Environmental and Experimental Biology (2013) 11: 205–214 *Original Paper*

Host preference of herbivorous arthropods feeding on *Ficus* (Moraceae) grown *ex situ* in Ukraine

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Abstract

Different plant taxa are known to be selectively preferred by particular herbivorous arthropod species. The goal of our study was to determine to what extent *Ficus*-feeding herbivores may display host preference with respect to plant infrageneric taxa under greenhouse conditions of a botanical garden. Using conventional methods for arthropod sampling in greenhouses, it was shown that the abundance and species richness of sucking herbivores on *Ficus* greatly depended on the taxonomic position of both herbivores and their host-plants. Herbivores of all found taxa tended to choose plants of subgenus *Urostigma* for feeding, while those of the subgenera *Synoecia* and *Sycidium* were mostly ignored by them. *Ficus* plants in general seemed to be most preferred by herbivores of the families Pseudococcidae and Tetranychidae among all the species found. This finding may potentially be useful in prediction of herbivore assemblage structure and feeding behaviour in *Ficus*-containing plant communities.

Key words: feeding behaviour; *Ficus*; greenhouse conditions; herbivore assemblages; host-plant taxa; plant-herbivore interactions; sucking herbivores.

Introduction

Ficus L. (Moraceae) is known to be one of the most species-rich angiosperm genera, which comprises about 750 species of pantropical distribution (Berg 1989). Due to high diversity of its morphological traits and growth strategies combined with the species richness, *Ficus* is considered to be an important component of tropical floras as well as one of keystone resources for herbivorous arthropods in the forests (Berg 1989; Berg, Wiebes 1992; Basset et al. 1997). In fact, *Ficus* is also highly widespread outside its natural range as cultivated, naturalised, or weedy plant, and many varieties have been bred from some of its species in order to improve their qualities for people's use. As a result, morphological variability and general range of the genus have consequently been highly broadened allowing new herbivore taxa to feed on these plants under the new growing conditions (e.g. Nadel et al. 1992; Basset et al. 1997). Some herbivore species are known to have become notorious *Ficus*-feeding pests of economic importance. This all makes *Ficus* quite a suitable genus for studying the structure of plant-associated arthropod assemblages. Being a single distinctive taxonomic group, *Ficus* can provide substantial material for herbivore community studies in terms of host morphologic variability, its natural distribution as well as the domestication level.

Literature on the analysis of herbivorous arthropod communities associated with plants of particular taxa is rare, despite the wide range of host records for numerous herbivores provided by various lists and catalogues, monographs, abstracts, and databases available both on-line and off-line (Basset et al. 1997; Novotny, Basset 2005). Our literature survey showed that *Ficus* has considerably been examined in terms of its mutualistic interactions with pollinating wasps of the family Agaonidae (Hymenoptera: Chalcidoidea) and some other related parasitic species. These insects consequently appeared to be the largest group within the known herbivore fauna of *Ficus*, as they were discovered to consume certain floral parts when developing within the syconia (e.g. Berg, Wiebes 1992; Compton et al. 1996; Basset et al. 1997). Substantive work was done by Basset et al. (1997) who compiled the literature data on arthropod fauna feeding on *Ficus* worldwide and conducted a profound field research in New Guinea together with other investigators (Novotny, Basset 1998; Basset, Novotny 1999; Novotny et al. 1999; Lepš et al. 2001; Novotny et al. 2002; Novotny et al. 2005).

In the studies on *Ficus*-associated arthropod communities, the mainly considered host-plant features are its geographical and habitat distribution (e.g. Basset et al. 1997; Basset, Novotny 1999; Lepš et al. 2001; Novotny et al. 2002; Novotny et al. 2005). Several studies have involved certain host-plant morphological traits (Basset, Novotny 1999; Ribeiro, Basset 2007) and phylogeny (Weiblen et al. 2006). Nevertheless, in spite of high morphological diversity of *Ficus,* which allows to identify different infrageneric taxa (e.g. Berg 1989; Berg, Wiebes 1992; Berg 2003a; Klimko, Truchan 2006; Sonibare et al. 2005), *Ficus*-feeding herbivore fauna has been seldom examined with regard to the host morphology and taxonomy. Moreover, no studies have dealt with herbivore community structure with respect to plant infrageneric position. Meanwhile, host-plant architecture has been shown to affect the composition of herbivore arthropod communities on plants of taxa other than *Ficus* (Peeters 2002).

In view of a morphological approach used for *Ficus* classification (Berg 2003a), the objective of the present study was to determine whether different *Ficus* infrageneric taxa support unique herbivorous arthropod fauna under similar environmental conditions of a greenhouse, and whether herbivore species tend to choose particular *Ficus* taxa for feeding. Both practical and theoretical aspects may be developed in the application of such data. Firstly, information on how feeding choice of a herbivorous arthropod depends on taxonomic position of *Ficus* host plants may be used in pest management to predict herbivore assemblage structure and possible sites of herbivore abundance in *Ficus* cultivation areas and in *Ficus*-containing plant communities. Secondly, this finding can lay a theoretical background for plant morphological studies to determine relationships between plant structural traits and host preference of herbivores in natural systems, which can increase our understanding of the ecology of host preference in *Ficus*-feeding herbivores.

Materials and methods

Area of the study

The study area consisted of four sites covering greenhouse plant collections of four botanical gardens in three cities of Ukraine:

Site A: Botanical Garden of the Ivan Franko National University of Lviv, Lviv city;

Site B: M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine, Kyiv city;

Site C: O.V. Fomin Botanical Garden of the Taras Shevchenko National University of Kyiv, Kyiv city;

Site D: Donetsk Botanical Garden of the National Academy of Sciences of Ukraine, Donetsk city.

The main characteristics of the sites are presented in Table 1. Each of the four greenhouse complexes consisted of several sections (i.e. greenhouses) with passages between them, and the plants of different taxonomic or ecological groups were grown in each of the sections under appropriate climatic conditions. *Ficus* plants are typically cultivated in non-specialized humid tropical and subtropical greenhouses together with many other plants of different origin and systematic position. In general, plant taxonomic composition in such greenhouses was more or less similar at the family scale in all four sites of the study, but some families varied in the species number represented. The number of cultivated plant species might change somewhat from year to year, which, however, did not influence the overall plant taxonomic diversity through the period of our study.

In greenhouses, climatic conditions are usually kept within the limits indicated in Table 1, with some day-night fluctuations. Soil conditions of *Ficus* cultivation were similar in all the sites. The data on greenhouse areas, plant collection structure, and environmental conditions were provided by curators of the greenhouse plant collections.

Biological material collection and identification

Sampling of arthropods on the cultivated plants was conducted during 2007-2013 in two to four replications per year at each site, except for site A where continuous observation over the whole period of the study was performed. Additionally, the assistance of greenhouse-working personnel was received in monitoring herbivore assemblages in greenhouses of sites B, C, and D to determine fluctuations in herbivore abundance and species composition.

In total, 54 *Ficus* species were examined, which were unevenly distributed among the sites (Table 2). The examined species were classified according to the recent classification of the genus *Ficus* (Berg 1986; Berg 2003a; Berg 2003b; Berg 2003c; Berg 2003d; Berg 2003e; Berg 2004a; Berg 2004b; Berg, Corner 2005). The synonymy and position of the species within the classification were checked using electronic sources (Global Biodiversity Information Facility, http://data.gbif.org; USDA Agricultural Research Service, http://www.ars-grin.gov;

Table 1. Characteristics of the study area sites. Full names and location of the sites can be found in Materials and methods. Climatic conditions are given for only the greenhouses where the studied *Ficus* were grown; the values were obtained for the whole period of the study

Site designation	Greenhouse area (m^2)	Climatic conditions (for six months of the hot and cold periods of year, mean ± SD)				Number of cultivated plant taxa	
		Temperature (°C)		Air humidity (%)		Species	Family
		IV-IX	X-III	IV-IX	X-III		
A	1565	23.7 ± 7.9	14.5 ± 4.8	91.8 ± 5.5	86.7 ± 4.6	1460	144
B	2300	25.4 ± 7.4	15.8 ± 3.8	92.3 ± 5.2	85.6 ± 3.7	2135	173
C	1250	24.7 ± 7.5	18.6 ± 4.7	93.1 ± 5.3	85.7 ± 4.5	3380	182
D	2720	24.8 ± 6.8	17.5 ± 4.6	91.4 ± 4.4	86.8 ± 4.3	1120	136

Table 2. *Ficus* species examined in the study and their status (marked with superscript letters) with respect to the occupation by herbivores revealed. The explanation for each species status is given in the text. [a], species occupied by many herbivore species (five and more) belonging to different taxa; [b], species highly occupied by representatives of certain herbivore taxa; [c], species not highly occupied by herbivores; [d], species free of herbivores or nearly not occupied

Subgenus	Section	Subsection	Species	Area of data collecting
Ficus	*Ficus*	*Ficus*	*F. afghanistanica* Warb.[d]	C, D
			F. carica L.[c]	A, B, C, D
			F. palmata Forssk.[c]	C, D
		Frutescentiae	*F. deltoidea* Jack[d]	A
			F. erecta Thunb.[a,b]	A, C, D
			F. formosana Maxim.[c]	B
Synoecia	*Kissosycea*	–	*F. hederacea* Roxb.[d]	B, D
	Rhizocladus	*Plagiostigma*	*F. pumila* L.[d]	A, B, C, D
			F. sarmentosa Buch.-Ham. ex. Sm.[d]	B
		Punctulifoliae	*F. sagittata* J. König ex Vahl[d]	A, B
			F. villosa Blume[d]	B
Sycidium	*Sycidium*	–	*F. aspera* G. Forst.[d]	B, C
			F. montana Burm.f.[c]	B, C
			F. ulmifolia Lam.[d]	C
	Palaeomorphe	–	*F. tinctoria* G. Forst. subsp. *gibbosa* (Blume) Corner[c]	A, D
			F. virgata Reinw. ex Blume[d]	C
Sycomorus	*Sycomorus*	*Sycomorus*	*F. mucuso* Ficalho[c]	B
			F. racemosa L.[b]	D
			F. sur Forssk.[a,b]	C, D
			F. sycomorus L.[c]	B, C, D
			F. vallis-choudae Delile[d]	D
		Neomorphe	*F. auriculata* Lour.[c]	A
	Sycocarpus	*Sycocarpus*	*F. hispida* L.f.[b]	B, C
			F. septica Burm.f.[d]	B
Pharmacosycea	*Oreosycea*	*Pedunculatae*	*F. callosa* Willd.[b]	A
Urostigma	*Americana*	–	*F. crocata* (Miq.) Miq.[d]	C
			F. luschnathiana (Miq.) Miq.[b]	B, C
			F. palmeri S. Watson[c]	A, C
	Urostigma	*Urostigma*	*F. lacor* Buch.-Ham.[c]	C
			F. laurifolia Hort. ex Lam.[c]	D
			F. religiosa L.[a,b]	A, B, C, D
			F. salicifolia (Vahl) C.C. Berg[c]	D
			F. virens Aiton[b]	A
		Conosycea	*F. altissima* Blume[d]	B
			F. benghalensis L.[a]	A, B, C, D
			F. benjamina L.[a,b]	A, B, C, D
			F. binnendijkii (Miq.) Miq.[a]	A, B, C, D
			F. drupacea Thunb.[a,b]	A, B, C, D
			F. microcarpa L.f.[c]	B, D
			F. retusa L.[c]	B, D
	Stilpnophyllum	*Stilpnophyllum*	*F. elastica* Roxb. ex Hornem.[a,b]	A, B, C, D
		Malvantherae	*F. macrophylla* Desf. ex Pers.[b]	A, B, D
			F. platypoda A. Cunn. ex Miq.[a,b]	A
			F. rubiginosa Desf. ex Vent[a]	A, B, C, D
			F. watkinsiana F.M. Bailey[a,b]	A, B, D

Table 2. /continued/

Subgenus	Section	Subsection	Species	Area of data collecting
	Galoglychia	*Platyphyllae*	*F. vasta* Forssk.[b]	A
		Chlamydodorae	*F. buxifolia* De Wild.[d]	A
			F. craterostoma Mildbr. & Burret.[c]	B, C, D
			F. lingua D. Wild. & T. Durand subsp. *lingua* D. Wild.[c]	B
			F. natalensis Hochst. subsp. *leprieurii* (Miq.) C.C. Berg[c]	A, B, C, D
			F. natalensis subsp. *natalensis* Hochst.[c]	A
			F. thonningii Blume[c]	D
			F. volkensii Warb.[c]	A
		Cyathistipulae	*F. cyathistipula* Warb.[c]	B, D
			F. lyrata Warb.[a]	A, B, C, D

Figweb, http://www.figweb.org/Ficus/index.htm) as well as available publications (van Greuning 1990; Berg, Wiebes 1992; Erhardt et al. 2002; Zhou, Gilbert 2003; Berg, Corner 2005; van Noort et al. 2007; Kumar et al. 2011; Chaudhary et al. 2012).

At each site, arthropods were sampled on all the individual plants (from one to three) of each *Ficus* species. The examined plants varied in height from one to 10 meters (except for climbers), mostly 3 to 5 m. The plant individuals grown less than one year in the collections as well as plant cultivars were not taken into account. Plants of other taxa grown in the same greenhouses with *Ficus* were also observed for herbivores.

For arthropod collecting and fixation conventional methods were used. Insects and mites were sampled with the use of a brush or an aspirator from different parts of the plant crown and stored in 70% ethanol. Sessile developmental stages of arthropods were collected by hand with small parts of the substratum (leaves and stems) (Tereznikova, Chumak 1989). The root system of the plants was impossible to observe, as it could lead to damage of the collection plants. Identification of arthropod species was made on the basis of their morphological traits by making temporary preparations (Tereznikova, Chumak 1989) and using appropriate identification keys (Borkhsenius 1963; Dyadechko 1964; Műller 1976; Mitrofanov et al. 1987; Akhatov et al. 2004). The degree of host-plant occupation by herbivores was determined visually for each herbivore species using a 10-point scale: 0 points – herbivore individuals are absent on the plant; 1 point – several herbivore individuals are present, less than 5% of the plant surface area is occupied by herbivore; 2 to 3 points – 6 to 25% of the plant surface area is occupied; 4 to 5 points – 26 to 50% of the plant surface area is occupied; 6 to 7 points – 51 to 75% of the plant surface area is occupied; 8 to 9 points – 76 to 100% of the plant surface area is occupied. To estimate herbivore preference, we used the values of plant occupation degree detected during the time when the herbivores of particular taxa were most abundant in the greenhouses.

Statistical analysis

Among *Ficus* infrageneric taxa, we chose subgenera to compare by herbivore preference; the use of taxa of lower ranks (sections and subsections) was assumed to provide no meaningful results because of too few species within these ranks in the study. The abundance and species richness of herbivores on their host-plants were estimated using three parameters: (1) plant occupation degree (as identified before), (2) herbivore species number on an individual plant species, and (3) percent of plant species within each *Ficus* subgenus colonized by herbivores of a particular taxa. For *Ficus* subgenera, mean values of (1) and (2) were calculated.

To estimate the influence of herbivore and host-plant taxonomic position on the abundance and species richness of herbivores, two-way factorial ANOVA was performed on (1), (2), and (3) using *Ficus* subgenera and herbivore families as factors. Also, a *t*-test was used to compare the same three parameters for different *Ficus* subgenera. Pearson correlations were determined between the numbers of examined and colonized *Ficus* species of each subgenus as well as between the latter and the number of herbivore species colonizing the plants.

Results

In total, 22 herbivore species were recorded on *Ficus* during the study (Table 3), which was 44.9% of the total herbivore arthropod species number found to feed on the greenhouse plants. *Ficus*-feeding Hemiptera represented 45.2% of all the hemipterous species found, Thysanoptera (Thripidae) – 87.5%, and Arachnida – 11.1%. These arthropod taxa were found to contribute most of the herbivore diversity and abundance in the study. Most of the species sampled on *Ficus* were also collected on a great quantity of other plants in the greenhouses (Table 3). The species listed in Table 3 occurred in all four sites of the study except for *Pseudococcus gahani* which was recorded only in site A, and *Chrysomphalus dictyospermi* and *Echinothrips americanus* both found in sites A, B, and C except D.

Table 3. Herbivores collected on *Ficus*, their host-plant taxa number and occupation degree in the study area. Species status marked with superscript letters is given according to Akhatov et al. (2004), Chumak (2010), and Chumak and Shkol'na (2004). The point values of plant occupation degree are given in the Materials and methods. [a], indigenous species; [b], cosmopolitan species; [c], new for Ukraine; [d], identified at the rank of a species complex (Chumak 2004)

Family	Species	Number of host plant taxa			Maximal value of *Ficus* occupation degree
		Total		*Ficus* species	
		Species	Family		
Insecta					
Aleyrodidae	*Trialeurodes vaporariorum* Westw.	85	43	1	4
Aphididae	*Aphis fabae* Scop.[a]	12	8	1	2
	Aulacorthum circumflexum Buckt.	82	34	2	2
	Myzus persicae Sulz.[a,b]	74	38	3	1
Pseudococcidae	*Planococcus ficus* Sign.	96	37	23	9
	Pseudococcus affinis Maskell	254	97	10	4
	Pseudococcus gahani Green	5	5	1	2
	Pseudococcus longispinus Targ.	78	40	5	1
Coccidae	*Coccus hesperidum* L.[b]	153	74	15	6
	Saissetia coffeae Walker	148	69	1	2
Diaspididae	*Aspidiotus nerii* Bouché[b]	74	32	6	4
	Aspidiotus spinosus Comst.	12	6	1	1
	Chrysomphalus dictyospermi Morg.	11	9	2	5
	Hemiberlesia lataniae Sign.	22	11	3	3
Thripidae	*Anaphothrips orchidii* Moulton	57	25	6	4
	Echinothrips americanus Morgan.[c]	12	8	1	3
	Frankliniella occidentalis Perg.[c]	84	17	6	1
	Heliothrips haemorrhoidalis Bouché	244	78	16	9
	Hercinothrips femoralis Reuter	47	23	1	1
	Parthenothrips dracaenae Heeger	112	47	4	1
	Thrips tabaci Lind.[a]	174	34	3	1
Arachnida					
Tetranychidae	*Tetranychus urticae* Koch.[a,b,d]	124	63	28	9

Herbivores recorded during the study were found to feed on 75.9% (41 species) of the examined *Ficus* species. Among the latter, 82.9% were occupied by scale insects and mealybugs in total (Coccoidea), 68.3% – by spider mites (Tetranychidae), 46.3% – by thrips (Thripidae), 14.6% – by aphids (Aphididae), and 2.4% – by one species of whiteflies (Aleyrodidae). The exact numbers of host-plant taxa for each herbivore species and family are presented in Tables 3 and 4. The tables show that the families Aleyrodidae, Aphididae, and Diaspididae were least frequent on *Ficus*, whereas Pseudococcidae and Tetranychidae were the most common ones.

Each *Ficus* species studied appeared to support the same herbivore fauna at the family scale from year to year at all the study sites. Furthermore, when taking into account the plants grown in the same greenhouses with *Ficus*, most of the widespread herbivore species were noticed to choose plants of the same families for feeding at each study site. However, the abundance of herbivore individuals could change depending on the period of year. In particular, there was a low quantity of herbivores in greenhouses for almost the whole cold period of year (see Table 1). Over the hot period, their quantity fluctuated mainly due to the effect of plant protection measures used in the greenhouses.

The values of herbivore abundance and species richness differed for each *Ficus* subgenus. Plants of subgenera *Synoecia, Sycidium*, and *Pharmacosycea* were characterized by the lowest herbivore diversity (Table 4). The species of five *Ficus* subgenera except *Urostigma* were mainly colonized by Pseudococcidae and Tetranychidae, while other insect families had sporadic occurrence on these plants. In general, for the species of those subgenera relatively poor herbivore fauna was characteristic (Table 4) along with mostly low degree of their occupation by herbivores (Table 2).

The subgenus *Urostigma* supported the highest herbivore diversity, both in general and for its individual species. Each herbivore family, except Tetranychidae, was represented here by larger amount of species, and especially Thripidae had higher species number in comparison with herbivore communities feeding on *Ficus* of other subgenera (Table 4). Furthermore, for each herbivore family, the number of *Urostigma* host-species was much larger than that of other

Table 4. Species richness of herbivores on *Ficus* host-plants belonging to different subgenera

Herbivore family	Number of herbivore species occupying *Ficus* plants of each subgenus (number of *Ficus* species occupied)						Total number
	Ficus	*Synoecia*	*Sycidium*	*Sycomorus*	*Pharmacosycea*	*Urostigma*	
Aleyrodidae	–	–	–	–	–	1 (1)	1 (1)
Aphididae	1 (1)	–	–	1 (1)	–	2 (4)	3 (6)
Pseudococcidae	3 (4)	–	1 (1)	3 (5)	1 (1)	4 (20)	4 (31)
Coccidae	1 (1)	–	–	1 (2)	–	2 (12)	2 (15)
Diaspididae	1 (1)	–	–	2 (2)	–	4 (9)	4 (12)
Thripidae	3 (1)	–	2 (1)	3 (2)	–	7 (15)	7 (19)
Tetranychidae	1 (3)	1 (1)	1 (1)	1 (5)	–	1 (18)	1 (28)
Total number	10 (4)	1 (1)	4 (3)	11 (6)	1 (1)	21 (26)	22 (41)

subgenera. Finally, *Urostigma* had considerably more highly occupied plants among its species, as compared to the other subgenera (Table 2).

Significant positive correlations were detected between the total number of examined *Ficus* species of each subgenus and the number of species occupied by herbivores ($r = 0.99$; $p < 0.05$) as well as between the latter and the number of herbivore species occupying the plants ($r = 0.92$). These correlations are, in fact, theoretically expected and do not reveal any relationships between herbivores and their host-plants. However, another predictable correlation – between the number of herbivore species of each family and the number of *Ficus* species they occupy – was found to be not significant ($r = 0.29$), which may give some additional evidence for the hypothesis that herbivore families tend to unequally prefer *Ficus* plants for feeding.

ANOVA results showed strong relation between herbivore abundance and species richness and *Ficus* host-plant taxonomic position at the subgenus scale (Table 5). At the same time, all the three parameters analysed were also significantly related to herbivore families. The results of *t*-test showed that the subgenera *Synoecia* and *Sycidium* are more or less significantly different from the others, except *Pharmacosycea*, with respect to all the parameters of herbivore abundance and species richness analysed (Table 6).

Herbivores of different taxa were found to co-occur on many *Ficus* hosts (Table 7). Notably, herbivores of a particular family shared from 80 to 100 % of their *Ficus* hosts with herbivores of other taxa. The largest frequency of co-occurrence was detected for Pseudococcidae and Tetranychidae, Pseudococcidae and Thripidae, and Thripidae and Tetranychidae (Table 7).

When considering *Ficus* host-plants at the scale of a species instead of subgenera, all the examined plants could be classified into four groups according to their occupation by herbivores.

(1) Species occupied by many herbivore species (five and more) belonging to different taxa – 12 species.

(2) Species highly occupied by representatives of particular herbivore taxa – 15 species. Although herbivores of different taxa were found to feed on these plants (because of this, some of the plants belong to the first group as well), some dominant species occurred with a notably high

Table 5. ANOVA results for the abundance and species richness of herbivores of different families among *Ficus* subgenera characterized by the three parameters. The subgenus *Pharmacosycea* is not included into analysis

Source	*SS*	*df*	*MS*	*F*	*P*	*F* critical
(1) Mean occupation degree						
Ficus subgenera	4.772	4	1.193	5.873	0.002	2.776
Herbivore families	5.373	6	0.895	4.409	0.004	2.508
Error	4.875	24	0.203			
(2) Mean herbivore species number on an individual plant species						
Ficus subgenera	0.963	4	0.241	10.212	< 0.001	2.776
Herbivore families	1.207	6	0.201	8.531	< 0.001	2.508
Error	0.566	24	0.024			
(3) Percent of plant species colonized						
Ficus subgenera	6428.829	4	1607.207	12.33	< 0.001	2.776
Herbivore families	8107.35	6	1351.225	10.366	< 0.001	2.508
Error	3128.493	24	130.354			

Table 6. Student coefficient values between *Ficus* subgenera compared for (1) mean value of occupation degree by herbivores of each family, (2) mean number of herbivore species of each family on an individual *Ficus* species, and (3) percent of *Ficus* species colonized by herbivores of each family. Its critical value for the $df = 12$ is 2.2. Significance level: **, $P < 0.01$; *, $P < 0.05$

Ficus subgenera	*Ficus*	*Synoecia*	*Sycidium*	*Sycomorus*	*Pharmacosycea*	*Urostigma*
(1) Mean occupation degree						
Ficus	0					
Synoecia	2.141	0				
Sycidium	1.57	1.246	0			
Sycomorus	0.163	2.615*	1,.78	0		
Pharmacosycea	0.209	0.966	0.794	0.283	0	
Urostigma	0.914	3.312**	2.699*	1.193	0.222	0
(2) Mean herbivore species number on an individual plant species						
Ficus	0					
Synoecia	2.958*	0				
Sycidium	1.867	1.349	0			
Sycomorus	0.216	2.952*	1.974	0		
Pharmacosycea	1.0	0.786	0.191	1.133	0	
Urostigma	1.012	3,.217**	2.476*	0,.802	1.692	0
(3) Percent of plant species colonized						
Ficus	0					
Synoecia	2.522*	0				
Sycidium	1.819	1.155	0			
Sycomorus	0.331	2.916*	2.211*	0		
Pharmacosycea	0.71	0.785	0.385	0.952	0	
Urostigma	0.999	3.741**	3.019*	0.665	1.449	0

occupation degree (5 to 9 points), whereas other herbivores were less abundant.

(3) Twenty species were not highly occupied by herbivores. From one to several herbivore species were recorded on these plants with a low occupation degree (1 to 3 points).

(4) Fifteen species were free of herbivores or nearly not occupied. Although sporadic herbivore individuals were found on some of these plants, their colonies were not observed to develop, suggesting their accidental occurrence.

The species belonging to each of the above groups are respectively marked in Table 2.

Discussion

One of the major limitations of the study is the large difference in the examined species number between *Ficus* taxa. For example, one half of all the species belong to one subgenus of the six. The subgenus *Pharmacosycea* is in contrast represented by only one species, which makes it difficult to treat and the probability would be too low for any interactions. It was not therefore used in the ANOVA analysis. Furthermore, the theoretically expected correlations mentioned in the Results section influenced the choice of parameters to estimate herbivore abundance and species richness. In particular, instead of using the total herbivore diversity in each *Ficus* subgenus, we chose to calculate the diversity in one species and to calculate the mean value for each subgenus. In addition, the difference in plant diversity between the study sites, though mentioned to be little at the family scale (see section Materials and methods), may have affected the herbivores' feeding preference. However, most of the examined *Ficus* plants have been grown in the collections for quite a long time, and polyphagous herbivores may have adapted to them, which though is not the case for recently introduced species (see Table 3).

The results of the study showed that the abundance and species richness of sucking arthropod herbivores on *Ficus* greatly depends on the taxonomic position of both herbivores and their host-plants, which is indicated by ANOVA results (Table 5). This should be taken into account when predicting assemblage structure and feeding behaviour of herbivores in *Ficus*-containing plant communities. In the greenhouses, *Ficus* plants in general seem to be most preferable for Pseudococcidae and Tetranychidae, but some species of Coccidae and Thripidae (Table 3) may also choose *Ficus* as suitable host. Hence, these herbivores are most likely to colonize and damage *Ficus* plants under the cultivation conditions of greenhouse. At the same time, most of those herbivore species, which were sporadic on *Ficus*, also had a wide range of host-plants from other taxa in the study area (Table 3). This demonstrates that *Ficus* is not preferred by them due to certain reasons.

Table 7. Number of *Ficus* species shared by herbivores of different taxa. Table cells with boldface indicate the number of *Ficus* species occupied by herbivores of only a particular family

Herbivore families	Aleyrodidae	Aphididae	Pseudococcidae	Coccidae	Diaspididae	Thripidae	Tetranychidae
Aleyrodidae	**0**						
Aphididae	1	**0**					
Pseudococcidae	0	4	**6**				
Coccidae	0	1	12	**1**			
Diaspididae	0	2	11	7	**0**		
Thripidae	1	6	15	7	9	**2**	
Tetranychidae	1	4	21	12	11	15	**3**

Among *Ficus* subgenera, *Urostigma* supports the most diverse and abundant herbivore fauna in our study. However, on plants of subgenera *Ficus* and *Sycomorus* several herbivore taxa were also detected, which belong to almost as many families as occur on *Urostigma* (Table 4). This suggests that herbivore richness may be limited due to the small amount of the examined plant species of those two subgenera, in comparison with *Urostigma*. Nevertheless, the mostly low degree of plant occupation by herbivores in the mentioned subgenera (Table 2) provides evidence that they are less preferred by most of the herbivore species. In contrast, the subdivision of the examined *Ficus* species into four groups according to their occupation by herbivores (Table 2) showed that some *Urostigma* species do not support a rich herbivore fauna. In particular, the less colonized species of *Urostigma* mainly belong to the section *Americana* and subsection *Chlamydodorae* (section *Galoglychia*) (Table 2). Some species of the other sections showed low colonization, which does not allow us to make any suggestions concerning host preference of herbivores at the level lower than subgenus.

Based on the obtained data and their analysis, we can thereby conclude that (1) herbivores of all the taxa in our study tended to choose *Urostigma* among all *Ficus* subgenera for feeding, (2) the plants of subgenera *Synoecia* and *Sycidium* in general are evidently not preferred by the herbivores, and (3) the plants of subgenera *Ficus* and *Sycomorus* seem to be mainly preferred by Pseudococcidae and Tetranichydae. This knowledge may be applied to manage herbivore arthropod assemblages in *Ficus*-containing plant communities under cultivation conditions. The information allows to predict to a greater or lesser extent the potential of plants of particular *Ficus* subgenera to be colonized by herbivores. Furthermore, the described tendencies of herbivore feeding behaviour on *Ficus* may be also relevant to natural conditions, which needs further investigation.

The cause of such feeding preference of herbivores is unknown, since many factors may influence host selection. These factors include, among others, the activity of beneficial organisms (i.e. predators and parasites of herbivores), competition between herbivores, and those connected with plant quality (its structural and biochemical traits), etc. (Price at al. 1980; Shapiro et al. 1986; Bernays, Chapman 1994; Denno et al. 2000; Awmack, Leather 2002; Peeters 2002). Additionally, although climatic conditions of *Ficus* growing were shown to be similar in all the study sites (Table 1), there was no possibility to measure the indices near the plant surface, which are known to affect arthropod's behaviour (Shapiro et al. 1986). Concerning beneficial organisms, our observations in accordance with the published data on the study sites (Chumak 2004) revealed a poor spontaneous fauna of these organisms in the greenhouses combined with their low efficiency in herbivore regulation. This allowed to ignore their effect in the study.

Literature survey showed that the herbivore species collected do not mainly co-occur with their *Ficus*-hosts in the wild. This indicates that there is no phylogenetic relationship between them. Although nearly all the herbivore species found are of tropical and/or subtropical origin (Akhatov et al. 2004; Chumak 2004), many of them are widespread in greenhouses throughout the Palaearctic and some species have cosmopolitan distribution (Table 3). Thus, possible long-term coexistence of the herbivores and their host-plants under the greenhouse conditions may have been of great importance for the development of host preference.

Due to the frequent co-occurrence of herbivore species on *Ficus* shown (Table 7), competition between them may have arisen, especially between those belonging to the same feeding guild. The herbivores collected in our study represent only a few guilds of sucking arthropods: mobile mesophyll-feeders (Thripidae and Tetranychidae) and phloem-feeders (mobile – Aphididae, and sessile – Aleyrodidae, Pseudococcidae, Coccidae, and Diaspididae), as defined by other investigators (Basset et al. 1997; Peeters 2002). Hence, competition should be assumed to have potentially influenced the host-plant range of herbivores in our study.

Since host-plant quality is known to determine herbivorous arthropod behaviour, development, and feeding choice (Price at al. 1980; Shapiro et al. 1986; Bernays, Chapman 1994; Awmack, Leather 2002), we suggest that plant features may greatly influence host preference of herbivores in our study. The only herbivores known to be polyphagous (Akhatov et al. 2004; Chumak 2004) were found to feed on the studied *Ficus* plants. These species had many host plants from various taxa and of various origins in the study area (Table 3), which enables them to flourish there, having quite poor limitations in food availability. However, these generalist species supposedly have similar requirements to the host-plant traits, which may be sustained by their frequent co-occurrence (Table 7). The plant traits, in turn, correspond or do not correspond to those requirements, which results in herbivores to choose particular plant species for feeding. This suggestion is rather speculative, and the explanation of the discovered tendencies in herbivore host preference will be a challenge for our future investigations.

Acknowledgements

I am pleased to thank Dr. Lydia Tasenkevich, Dr. Nataliya Kalinovych, and Dr. Andriy Prokopiv, and the anonymous reviewer for reviewing this manuscript, helpful discussions and comments. Thanks to curators of greenhouse plant collections – Dr. Lyudmyla Buyun, Dr. Vira Nikitina, Dr. Olha Usoltseva, and M.Sc. Nadiya Lutsyshyn for providing the data on greenhouse conditions and permissions to work in greenhouses of the botanical gardens. Thanks to Dr. Petro Chumak, M.Sc. Ivan Strelnikov, and M.Sc. Nataliya Shchekhorska for assistance in monitoring herbivore assemblages, data collecting, and arthropod identification.

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Received 20 October 2013; received in revised form 28 November 2013; accepted 15 December 2013