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Dense white trichome production by plants as possible mimicry of arthropod silk or fungal hyphae that deter herbivory

Kazuo Yamazaki [a,*,1], Simcha Lev-Yadun [b,1,2]

[a] Osaka City Institute of Public Health and Environmental Sciences, 8-34 Tojo-cho, Tennoji, Osaka 543-0026, Japan
[b] Department of Biology and Environment, Faculty of Natural Sciences, University of Haifa – Oranim, Tivon 36006, Israel

HIGHLIGHTS

- Anti-herbivory animal mimicry by plants has been rarely recognized.
- Several plants growing in Israel, Estonia, Greece and Japan have dense thread-like trichomes.
- These trichomes resemble spider webs or other arthropod silk nests.
- Spider webs are dangerous objects for herbivores because of the predatory habit and toxins.
- The trichomes may deter herbivores by visual mimicry or perceptual exploitation.

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ABSTRACT

Some spiders are well-known to mimic flowers or other plant surfaces in order to be cryptic to both their prey and their predators. We propose that dense, thread-like white trichomes of some plants from Estonia, Greece, Israel and Japan visually mimic spider webs, lepidopteran and spider-mite web nests and plant-pathogenic fungi, and that it may result in reduced herbivory, since various herbivores avoid spider- or other arthropod webs to circumvent predation or toxic attacks, or refrain from colonizing plants that have already been occupied by other herbivores and pathogens. Spiders and other web-forming arthropods are also the prey of certain vertebrate predators and wasps, and therefore such predators may be attracted to these web-like plant structures and prey on the invertebrate herbivores occupying them. We do not dismiss the possibility that these web-like structures may also have other defensive or physiological functions or that they are not classic mimics but rather exploit the herbivore's perceptual state concerning the avoidance of potentially risky objects.

1. Introduction

Plants employ various predators and parasitoids as bodyguards that act as an indirect defense against herbivores (Dicke and Sabelis, 1988; Heil, 2008). Well-known allies of plants are ants, predatory mites and parasitoids. Many myrmecophytes (ant-plants) make living space (i.e., domatia) and nourish their ants via extrafloral or floral nectaries and by solid food bodies. Mutualistic ants use the domatia and/or foods and in turn defend their host plants from various natural enemies including herbivorous arthropods, mammals and even from other plant competitors (Janzen, 1966; Yano, 1994; Frederickson et al., 2005; Heil, 2008). Although aphids and other hemipterans are sometimes important plant enemies, they secrete honeydew that in turn attracts ants, resulting in the protection of the plants from various herbivores (Styrsky and Eubanks, 2007; Yamazaki, 2008a, 2008b). Several plants emit herbivore-induced volatiles to attract predatory mites (Dicke and Sabelis, 1988; Dicke et al., 1990; Takabayashi and Dicke, 1996) and parasitoids (van Poecke et al., 2001; Shiojiri et al., 2010).

Spiders are very common predators of various herbivorous arthropods in natural habitats (Nyffeler et al., 1994; Nyffeler, 2000) and their activity results in positive effects on plant growth (e.g., Louda, 1982; Wise, 1993; Nyffeler et al., 1994). Thus, various plant species actually form some facultative partnerships with spiders. For example, *Chamaecrista nictitans* (Fabaceae) herbs in the USA attract jumping spiders in addition to ants via extrafloral nectar, and the resulting reduced herbivory allows for an increased seed set (Ruhren and Handel, 1999). Similarly, *Acacia lingulata*

* Corresponding author. Tel.: +81 6 6771 3196; fax: +81 6 6772 0676.
E-mail addresses: kazuo-yamazaki@city.osaka.lg.jp (K. Yamazaki), levyadun@research.haifa.ac.il (S. Lev-Yadun).
[1] Both authors equally contributed to this paper.
[2] Tel.: +972 522 781245.

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(Fabaceae) shrubs in Australia bear extrafloral nectaries and attract and harbor a subsocial amaurobiid spider species that makes dense webs on the plants, thus reducing seed predation by bugs, wasps and weevils (Whitney, 2004). A different strategy is employed by *Trichogoniopsis adenantha* (Asteraceae) and *Rhynchanthera dichotoma* (Melastomataceae) shrubs in South America. These plants are equipped with glandular trichomes that capture tiny arthropods. Lynx spiders prey on free-ranging herbivorous arthropods found on the plants, and also feed on the prey trapped by the trichomes, resulting in a reduction in herbivory (Romero et al., 2008; Morais-Filho and Romero, 2010; Krimmel and Pearse, 2013).

When plants can effectively mimic the actual signals of their bodyguards, or of reliable cues for their activity, they may benefit from the protection from herbivores without investing in volatiles, nectar, and cavities for housing. Such examples of herbivore-enemy mimicry by plants have rarely been recognized, although several cases of defensive arthropod mimicry by plants were advocated (e.g., Rothschild, 1974; Lev-Yadun and Inbar, 2002; Lev-Yadun and Ne'eman, 2012; Lev-Yadun, 2013; Yamazaki and Lev-Yadun, 2014) and sometimes demonstrated by experiments (e.g., Shapiro, 1981; Williams and Gilbert, 1981). One example of apparent arthropod mimicry by plants is swarming ant mimicry by short dark stripes and dots found on stems, branches and petioles of *Xanthium trumarium* (Asteraceae) and *Arisarum vulgare* (Araceae) (Lev-Yadun and Inbar, 2002) and by flowers of several *Passiflora* spp. (Passifloraceae) (Lev-Yadun, 2009). Because ants attack various herbivorous arthropods and mammals, many herbivores avoid ants. It has thus been proposed that ant-mimicking plants may incur less damage by herbivores (Lev-Yadun and Inbar, 2002; Lev-Yadun, 2009).

Taking into account the fact that spiders are also abundant and ubiquitous predators on plants, plants are expected to mimic spider cues for their defense. Also, as plants already used by herbivorous arthropods are inferior food sources (Karban and Baldwin, 1997) or turn into dangerous habitats that attract natural enemies (Niemelä and Tuomi, 1987; Kessler and Baldwin, 2001), plants may mimic the cues of the herbivores. We have thus explored this issue and propose that certain plants indeed mimic spider webs, lepidopteran and spider-mite web nests for defense.

Visual fungal-web mimicry by plants as defense from herbivory has been proposed for various plants that have white leaves (Lev-Yadun, 2006) or white variegation (Lev-Yadun, in press) because fungal-infested plants may be toxic.

2. Materials and methods

During the years of field work on defensive animal mimicry by plants in Japan, (K.Y.) examined various plants including herbs, climbers, shrubs and trees in urban parks, arable lands, riverbanks and forests in central Japan from March to November in 2010–2012. Each site in Japan was visited at least twice to inspect both early and mid-growing stages of plants. Parallel field work was conducted in Israel (1995–2013), the environs of Makri in northern Greece (summer of 2003), and in the Baltic coastal region of Estonia (summer of 2006) (S.L-Y.). We noticed apparent visual

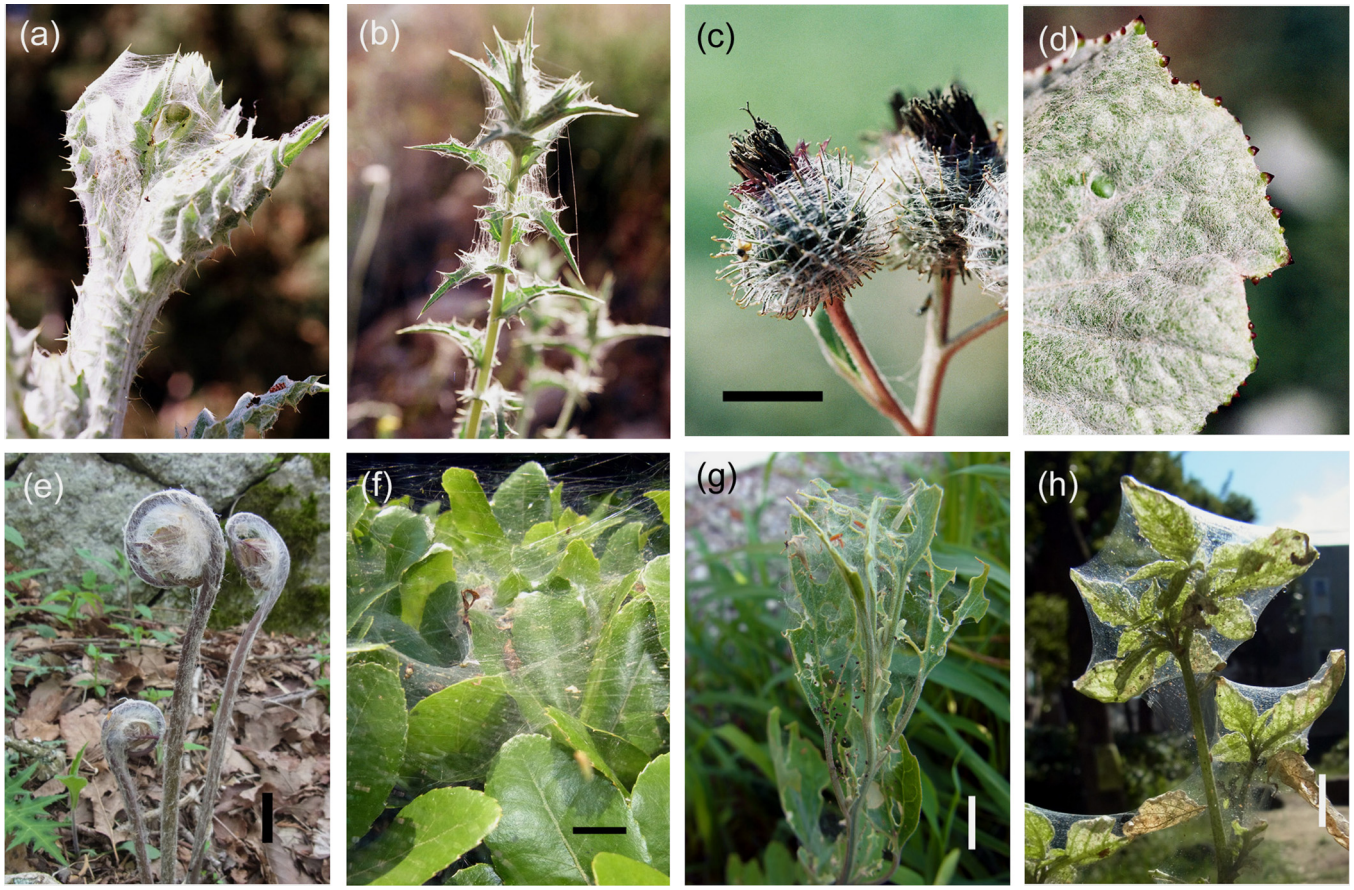

Fig. 1. Spider-web-like trichomes (a–e) and web nests of spiders, caterpillars and mites (f–h). (a) New buds of *Onopordum* from Israel, (b) *Carthamus* sp. from Greece, (c) flower heads of *Arctium tomentosum* from Estonia, (d) a new and still small leaf of *Tussilago farfara* from Estonia, (e) new fronds of *Osmunda japonica* from Japan, (f) sheet web of *Agelena silvatica* (Agelenidae), from Japan, (g) web nest of *Scythris sinensis* (Scythrididae), from Japan, and (h) web of *Tetranychus evansi* (Tetranychidae) from Japan. Scale bar: 10 mm.