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Dictyophara europaea (Hemiptera: Fulgoromorpha: Dictyopharidae): description of immatures, biology and host plant associations

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Abstract

The European lantern fly *Dictyophara europaea* (Linnaeus, 1767), is a polyphagous dictyopharid planthopper of Auchenorrhyncha commonly found throughout the Palaearctic. Despite abundant data on its distribution range and reports on its role in the epidemiology of plant-pathogenic phytoplasmas (*Flavescence dorée*, FD-C), literature regarding the biology and host plants of this species is scarce. Therefore, the aims of our study were to investigate the seasonal occurrence, host plant associations, oviposition behaviour and immature stages of this widespread planthopper of economic importance. We performed a 3-year field study to observe the spatio-temporal distribution and feeding sources of *D. europaea*. The insects's reproductive strategy, nymphal molting and behaviour were observed under semi-field cage conditions. Measurement of the nymphal vertex length was used to determine the number of instars, and the combination of these data with body length, number of pronotal rows of sensory pits and body colour pattern enabled the discrimination of each instar. We provide data showing that *D. europaea* has five instars with one generation per year and that it overwinters in the egg stage. Furthermore, our study confirmed highly polyphagous feeding nature of *D. europaea*, for all instars and adults, as well as adult horizontal movement during the vegetation growing season to the temporarily preferred feeding plants where they aggregate during dry season. We found *D. europaea* adult aggregation in late summer on *Clematis vitalba* L. (Ranunculaceae), a reservoir plant of FD-C phytoplasma strain; however, this appears to be a consequence of forced migration due to drying of herbaceous vegetation rather than to a high preference of *C. vitalba* as a feeding plant. Detailed oviposition behaviour and a summary of the key discriminatory characteristics of the five instars are provided. Emphasis is placed on the economic importance of *D. europaea* because of its involvement in epidemiological cycles of phytoplasma-induced plant diseases.

Keywords: behaviour, immatures, morphology, oviposition, phytoplasma vector, seasonal occurrence

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Introduction

Restricted to the Palaearctic region, the genus *Dictyophara* Germar, 1833 consists of approximately 40 species currently divided into the five subgenera, according to length, thickness and general shape of cephalic process (Emeljanov, 2003).

Dictyophara europaea (Linnaeus, 1767) is a type of species for the genus. In addition to *D. europaea* the subgenus *Dictyophara* consists of three closely related species: *Dictyophara asiatica* Melichar, 1912, *Dictyophara lindbergi* Metcalf, 1955, and *Dictyophara subsimilis* Linnavuori, 1953. According to the literature records, *D. europaea* (European lantern fly) is a polyphagous phloem-feeding planthopper species commonly found across the Western Palaearctic, with a single report from Northwestern China (Song & Liang, 2008).

Although a very common member of the Auchenorrhyncha fauna across its distribution range, data regarding the biology of the European lantern fly are scarce and often restricted to a few aspects related only to feeding patterns, habitat characteristics and distribution (Nickel, 2003). With regard to the feeding habits of *D. europaea*, there is a general consensus about the polyphagous nature of this insect. Holzinger *et al.* (2003) state that the species is associated with dicotyledonous herbs, grasses and shrubs. According to Biedermann & Niedringhaus (2004), *D. europaea* exploit diverse herbaceous plants and grasses for feeding. Melichar (1912) reported that this species is frequently found on *Achillea millefolium* L. (Asteraceae), whereas Lessio & Alma (2008) reported that *D. europaea* is common on *Amaranthus retroflexus* L. (Amaranthaceae) and *Urtica dioica* L. (Urticaceae) and that *A. retroflexus* is a suitable host plant for rearing under laboratory conditions. However, Filippin *et al.* (2009*a*) have regularly found *D. europaea* in association with the climbing shrub *Clematis vitalba* L. (Ranunculaceae) in vineyard ecosystems.

Regarding the habitat associations, the European lantern fly is frequently found on ruderal, xerothermic and sunny hillsides, preferentially in disturbed patches with some bare ground places where females presumably oviposit in the soil (Holzinger & Hausl-Hofstätter, 1994; Biedermann & Niedringhaus, 2004). Some additional notes on the biology of *D. europaea* are presented by Nickel (2003) and Nickel & Remane (2002), who state that this planthopper is univoltine and overwinters in the egg stage, with a distribution range across the Western Palaearctic.

Interest regarding the biology, host plant associations and general behaviour of *D. europaea* has increased recently due to evidence of its involvement in the transmission and epidemiology of *Flavescence dorée* (FD) phytoplasma disease of grapevine (Filippin *et al.*, 2009*a*). The FD phytoplasma has a quarantine status in the EU and severely affects vineyards and vine production in several European countries (Steffek *et al.*, 2007), with several epidemic outbreaks in the past decades. Phytoplasmas are wall-less, phloem-limited, non-culturable prokaryotes of the class Mollicutes and cause several hundred diseases in both wild and cultivated plants. Because they cannot be cultured on artificial medium and lack stable phenotypic characters, classification of these bacteria has been based on highly conserved 16S rRNA gene sequences (Lee *et al.*, 1998) and other conserved genes (Lee *et al.*, 2010) into distinct groups, subgroups and species accommodated within provisional genus-level taxon *'Candidatus* Phytoplasma' (IRPCM, 2004). Phytoplasmas are characterized by obligate transmission by insects, parasitic plants or grafting (Hogenhout *et al.*, 2008). Insect vectors of phytoplasmas include leafhoppers, planthoppers and psyllids belonging to the suborders Auchenorrhyncha and Sternorrhyncha of order Hemiptera.

The role of *D. europaea* in the epidemiological cycle of FD phytoplasma (16SrV group, subgroup C) has been documented after experimental transmission of this phytoplasma from naturally-infected *C. vitalba* to healthy grapevine seedlings and molecular tracing of the phytoplasma strains (genotypes) via multilocus typing (Filippin *et al.*, 2009*a*). Furthermore, Filippin *et al.* (2009*b*) and Cvrković *et al.* (2010) reported the presence of another phytoplasma in *D. europaea*, namely, the stolbur phytoplasma (16SrXII-A subgroup, *'Candidatus* Phytoplasma solani'), which induces *Bois noir* disease in grapevine and stolbur disease in solanaceous crops (Quaglino *et al.*, 2013). Subsequently, Mitrović *et al.* (2012) confirmed this finding and identified the presence of a third phytoplasma in analyzed specimens of European lantern fly collected in Serbian vineyards, a strain associated with bushy stunt in *Picris hieracioides* L. (Asteraceae) (16SrII-E subgroup). The recent finding of substantially higher rate of FD phytoplasma infection in some populations of *D. europaea* (Krstić *et al.*, 2012) initiated a study on the population genetics peculiarities of this planthopper and interaction with the pathogen (Krstić & Jović, in preparation).

Given its polyphagous feeding behaviour, the potential of acquiring and possibility of spreading three phylogenetically distinct phytoplasma groups has made *D. europaea* a tentatively important link in the understanding epidemiological cycles of the above, and likely other, phytoplasma-induced plant diseases. Because pathogen dissemination and disease transmission cycle(s) are directly influenced by any change in the population biology and host plant preference of the vector (Imo *et al.*, 2013), knowledge on the biology and plant associations of *D. europaea* has become especially important for elucidating phytoplasma disease cycles and developing measures of disease control. In this regard, details on the vector species biology, behaviour and methodological approaches in laboratory rearing are valuable for all future transmission assays, epidemiological studies and monitoring. The present paper provides new information on the biology, seasonal occurrence and host plant associations of *D. europaea* based on the observation in the natural habitats and under controlled semi-field conditions. Description of immature stages and behaviour of the nymphs are provided as well as insight into the oviposition behaviour of this planthopper species.

Materials and methods

Study sites and insect sampling

The *D. europaea* adults used in this study were monitored and collected during 2010–2012 from four selected locations in Serbia where this planthopper is recorded as being relatively abundant (fig. 1). The morphological identification of the collected specimens was confirmed using the description provided by Holzinger *et al.* (2003). Temporal variation in the occurrence and abundance of *D. europaea* was monitored during the 2011 and 2012 seasons at all four locations; calculations were performed after collecting specimens along five diagonal transects of 30 m long per site, every 15 days from the beginning of July to the end of the September. Standard entomological nets and mouth aspirators were used to collect the planthoppers. The collected specimens were counted and then released back onto the vegetation.

The first location (Loc-1) was in the vicinity of the town Topola in Central Serbia (N44 13.714, E20 41.112), where *D. europaea* individuals were collected from semi-ruderal abandoned meadow with *Salvia pratensis* L. (Lamiaceae) covering of approximately 30% of the surface. *Crepis foetida* L. (Asteraceae) and *Plantago lanceolata* L. (Plantaginaceae)

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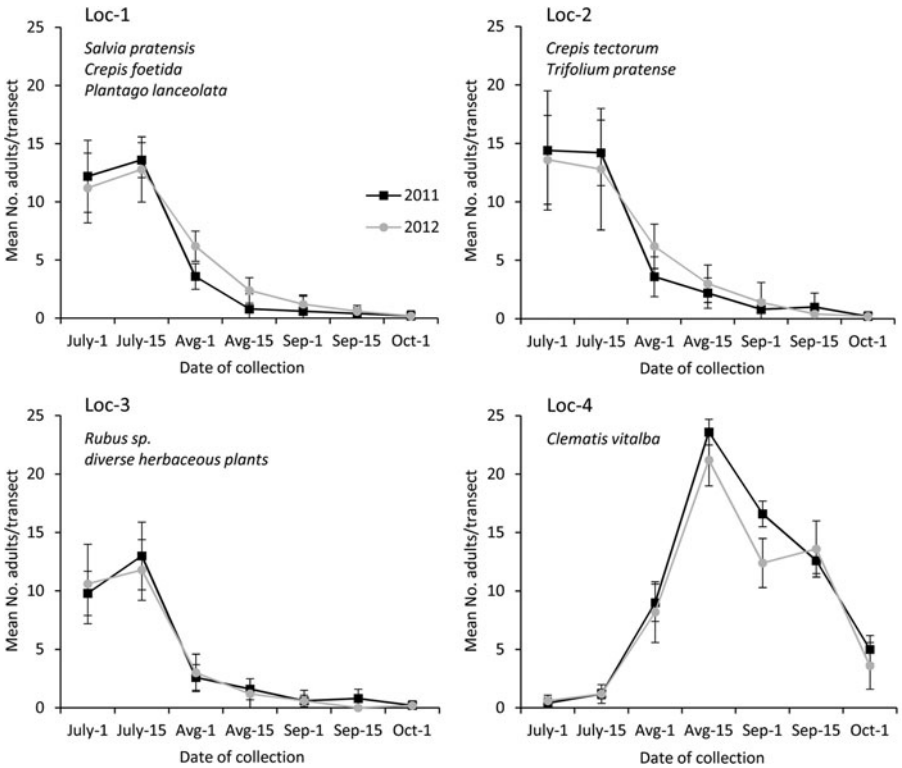

Fig. 1. Seasonal occurrence of *Dictyophara europaea* adults in 2011–2012 at four locations (Loc#) in Serbia with different vegetation cover (July–October). Bars indicate ± SD of the mean.

were the second and third most dominant plant species at the habitat with total cover of approximately 10%, intermixed with diverse legume plant species (*Trifolium* sp., *Onobrychis* sp. and *Lathyrus* spp.) and various grasses (mostly *Hordeum murinum* L. (Poaceae), *Cynodon dactylon* (L.) Pers. (Poaceae), *Festuca* spp., *Agropyron* spp., *Dactylis* spp.)

The second location (Loc-2) was a xerothermic hillside meadow with the Southwestern exposure close to the town Mladenovac, also in Central Serbia (N44 24.204, E20 44.575). *Crepis tectorum* L. (Asteraceae) was the most abundant plant species covering over 60% of the meadow, with red clover (*Trifolium pratense* L. (Fabaceae)) up to 20%, while the heart clover (*Medicago arabica* (L.) Huds. (Fabaceae)), *Mentha arvensis* L. (Lamiaceae) and *A. millefolium* (Asteraceae) were less abundant, with about 2% of the plant coverage.

The third location (Loc-3), near the town Negotin in Eastern Serbia (N44 16.605, E22 30.595), had a moderate slope with a Southwestern exposure and diverse plant coverage, growing on loam-sandy soil; the vegetation consisted of almost equal proportions of *Rubus* sp. (Rosaceae), *Linaria genistifolia* (L.) Mill. (Plantaginaceae), *Linaria vulgaris* Mill. (Plantaginaceae), *Kickxia elatine* (L.) Dumort. (Plantaginaceae), *S. pratensis* (Lamiaceae), *C. foetida*, *Knautia arvensis* (L.) Coult. (Caprifoliaceae), *Xanthium italicum* Moretti (Asteraceae), *Xeranthemum annuum* L. (Asteraceae), *Carduus acanthoides* L. (Asteraceae), *Centaurea stoebe* L. (Asteraceae), *Althaea officinalis* L. (Malvaceae), *Lepidium campestre* (L.) W.T. Aiton (Brassicaceae), *Lotus corniculatus* L. (Fabaceae), *Dorycnium herbaceum* Vill. (Fabaceae), *Lathyrus tuberosus* L. (Fabaceae), *Hypericum perforatum* L. (Hypericaceae) and grasses from the genera *Brachypodium*, *Phleum*, *Ammophila*, *Agrostis*, *Apera*, *Festuca*, *Bromus* and *Poa*.

The fourth location (Loc-4) was an abandoned vineyard in the village Jasenovik (N43 21.993, E22 01.256) near Nis in Southern Serbia. Approximately 80% of the ground surface at this location was covered with a climbing shrub *C. vitalba*. This site was used as a control for comparison of the influence of diverse vegetation on the seasonal occurrence of *D. europaea* because it was the only site with dominant shrub vegetation. In addition, *D. europaea* occurrence at this site was documented and monitored since 2005 for the purpose of epidemiological studies of FD phytoplasma transmission and spread (Filippin *et al.*, 2009*a*; Mitrović *et al.*, 2012).

For laboratory rearing, planthoppers were collected from several sites in the Topola district, mostly from *S. pratensis* and on patches of *C. vitalba*. Collections were performed in 2010 and 2011 from the beginning of July until the end of September to provide a sufficient number of specimens for oviposition and to gather information on adult behaviour and the condition in the natural environment during entire flight period. The collected adults were subsequently set in capped, well-ventilated plastic cylinders (10 × 35 cm) and transported to the laboratory in mobile refrigerators at 15°C.

Insect rearing

Insects collected for laboratory rearing were arranged in two types of cages that enabled observations related to adult behaviour under controlled conditions. During July of 2010 and 2011, batches of 200 adults, collected from several

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locations within the vicinity of the town Topola (mostly from *S. pratensis*), were placed in each of three mesh field cages (210 × 210 × 190 cm), respectively. The cages were planted with *S. pratensis*, *C. foetida*, *P. lanceolata*, *L. vulgaris* and *Agropyron repens* (L.) *P. Beauv*. (Poaceae) previously germinated from seeds and then used as a food resource for the released adults. The behaviour of the adults was monitored weekly for 1 h between 8 and 9 AM, noon and 1 PM, and from 5 to 6 PM. In addition, close-up monitoring of the oviposition behaviour of *D. europaea* was performed daily in four mobile frame cages (30 × 30 × 45 cm) placed into large pots filled with soil (40 × 40 × 16 cm). Two sides of the cages were covered with transparent glass (3 mm) and two with mesh for ventilation. The cages were planted with above noted plants, and kept in an outdoor insectarium. A total of 40 adults per mobile frame cage were released and their behaviour was monitored for 3 months (until the end of September). After the observed adults died, the cages were left in the outdoor conditions until spring. The behaviour of *D. europaea* nymphs and adults was monitored in both types of cages.

Nymph rearing under the laboratory conditions

A total of 30 soil particles containing eggs ('soil nests') were collected from the mobile framed cages and placed in Petri dishes (9 cm diameter) on wet filter paper and kept at 4–6°C from November until the beginning of March. These eggs were transferred at room temperature (23 ± 1°C) at the beginning of March following the increase in the outdoor temperature, and the soil particles were subsequently kept at room temperature until first-instar nymph emergence. Between 13 and 23 May 2011, a total of 73 N1 nymphs emerged. Young seedlings of *C. foetida*, *S. pratensis* and *Lolium perenne* L. (Poaceae) were placed in the Petri dishes as a food source for the N1 nymphs. The newly hatched nymphs were kept in Petri dishes on the young germinated seedlings for the next 10 days; when the nymphs reached the N2–N3 instars, they were transferred to framed cages with potted seedlings of *C. foetida*, *S. pratensis*, *P. lanceolata* and *L. vulgaris* as a food source for further nymph development.

Morphological study

The terminology of morphological characters and descriptors used in this paper was adopted from Snodgrass (1935) and Holzinger *et al*. (2003). To estimate the number of instars, the vertex length was measured with a Leica MS5 binocular tube using high magnification (40× or 64×) for the first three instars; 25× and 16× was used for N4–N5 and adults, respectively. The measurements were combined with morphological peculiarities between successive molted instars visually observed during the rearing. The multimodal frequency distribution was used as an indirect method to confirm the number of instars under the assumption of the normal distribution of vertex length across all instars (McClellan & Logan, 1994; Delbac *et al*., 2010). Furthermore, we tested the use of Dyar's rule (Dyar, 1890), which assumes a constant growth ratio of measures of successive instars and is used as an aid for determining the number of instars. Therefore, we compared the observed growth ratio and calculated growth ratio, i.e., the mean vertex length of instar N_i/mean vertex length of instar N_{i-1}, according to Hsia & Kao (1987). Images of nymphs and the caudal end of the female abdomen from the ventral side were obtained using a JSM 6460 Scanning Electron Microscope (JEOL USA Inc., Peabody, MA, USA).

Fecundity

Mean fecundity was calculated using the females reared in mobile frame cages. A total of 30 females were dissected at the end of August and the beginning of September 2012, when the first oviposition events were recorded under the cage conditions. Only fully developed eggs were counted.

Parasitism

Field-collected adults of *D. europaea* were checked for dryinid larvae, and three specimens were subjected to molecular identification. Larval tissue was carefully removed from the host and DNA was extracted using Dneasy® Blood & Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. The barcoding region of the mitochondrial cytochrome oxidase subunit I gene (mt*COI*) was amplified using the primers LCO1490 and HCO2198 (Folmer *et al*., 1994). The obtained amplicons were sequenced (Macrogen Inc., Seoul, South Korea), resulting sequence was deposited in the GenBank database under accession number KT852981, and compared with publicly available data using BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi) and BOLD (http://www.boldsystems.org/index.php/IDS_OpenIdEngine) search tools.

Results

Field-observed seasonal occurrence, feeding sources and parasitism

The temporal dynamics and seasonal occurrence of *D. europaea* adults observed in the field were similar in the 2 consecutive years monitored (2011, 2012). During July, there were no substantial differences among the abundance of *D. europaea* adults at the three studied locations with herbaceous vegetation or along the transects; the random distribution of adults was observed inside the studied plots (Loc-1, -2 and -3; fig. 1). The number of adults substantially declined at these locations during August when only a few individuals could be collected per location. This coincided with hitherto desiccation of the herbaceous plants forming the vegetation cover during July. More careful inspection of these sites during August and September indicated that the adults of *D. europaea* aggregated on those plant species better adapted to drought conditions (e.g., *S. pratensis*) or migrated to the shrubs growing close to the meadows. *C. vitalba* was observed at all three locations as one of the preferred plant of *D. europaea* aggregation at the end of August and during early September.

However, at the fourth location, where *C. vitalba* was the dominant plant species, the temporal occurrence of *D. europaea* adults exhibited different dynamics (fig. 1, Loc-4), confirming a previous observation of late-summer aggregation on shrubs. Prior to the beginning of August, only single individuals of *D. europaea* adults were collected, whereas the peak occurrence was recorded in mid-August and at the beginning of September. In addition, the total number of collected individuals was higher compared with the other three locations, especially with regard to the time of the population peak. This appears to be a consequence of the forced aggregation of

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adults due to the drying of the herbaceous vegetation rather than to a higher preference for *C. vitalba* as a feeding plant.

At all the four locations adults parasitized with dryinid wasps (Hymenoptera, Dryinidae) were observed. The average parasitoid infection rate was 1.6% ($n = 560$), which according to Denno & Roderick (1990), does not affect the population dynamics of the host. The molecular identification of parasitoid species associated with *D. europaea* revealed 22–28% of genetic divergence compared with the publicly available data. Due to the limited number of species and/or barcode records of the Dryinidae family available in BOLD and NCBI GenBank and because many of them exhibit genetic distances greater than 20%, even up to 25%, we could only confirm identification at the family level.

Reproductive behaviour

Under the cage conditions, the adults demonstrated polyphagous behaviour by feeding on all the plant species available. A total of 69 copulations were recorded in the field mesh cages and 18 in the mobile frame cages. Copulations were observed during August in the noon hour (12–13 h). Mortality among the caged specimens was not recorded during July or in the first half of August. Mortality increased slightly from mid-August and affected male specimens, i.e., most likely the males that had previously participated in copulation. Under the cage conditions, all males had died by mid-September. A decreasing number of males was also observed in the field populations of *D. europaea* at all four locations.

The oviposition behaviour of *D. europaea* was studied under the semi-field cage conditions. First ovipositions were observed during the last week of August, both in 2010 and 2011. Prior to the oviposition period, the females spent most of the day at the soil surface. As a consequence, the apical end of the wings of these females became evidently ragged. Oviposition occurred at the soil surface; before laying eggs, the females collected soil particles at the caudal end of the abdomen by secreting a sticky fluid that turned the soil particles into mud. Consequently, the mud filled the space between the anal segment and the third valvula that are surrounding the ovipositor shaft (fig. 2a–c). The females employed the anal segment and the third valvula to shuffle and scroll the mudded soil, making an irregular oval formation up to 4 mm in diameter. The females oviposited 2–4 eggs inside the muddy soil which subsequently fell off onto the soil surface (fig. 2d, e). The mean fecundity of dissected females was 41.9 ± 11.0 (range 24–63, $n = 30$).

Post-hibernation emergence

The emergence of N1 nymph inside the cages under outdoor conditions was observed in the middle of May. The same was true for eggs collected from the mobile framed cages and later kept for laboratory observation. From four mobile framed cages set up in 2010, a total of 560 nymphs emerged during May 2011. The emerged nymphs were successively collected for morphological studies of instars. In addition, rearing of *D. europaea* in three field mesh-cages resulted in the emergence of 421, 480 and 544 adults, respectively.

Morphology and behaviour of immature stages and adults

The five instars were determined on the basis of the vertex length (fig. 3) and morphological characters (fig. 4, table 1). The first two instars were selected visually, i.e., for measurements of N1 instars, *ex ovo* emerged nymphs were used, whereas molted N1 nymphs were used for N2 instars. Only molted nymphs were selected for the morphological analysis of late instars. A total of 223 nymphs and 30 adult specimens (15 males and 15 females) were used for measurements of the vertex and body length.

Eggs

(Fig. 2f) – elongated, oval, yellowish-green, with chorion translucent, in length 0.93 ± 0.05 mm (range 0.88–1.02, $n = 25$), 0.42 ± 0.01 mm wide (range 0.40–0.45, $n = 25$). The cephalic end of the egg is pearl white in colour, armed with a bundle of shortly elongated processes (0.12 ± 0.02 mm, range 0.07–0.17, $n = 25$). *D. europaea* overwinters in the egg stage.

First-instar nymph

N1 (figs 4a and 5a). Mean vertex length of 0.34 ± 0.03 mm (range 0.29–0.38, $n = 34$) and body length (cephalic processus included) 1.12 ± 0.09 mm (range 0.94–1.25, $n = 34$); bicoloured, head and thorax dark brown–black, abdomen pearl white, nearly translucent; vertex and frons dark brown–black with black and pearl white spot patterns between the median and lateral carina of frons; pronotum with a single row of six sensory pits dorsally; legs white. Just after the start of feeding, the nymphs secrete several hair-like wax excrements caudally. The first-instar nymphs are motionless, do not change feeding position and become into N2 instars after 3–4 days at room temperature (23 ± 1°C).

Second-instar nymph

N2 (figs 4b and 5b). Mean vertex length of 0.52 ± 0.04 mm (range 0.40–0.59, $n = 31$) and body length (cephalic processus included) 2.60 ± 0.19 mm (range 2.02–2.98, $n = 31$). Nymphs multicoloured, most often with the ground colour of the head and the thorax, grey–green with white patterns, with some specimens coloured with paler or darker nuances of brown; ground colour of abdomen pearl white, with wide coloured patterns on tergites medially and laterally and five rows of white dots dorsally; vertex and frons grey-green with black and white spots patterns between the median and lateral carina of frons; pronotum with a single row of seven sensory pits dorsally; legs greenish-white. Second-instar nymphs are also motionless, molting into N3 instars after 5–6 days at room temperature.

Third-instar nymph

N3 (figs 4c and 5c). Mean vertex length of 0.83 ± 0.06 mm (range 0.71–1.02, $n = 48$) and body length (cephalic processus included) 3.63 ± 0.31 mm (range 2.42–4.5, $n = 48$). Nymphs multicoloured, most often the ground colour of the head and the thorax are olive-green with rare white patterns; abdomen usually somewhat brighter in colour with five rows of white dots dorsally; vertex and frons olive-green with black and pearl white spots patterns between the median and lateral carina of frons; pronotum with two rows of sensory pits dorsally; legs pale green. Third-instar nymphs are more active but

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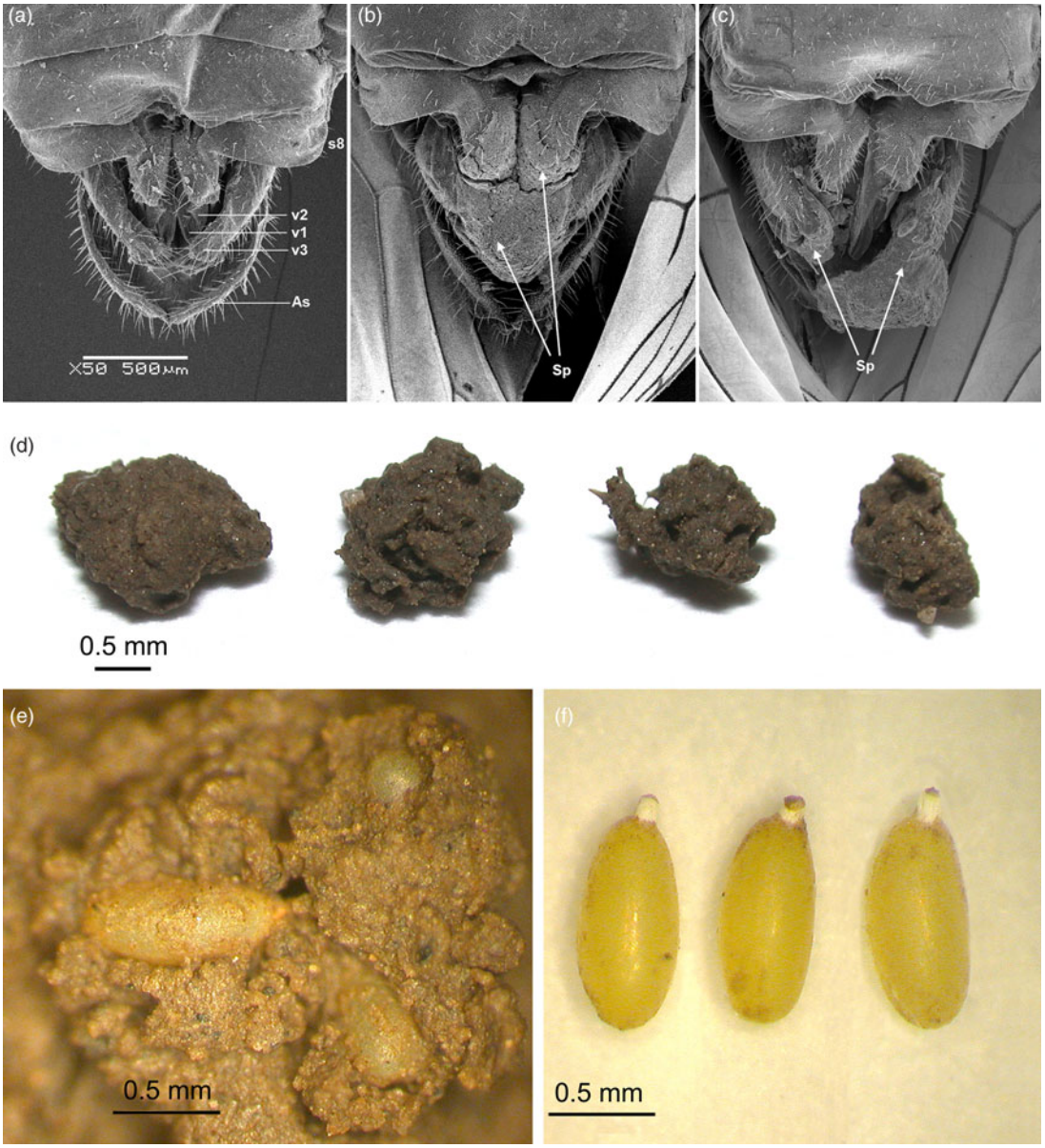

Fig. 2. Characteristics of the female genital apparatus, eggs and 'soil nests' of *Dictyophara europaea*: (a) Caudal end of the abdomen ventrally with the morphological structures of female genitalia involved during oviposition process: s8 – eight sternit; v1 – first valvula; v2 – second valvula; v3 – third valvula; as – anal segment. (b and c) Caudal end of the abdomen ventrally filled with liquid mud, i.e., soil particles (Sp). (d) View of soil particles with deployed eggs dropped by the female during oviposition. (e) View of the egg positions inside the oviposited 'soil nests'.(f) View of eggs extracted from 'soil nests'.

situate at the basal stem parts of plants during feeding, molting into N4 instars after 6–8 days at room temperature.

Fourth-instar nymph

N4 (figs 4d and 5d). Mean vertex length of 1.15 ± 0.04 mm (range 1.04–1.24, $n = 80$) and body length (cephalic processus included) 5.19 ± 0.32 mm (range 4.53–5.98, $n = 80$). Nymphs are multicoloured, very often green or olive-green with pale brown nuances, but in some specimens the ground colour is pale brown, dark brown or rarely reddish-brown; abdomen somewhat brighter in colour with four rows of white dots dorsally; frons with black and pearl white spots patterns between the median and lateral carina of frons; pronotum with three rows of sensory pits dorsally; legs pale green. Fourth-instars nymphs are more active, frequently changing position during feeding. The N4 nymphs molted into N5 instars after 7–10 days at room temperature.

Fifth-instar nymph

N5 (figs 4e and 5e). Mean vertex length of 1.31 ± 0.05 mm (range 1.21–1.39, $n = 30$) and body length (cephalic processus included) 6.23 ± 0.47 mm (range 5.41–7.11, $n = 30$). Nymphs

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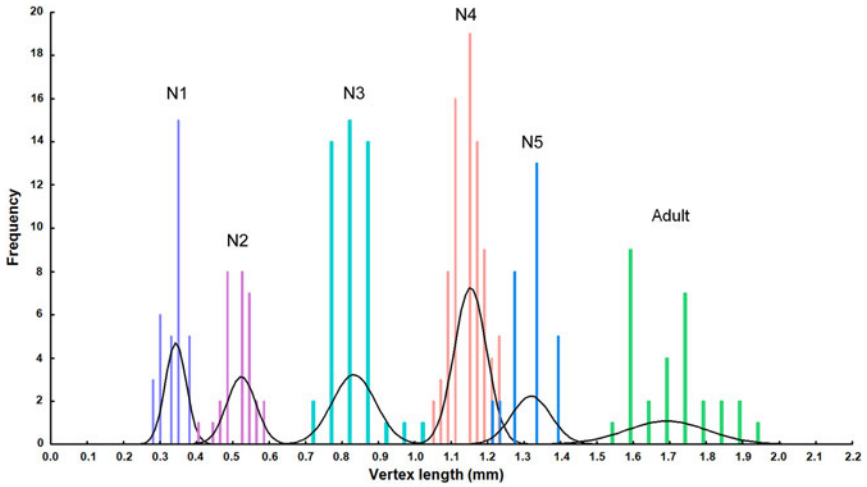

Fig. 3. Multimodal frequency distribution of the observed vertex length of N1–N5 instars and the adult stage of *Dictyophara europaea*.

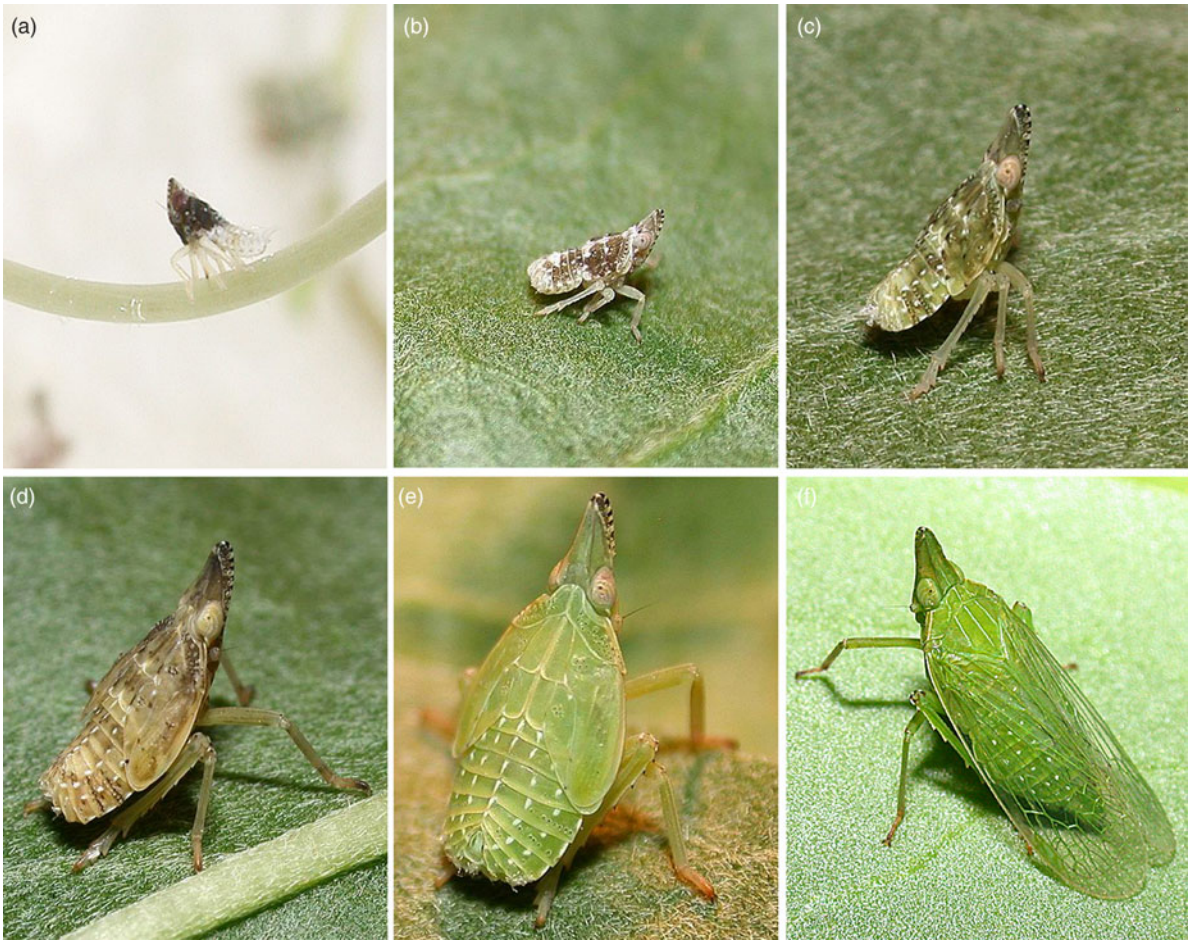

Fig. 4. View of instars and adult of *Dictyophara europaea*. (a) First-instar nymph. (b) Second-instar nymph. (c) Third-instar nymph. (d) Fourth-instar nymph. (e) Fifth-instar nymph. (f) Adult.

are usually entirely green, abdomen with five rows of white dots dorsally; frons with black and pearl white spots patterns between the median and lateral carina of frons; pronotum with three or four rows of sensory pits dorsally; legs pale green, tarsi yellowish-brown. Fifth-instar nymphs are very active, frequently changing feeding sources. The N5 nymphs

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Table 1. Summary of the key discriminatory characteristics of *D. europaea* instars.

Instar	Mean vertex length ± SD/ range (mm)	Mean body length ± SD/ range (mm)	Body colour pattern	Number of rows of pronotal sensory pits	Instar mobility
N1	0.34 ± 0.03/ 0.29–0.38	1.12 ± 0.09/ 0.94–1.25	bicolour	1	no
N2	0.52 ± 0.04/ 0.40–0.59	2.60 ± 0.19/ 0.94–1.25	multicolour	1	no
N3	0.83 ± 0.06/ 0.71–1.02	3.63 ± 0.31/ 2.42–4.5	multicolour	2	medium
N4	1.15 ± 0.04/ 1.04–1.24	5.19 ± 0.32/ 4.53–5.98	multicolour	3	medium
N5	1.31 ± 0.05/ 1.21–1.39	6.23 ± 0.47/ 5.41–7.11	unicolour (green)	3 (4)	high

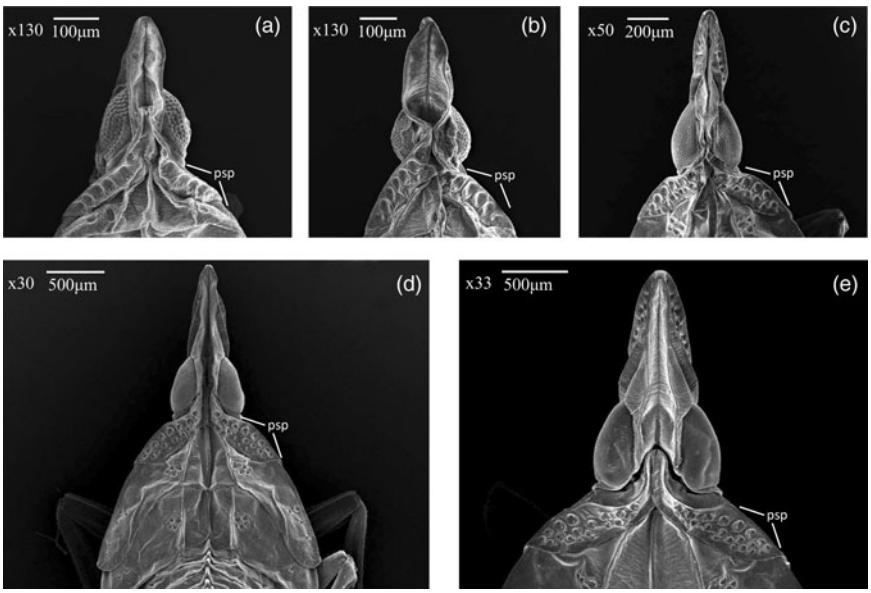

Fig. 5. Pronotal sensory pits (psp) of *Dictyophara europaea* instars. (a) First-instar nymph. (b) Second-instar nymph. (c) Third-instar nymph. (d) Fourth-instar nymph. (e) Fifth-instar nymph.

molted into the adult stage after 8–12 days at room temperature.

Each new instar showed an increase in vertex length with a mean growth rate of 1.41, as calculated according to Dyar's rule (table 2). Although originally developed as a method for determining the number of instars of Lepidoptera, Dyar's rule can be applied to the planthopper *D. europaea* because the calculated vertex lengths of almost all instars were within the range of the observed values. However, the growth ratio for the late instars of *D. europaea*, as opposite to Dyar's rule, actually decreased, which could be due to a number of environmental factors (Klingenberg & Zimmermann, 1992; Hunt & Chapman, 2001).

Multimodal frequency distribution (fig. 3) confirmed two observations regarding the instars: that *D. europaea* has five instars and the overlap in vertex length between the N4 and N5 instars. Namely, some of the large N4 and small N5 instars have identical vertex length. However, misclassification between these two instars was excluded because of the clear distinction in body colour and morphological characteristics (table 1).

Morphology of adults

Mean vertex length of 1.68 ± 0.11 mm (range 1.51–1.92, n = 30) and mean body length (cephalic processus included) of the adults is 9.25 ± 1.03 mm (range 7.5–12.1, n = 30). Mean length of males is 8.49 ± 0.44 mm (range 7.5–9.1, n = 15) and 10.0 ± 0.88 mm (range 9.0–12.1, n = 15) for females. Ground colour is entirely green; fastigium with few black spots. Cephalic process (fig. 4f) slightly upturned, nearly cuneiform, twice longer than the pronotum, vertex relatively broad with lateral margins strongly carinate, tortuously diverging towards the eyes; the median carina of vertex slightly shallow apically, distinctively visible at its basal half, white in colour. Pronotum and mesonotum with median and lateral carina distinct white coloured. Abdomen with six rows of white spots dorsally. Wings are hyaline transparent, longer than abdomen. Legs

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Table 2. Measurements of vertex length in instars of *D. europaea* and calculated vertex length according to Dyar's rule.

Instar	Sample size	Mean vertex length ± SD (mm)	Range of vertex length (mm)	Observed growth ratio[1]	Mean observed growth ratio	Calculated vertex length (mm)[2]
N1	34	0.34 ± 0.03	0.29–0.38			0.34
N2	31	0.52 ± 0.04	0.40–0.59	1.53		0.48
N3	48	0.83 ± 0.06	0.71–1.02	1.59	1.41	0.68
N4	80	1.15 ± 0.04	1.04–1.24	1.38		0.96
N5	30	1.31 ± 0.05	1.21–1.39	1.14		1.35

[1]Vertex length of instar N_i/vertex length of instar N_{i-1}.
[2]Vertex length of $N_{i+1} = N_i$ multiplied by the mean observed growth rate (1.41).

pale green; distal end of fore tibia and tarsomeres brown in colour; hind tibia with seven apical black-tipped spines, first and second tasomeres with approximately 16–20 black-tipped apical spines, respectively. Adults are very active during day time, frequently changing their position and feeding sources. No higher preference for any of the plants offered as a food source was observed, thus confirming the highly polyphagous behaviour of *D. europaea*.

Discussion

Data on the biological properties and peculiarities of particular organisms, especially those with economic or environmental impact, are of primary interest for a full understanding of their role and interaction with the environment. In general, the biology of dictyopharids is poorly known and data regarding life history are only available for a few species from the Palaearctic (Melichar, 1912; Holzinger & Hausl-Hofstätter, 1994; Nickel & Remane, 2002; Holzinger *et al*., 2003; Nickel, 2003; Lessio & Alma, 2008; D'Urso & Mifsud, 2012; Burrows, 2014), Nearctic (Wilson & McPherson, 1981; Wilson & Wheeler, 1992, 2005; McPherson & Wilson, 1995; Liang & Wilson, 2002) and Neotropical (Hernández *et al*., 2011; Remes Lenicov *et al*., 2012) regions.

D. europaea is relatively common polyphagous planthopper widely distributed in the Western Palaearctic, with a recently published record that confirmed its wider distribution to Western China (Song & Liang, 2008). Although *D. europaea* is treated as a common species and acts as a natural vector in the epidemiology of FD-C phytoplasma (Filippin *et al*., 2009*a*), information about the life history of this planthopper is scarce in the literature. An exception is the contribution of Lessio & Alma (2008), who reported polyphagous feeding behaviour of *D. europaea* but also a possible close association with *A. retroflexus* and *U. dioica* as preferred host plants for nymphs and adults. However, this study was limited to the scope of the vineyard agroecosystems in Northern Italy, and in the same region, *D. europaea* was also found to be associated with *C. vitalba* plants (Filippin *et al*., 2009*a*). This further emphasizes the need for more precise definitions of its feeding sources and behavioural characteristics. In our study, we applied a wide methodological approach, based primarily on extensive observations of *D. europaea* field populations and caged adults using several rearing methods, which allowed us to observe the morphological and behaviour peculiarities of all developmental stages.

To date, only the oviposition behaviour of the Neotropical dictyopharid species *Taosa longula* Remes Lenicov, 2010, in association with water hyacinth (*Eichhornia crassipes*, Pontederiaceae) has been studied in detail (Hernández *et al*., 2011). During oviposition, *T. longula* females utilize the first valvula, armed with a row of strongly sclerotized bifurcate teeth, to penetrate the inside plant tissue prior to egg laying. Wilson & McPherson (1981) reported occasional oviposition of the Nearctic dictyopharid species *Nersia florens* Stål, 1862 under laboratory conditions but without any details. Regarding *D. europaea*, Nickel (2003) stated that oviposition is performed into soil, though this was never supported with concrete observation. Although without data for *D. europaea*, Wilson *et al*. (1994) describe the ovipositor structure of the members of Dictyopharidae as the Fulgorid type for egg deposition by 'raking or sweeping substrate and placing eggs therein', while Emeljanov (1987) defined the ovipositor of the Dictyopharidae as a 'raking-kneading ovipositor'.

Our study revealed that the oviposition behaviour of *D. europaea* is a complex process, leading to the optimal protection of eggs, hidden in soil particles and then dropped onto the soil surface ('soil nests'). Such an oviposition strategy is beneficial at several levels. Because egg mortality plays a major role in the population biology of planthoppers (Denno & Roderick, 1990, and the references therein), such oviposition manner provides a good protection for eggs because the soil particles (with eggs) are highly camouflaged, becoming an integral part of the soil superficial layer, thus difficult for the detection by predators. In addition, these small soil particles filled with eggs may facilitate egg dispersal by wind and consequently contributes to the successful spread of the *D. europaea* throughout environments. Lastly, the observation of females depositing 2–4 eggs per single oviposition event represents a way of minimizing the risk and increasing survival (Prestidge, 1982), acting according to the general predictions of the bet-hedging strategy (Olofsson *et al*., 2009).

Similar to other members of the Dictyopharidae family, *D. europaea* has five instars. Only the first- and fifth-instar nymphs show stable colour patterns, which are bicoloured and entirely green, respectively. In contrast, the nymphs of the second–fourth-instar exhibit highly variable colour patterns. The vertex length of the instars, combined with the number of pronotal rows of sensory pits, allows for high accuracy in distinguishing instars. As the first and second-instars are motionless and behave sedentarily with practically no attempt to shift host or range, the polyphagous ability of *D. europaea* nymphs is of great importance to their successful development before they reach the later instars, a time when nymphs demonstrate higher mobility. In contrast, the winged adults are good flyers and may successfully migrate relatively long distance (Burrows, 2014). The high mobility of adults in the late summer with the purpose of aggregation on plants better adapted to drought and dry conditions represents a horizontal spatial distribution of this species through the habitat. The

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long period of adult activity, which extends up to 4 months (from the end of June to the beginning of October), combined with its polyphagous behaviour, is of particular interest and confers on *D. europaea* the possibility of successful dispersal and settlement in different biotopes.

Recently, increasing interest towards *D. europaea* has been motivated by its role in plant pathogen transmissions, primarily that of obligate bacteria from the genus '*Candidatus* Phytoplasma'. The transmission pathways of vector-borne plant diseases are determined by the vector feeding preferences, reservoir plants acting as common hosts of vector and pathogen, and ability of the vector to acquire a pathogen from a reservoir source and inoculate other plants (Kosovac *et al*., 2016). Accordingly, *D. europaea* should be treated as a potentially multilateral vector in the transmission of diverse phytoplasmas because several phylogenetically divergent types of phytoplasmas of the 16SrII, 16SrV and 16SrXII groups have been found in this planthopper (Filippin *et al*., 2009*a*, *b*; Cvrković *et al*., 2010; Mitrović *et al*., 2012). Thus, knowledge on the biology of *D. europaea* is critical for understanding the epidemiological pathways in which it could be involved. Probably, the most important involvement of this planthopper is in the transmission of the grapevine disease FD, caused by a phytoplasma belonging to the 16SrV-C subgroup (FD-C), which severely affected several grapevine regions in Northern Italy (Angelini *et al*., 2001), Slovenia (Mehle *et al*., 2011) and Serbia (Duduk *et al*., 2004; Krnjajić *et al*., 2007), with great economic losses in vine production.

Our field study described the seasonal phenology and observed the late summer aggregation of *D. europaea* on *C. vitalba*, the plant documented as a main reservoir plant of FD-C type of FD phytoplasma across Northern Italy and the Balkans (Filippin *et al*., 2009*a*). Our study also confirmed that the flight activity of *D. europaea* adults is nearly 4 months; during this time, the planthopper may acquire phytoplasmas from different plant sources and spread them throughout the environment, which strongly implies its important role in the epidemiology of plant diseases for which a phytoplasma is the causal agent.

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