and opened the seeds under a (×40) binocular microscope. All the bags were 10 cm × 5 cm, and they were fastened to the inflorescence base with plastic wires.

To check for the effectiveness of the thrips exclusion treatment, we put two additional bags per plant in Mas del Peraire site, and we inspected them twice in the middle of the flowering season (half of the bags on March 26 and the other half on April 9). Thrips were detected in 23% of the inflorescences bagged with 1-mm-mesh bags, but no thrips were detected in any of the inflorescences bagged with 250-μm-mesh bags; therefore, we consider the thrips exclusion treatment effective (see Moog et al. 2002 for a similar experiment). Inflorescence longevity was positively affected by bags. In several pollination experiments between 2000 and 2005, flowers with bags excluding pollinators, as used in the control and only thrips treatments, lived 1–2 d longer than control inflorescences.

Percentage of inflorescences with fruits, number of fruits per inflorescence, and the number of filled seeds per fruit were used as indicators of fecundity. Generalized linear mixed-effects models with quasi-Poisson distribution of errors were applied to the number of fruits per inflorescence and the rate of filled seeds, considering bagging treatment and site as factors. Because we were interested in the effects of the bagging treatment on reproductive output of a random sample of mothers, we used plant individual as random effect in these models. A dispersion parameter was included in the model to account for overdispersion. We used the "glmmPQL" option in the MASS library on the R statistical package (Ihaka and Gentleman 1996; Venables and Ripley 2002).

Nectar Consumption by Thrips

In March 2003, we performed an experiment to check for the consumption of nectar by thrips at Mas del Peraire site. Using 250-μm-mesh tulle bags, we bagged 18 inflorescences, each containing open and closed flowers, on six *A. uva-ursi* plants, to prevent access to thrips; we also marked 18 inflorescences as controls. All the inflorescences of the bagging treatment were inspected before and after the experiment for the absence of thrips. Twenty-four hours after bagging, we cut the inflorescences and measured the nectar content of all the open flowers with a 5-μL microcapillary tube. We controlled for insects other than thrips, visiting the experimental plants in three 1-h periods during the experiment. Bumblebees were the only insects we observed, and in spite of their very low numbers (<1 individual/h), all control plants visited by bumblebees during the observations were discarded from the analysis (two plants). A Mann-Whitney test was used for comparisons of nectar content due to lack of normality of the data.

Results

Presence of Thrips in Plants

We found thrips on ~45% of the plants in all studied populations and years, and 5%–22% of the inflorescences of these individual plants had thrips (table 1). Variation in the number of inflorescences with thrips within individuals accounted for more than 60% of the variance of the presence of thrips in flowers, and the remaining variance was explained by the variation within and among populations (fig. 1). These results were consistent in both years, but the portion of variation explained by the among-population level in 2004 was twice the contribution of the within-population level, and this relation reversed in 2005.

Five hundred fifty-four specimens of seven species of thrips were recorded. Of these, six species belonged to the family Thripidae and were almost all female individuals of *Thrips australis*, *Thrips major*, *Thrips tabaci*, *Thrips vulgatissimus*, *Oxythrips* sp., and *Ceratothrips ericae*. One species, *Haplothrips setiger*, belonged to the family Phlaeothripidae and included both sexes. Several larvae were determined only as larvae of Terebrantia or Tubulifera. Most of the individuals belonged to *H. setiger* (64% of the individuals) and *C. ericae* (32% of the individuals), and this preponderance was constant in all the studied populations.

Bag Experiments

In total, 221 fruits from 307 inflorescences, each with five flowers on average, were produced in the experiment; there were 116 fruits from the plants of San Ginés and 105 fruits from Mas del Peraire site plants.

Fewer than 13% of the inflorescences from the thrips-exclusion treatment had fruits, in contrast to more than 30% of the inflorescences from the thrips-only treatment and more than 60% of the inflorescences that were open to all potential pollinators. The inflorescences of the thrips-exclusion treatment produced fewer than 0.15 fruits per inflorescence on average (fig. 2), whereas the inflorescences of the thrips-only treatment and those of the control treatment produced on average more than 0.6 and 1.4 fruits per inflorescence, respectively. These differences among treatments in the number of fruits per inflorescence were significant, but neither site nor site × treatment interaction had significant effects on the variable (fig. 2).

Each fruit had an average of 0.6 filled seeds per fruit, and this was similar for the fruits of all treatments and populations (see fig. 2). We did not find effects of the predictor variables (site and treatment) on the percentage of filled seeds per fruit.

Nectar Consumption by Thrips

Forty flowers were used for comparisons, 26 from bagged inflorescences and 14 from open ones, after discarding four inflorescences visited by bumblebees. Flowers from bagged inflorescences had 20 times more nectar than flowers from open inflorescences (0.650 ± 0.118 vs. 0.033 ± 0.019 μL), and these differences were statistically significant ($U = 19{,}000$, $P < 0.001$).

Discussion

The experimental results support the hypothesis of thrips pollination. Nearly one-third of the inflorescences of *Arctostaphyllos uva-ursi* produced fruits when they were exposed to the presence of thrips only, and they generated on average 0.6 fruits per inflorescence. When we excluded all the pollinators, 13% of the inflorescences produced fruit, and they produced fewer than 0.2 fruits per inflorescence. So, by discounting the fruits produced without the contribution of any insect, we conclude that at least 85% of the fruits produced when the

Table 1

Percentage of Individuals with Thrips in at Least One Inflorescence, and Percentage of Inflorescences with Presence of Thrips for the Four Populations and the Two Studied Years

	SA		SG		MP		LP	
	2004	2005	2004	2005	2004	2005	2004	2005
Plants with thrips (%)	20	40	80	40	40	46.7	40	46.7
Inflorescences/plant with thrips (%; $X \pm$ SE)	5.0 ± .0	10.0 ± 1.6	10.8 ± 3.7	9.2 ± 2.7	17.8 ± 4.3	22.1 ± 5.3	9.2 ± 2.0	11.4 ± 4.0

Note. SA = Sierra Alta, SG = San Ginés, MP = Mas del Peraire, and LP = La Palmereta.

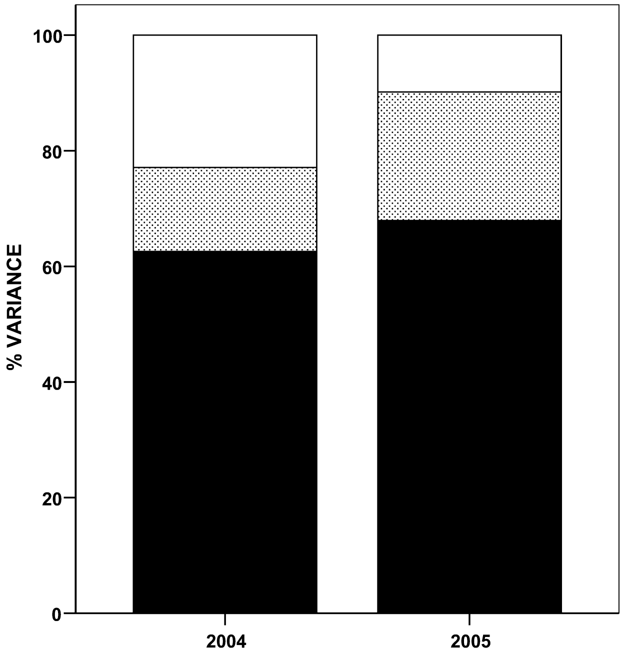

Fig. 1 Relative contribution of the different study levels to the amount of variation in the number of inflorescences with thrips: within individuals (black bars), within populations (gray bars), and among populations (white bars).

flowers of *A. uva-ursi* were accessible only to thrips are the consequence of thrips activity, and, therefore, thrips might account for 20% of the fruits produced in the control inflorescences. The remaining 80% of fruits presumably resulted from pollination by other insects. Although pollen diameter (44–64 μm) is smaller than 250-μm mesh and could allow pollen to enter, wind pollination is improbable because the corolla throat faces downward, styles and anthers are not exserted (negative values), and pollen production is low (505 ± 44 tetrads per anther). Bumblebees (*Bombus* sp. pl.) and social and solitary bees (*Apis mellifera*, *Anthophora*, *Andrena*, *Colletes*, etc.) are the most frequent insects observed visiting the *A. uva-ursi* flowers (Warming 1908; Hagerup 1954; Haslerud 1974; P. García-Fayos, personal observations), although some butterflies and large flies were observed rarely (P. García-Fayos, personal observation). The contribution of thrips to pollination in our experiment may have been inflated by the protection that bags conferred to thrips against predators because many such potential predators are insects greater than the 0.25-mm-sized mesh we used (Lacasa and Llorens 1998). However, the constant presence and abundance of thrips in flowers of *A. uva-ursi* suggest that predators have a limited effect on thrips abundance.

Given that there was no other plant species flowering at the same time as *A. uva-ursi* in the studied sites, nectar and pollen of this species are the only foods available for the thrips, thus reinforcing the role of the thrips as pollinators of *A. uva-ursi* flowers. There was an exception in La Palmereta, the site with the warmest climate, where *Erica multiflora* (Ericaceae), *Rosmarinus officinalis* (Lammiaceae), *Thymelaea tinctorea* (Thymeleaceae), and *Ulex parviflorus* (Fabaceae) were also flowering at the same time, and their flowers contained many *Haplothrips setiger*, *Ceratothrips ericae*, *Thrips vulgatissimus*, and *Odontothrips* sp. We cannot identify this species of *Odontothrips*, but it appeared to be identical to the *Odontothrips* species we found on the neighboring *A. uva-ursi* plants. The presence of these adult thrips on *A. uva-ursi* is probably circumstantial because *Odontothrips* species breed specifically in the flowers of particular Fabaceae (zur Strassen 2003).

Two species of thrips accounted for more than 95% of the individuals we found in the flowers of *A. uva-ursi* at the four sites studied. True host relationships of thrips species are very difficult to establish because adults often fly actively and disperse. For an understanding of thrips biology, it is essential to distinguish between the "finding-place" of a species and its "host-plant," although most publications about thrips confuse these two situations (Mound and Marullo 1996).

Cetatothrips ericae is host specific to flowers in the Ericaceae family (*Calluna*, *Erica*, *Vaccinium*, and *Arctostaphylos*; zur Strassen 2003). In the Faroes Island, where large pollinating insects are rare and long periods of heavy rain make wind pollination uncertain, *C. ericae* is the most important pollinator of *Calluna* in many summers. Often four to six young adults live inside each flower, feeding on the surface of the nectaries at the base of the petals, where even the mouth parts of bees cannot penetrate (Lewis 1973). *Haplothrips setiger* is a phleothripid that is host specific to flowers of Asteraceae (*Senecio*, *Pyrethrum*, *Inula*, *Leontodon*, *Leucanthemun*; Goldarazena 1996). This typically Mediterranean species flies actively when temperatures are warm, thus dispersing and colonizing new areas (Goldarazena 1996; Goldarazena and Mound 1997). *Thrips australis* is largely host specific on *Eucalyptus*, and it has been spread around the world by the global horticultural trade (Moritz et al. 2004). *Thrips vulgatissimus* is distributed in Europe, North America, and Palearctic Asia and is common in many plants, although it seems to be more frequently associated with Apiaceae and Compositae (zur Strassen 2003). *Thrips tabaci* and *Thrips major* are both polyphagous thrips (Mound et al. 1976), but their usual hosts are Rosaceae and Compositae species. Because they do not oviposit on *A. uva-ursi*, their presence in the flowers of *A. uva-ursi* has to be considered occasional. The food taken by these species probably includes the cell contents of pollen grains and of flower tissues such as petals and anthers. So, their contribution to pollination of *A. uva-ursi* may be negligible.

Because thrips were found in *A. uva-ursi* inflorescences in every population and year and because pollination success by thrips was not affected by site, we suggest that thrips pollination of this plant may be considered a general phenomenon that is not restricted to the Arctic plant populations, where thrips pollination in Ericaceae plants was first proposed (Hagerup 1950). Supporting this view is the constant presence in all our studied populations of *C. ericae*, the main thrips pollinator found in northern Ericaceae species (Hagerup 1950; Hagerup and Hagerup 1953; Kirk 1984). *Haplothrips setiger*, the most abundant and constant thrips species in the *A. uva-ursi* populations studied, may be playing the same role as *C. ericae* but in our warmer Mediterranean climate. Further research is needed on this thrips. Another potential pollinator of *A. uva-ursi* in southern European areas that needs investigating is *Orothrips priesneri* (Aeolothripidae). Although this species has

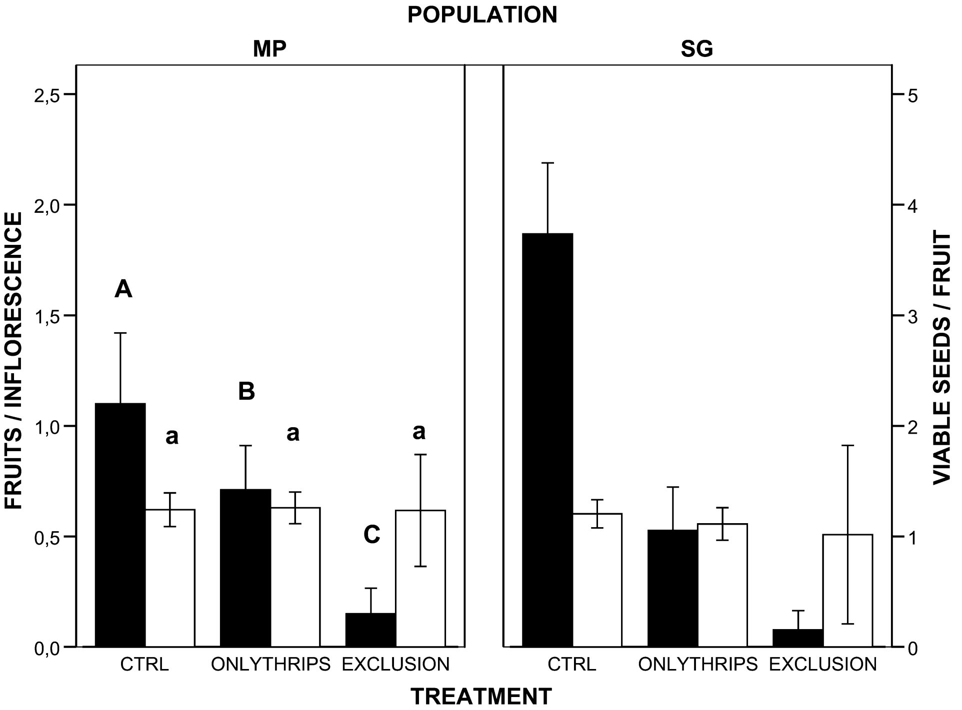

Fig. 2 Mean ± SE of the number of fruits per inflorescence (black bars) and of the number of viable seeds per fruit (white bars) resulting from bagging treatment (CTRL = flowers available for all potential pollinators; ONLY THRIPS = flowers available only for thrips; EXCLUSION = exclusion of all potential pollinators) and population (MP = Mas del Peraire; SG = San Ginés). Different letters over the bars indicated significant statistical differences at 0.05 level in the mean values of the variables among treatments (capital letters for fruits; lowercase letters for seeds). Neither population nor its interaction with the bagging treatment had significant influence on the variables.

been reported breeding only in the flowers of some European Rosaceae (zur Strassen 2003), its congener *Orothrips kelloggii* is the most common thrips in the flowers of *Arctostaphyllos pungens* in the western United States (Bailey 1957).

Our results showed that the presence of thrips is irregular within the inflorescences of a plant and also within the plants of a population. This may account for the contradictory conclusions of previous observers concerning thrips pollination in Ericaceae (Haslerud 1974; Mahy et al. 1998); it is also a warning about drawing inferences from inadequate sampling. Only by sampling many plant individuals and many flowers within individuals can a good estimate be obtained concerning the association of a thrips species with a particular plant species.

Additional support for the hypothesis of pollination of *A. uva-ursi* by thrips came from some casual observations of the presence of *A. uva-ursi* pollen grains on the bodies of thrips and of thrips contact with stigmas (P. García-Fayos, personal observation). Although pollen presence on thrips is not conclusive without experimental evidence, it has been the most widely used evidence by researchers to support pollination by thrips (Hagerup and Hagerup 1953; Luo and Li 1999; Frame and Durou 2001; Mound and Terry 2001; Williams et al. 2001; Bhattacharya and Mandal 2004; Cornara et al. 2005; Schwartz-Tzachor et al. 2006).

Self-fertilization in *A. uva-ursi* seems to have a low incidence. Inflorescences in the exclusion treatment produced flower-to-fruit ratios ~100 times smaller than those of control inflorescences and 20 times smaller than those of the thrips-only treatment. Hence, the low fertility values in the experiment prevent any interpretation about mechanisms of self-pollination. Because flowers of *A. uva-ursi* are self-compatible (P. García-Fayos, unpublished data) and because of the narrow distance between anthers and stigma, self-pollination must occur accidentally once the stigmas are receptive and wind shakes the flowers, throwing pollen up from the anthers (Hagerup 1954). Bags might have increased wind resistance of the inflorescences thus amplifying the wind-shaking force and enhancing self-pollination opportunities. So, even the low fertilization results obtained in the exclusion treatment may be an overestimation of spontaneous self-fertilization.

Results of our nectar experiment, together with those of Hagerup (1950), indicate that nectar consumption by thrips may be common, despite the lack of absolute control over other potential nectar consumers in our experiment (see also Kirk 1984 for a broader discussion). However, although thrips do not actively consume nectar, the pollen grains they usually carry on their bodies even when they feed on pollen would accidentally contact stigmas (Kirk 1985). The small size of these insects and the relatively few pollen grains each individual can carry are compensated for by the great numbers of individuals present in the flowers. In conclusion, our results point out that thrips pollination in *A. uva-ursi* is ubiquitous throughout the range *of A. uva-ursi* and can account for about 20% of total pollination success.

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Literature Cited

Ananthakrishnan TN 1993 The role of thrips in pollination. Curr Sci 65:262–264.

Bailey SF 1957 The thrips of California. I. Suborder Terebrantia. Bull Calif Insect Surv 4:143–220.

Baker JD, RW Cruden 1991 Thrips-mediated self-pollination of two facultatively xenogamous wetland species. Am J Bot 78:959–963.

Bhattacharya A, S Mandal 2004 Pollination, pollen germination and stigma receptivity in *Moringa oleifera* Lamk. Grana 43:48–56.

Bournier A 1983 Les thrips: biologie, importance agronomique. Institut National de la Recherche Agronomique, Paris.

Cornara L, B Borghesi, E Caporali, G Casazza, E Roccotiello, G Troiano, L Minuto 2005 Floral features and reproductive ecology in *Thymelaea hirsuta* (L.) Endl. Plant Syst Evol 250:157–172.

Frame D, S Durou 2001 Morphology and biology of *Napoleonaea vogelii* (Lecythidaceae) flowers in relation to the natural history of insect visitors. Biotropica 33:458–471.

Goldarazena A 1996 Contribution to the knowledge of the Thysanoptera of Navarre (orden Thysanoptera, clase Insecta). PhD diss. University of Navarre.

Goldarazena A, L Mound 1997 Introducción a la fauna de los tisanópteros (Cl. Insecta; O. Thysanoptera), de Navarra, sus plantas hospedadoras y su distribución. I. Terebrantia. Rev Mus Cienc Nat Alava 12:167–202.

Hagerup E, O Hagerup 1953 Thrips pollination of *Erica tetralix*. New Phytol 52:1–7.

Hagerup O 1950 Thrips pollination in *Calluna*. K Dan Vidensk Selsk Biol Medd 18:1–16.

——— 1954 Autogamy in some drooping bicornes flowers. Bot Tidsskr 51:103–116.

Haslerud HD 1974 Pollination of some Ericaceae in Norway. Nord J Bot 21:211–216.

Ihaka R, R Gentleman 1996 R: a language for data analysis and graphics. J Comp Graph Stat 5:299–314.

Kirk WDJ 1984 Pollen-feeding in thrips (Insecta: Thysanoptera). J Zool 204:107–117.

——— 1985 Pollen-feeding and the host specificity and fecundity of flower thrips (Thysanoptera). Ecol Entomol 10:281–289.

Lacasa A, JM Llorens 1998 Thrips y su control biológico. Vol 2. Pisa Editions, Alicante.

Lewis T 1973 Thrips: their biology, ecology and economic importante. Academic Press, London.

Luo YB, ZY Li 1999 Pollination ecology of *Chloranthus serratus* (Thunb.) Roem. et Schult. and *Ch. fortunei* (A. Gray) Solms-Laub. (Chloranthaceae). Ann Bot 83:489–499.

Mahy G, J De Sloover, A-L Jacquemart 1998 The generalist pollination system and reproductive success of *Calluna vulgaris* in the Upper Ardenne. Can J Bot 76:1843–1851.

Momose K, T Nagamitsu, T Inoue 1998 Thrips cross-pollination of *Popowia pisocarpa* (Annonaceae) in a lowland Dipterocarp forest in Sarawak. Biotropica 30:444–448.

Moog U, B Fiala, W Federle, U Maschwitz 2002 Thrips pollination of the dioecious ant plant *Macaraga hullettii* (Euphorbiaceae) in Southeast Asia. Am J Bot 89:50–59.

Moritz G, LA Mound, DC Morris, A Goldarazena 2004 Pest thrips of the world—visual and molecular identification of pest thrips. Center for Biological Information Technology, University of Queensland, http://www.cbit.uq.edu.au/software/pestthrips/default.htm (accessed August 9, 2007).

Mound LA, R Marullo 1996 The thrips of Central and South America: an introduction (Insecta: Thysanoptera). Memoirs of entomology, international. Vol 6. Associated, Gainesville.

Mound LA, GD Morison, BR Pitkin, JM Palmer 1976 Thysanoptera. Handbooks for the identification of British insects. Vol 1. Royal Entomological Society, London.

Mound LA, I Terry 2001 Thrips pollination of the central Australian cycad, *Macrozamia macdonnellii* (Cycadales). Int J Plant Sci 162: 147–154.

Pérez-Cueva A 1994 Atlas climàtic de la Comunitat Valenciana. Conselleria d'Obres Públiques Urbanisme i Transport–Generalitat Valenciana, Valencia.

Sakai S 2001 Thrips pollination of androdioecious *Castilla elastica* (Moraceae) in a seasonal tropical forest. Am J Bot 88:1527–1534.

Schwartz-Tzachor R, A Dafni, SG Potts 2006 An ancient pollinator of a contemporary plant (*Cyclamen persicum*): when pollination syndromes break down. Flora 201:370–373.

Terry I 2001 Thrips: the primeval pollinators? Pages 157–162 *in* R Marullo, L Mound, eds. Thrips and tospoviruses. Proceedings of the 7th international symposium on Thysanoptera, Reggio Calabria, Italy, July 2–7. http://www.ento.csiro.au/thysanoptera/symposium.html (accessed August 9, 2007).

Venables WN, BD Ripley 2002 Modern applied statistics with S. Springer, Heidelberg.

Warming E 1908 Arctic flowering plants. Medd Gronl 36:1–71.

Williams GA, P Adam, LA Mound 2001 Thrips (Thysanoptera) pollination in Australian subtropical rainforests, with particular reference to pollination of *Wilkiea huegeliana* (Monimiaceae). J Nat Hist 35:1–21.

Zamora R 1999 Conditional outcomes of interactions: the pollinator-prey conflict of an insectivorous plant. Ecology 80:786–795.

Zerega NJC, LA Mound, GD Weiblen 2004 Pollination in the New Guinea endemic *Antiaropsis decipiens* (Moraceae) is mediated by a new species of thrips, *Thrips antiaropsidis* sp. nov. (Thysanoptera: Thripidae). Int J Plant Sci 165:1017–1026.

zur Strassen R 2003 Die terebranten Thysanopteren Europas und des Mittelmeer-Gebietes. Die Tierwelt Deutschlands. Vol 74. Goecke & Evers, Frankfurt.