High host plant aggregation
involves uniform gall distribution and high prevalence:
the case of wild roses and Bedeguar gall wasps (*Diplolepis rosae*)

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Abstract. We studied the effect of rose shrub spatial pattern and density toward its parasitism by *Diplolepis rosae* gall wasps, considering host shrubs' size. There were eight sample sites on dry pastures and/or on the edges of these pastures. Our results show that high densities rose shrubs show uniform distribution, while the low densities ones appear aggregated. Gall density and prevalence are affected by host plant aggregation. Gall aggregation is inversely related with host plant aggregation. The plant architecture hypothesis regarding rose shrub size was not supported.

Introduction

Host-specific phytophagous insects are usually patchily distributed within the populations of their host plants (Egan & Ott 2007) because high-quality plants are phenotypic and/or genotypic islands within a number of lesser-quality hosts (Janzen 1968). Host plant variation determines the distribution patterns of herbivores on their host plants (Egan & Ott 2007, Gripenberg & Roslin 2005). Studies regarding insect herbivory frequently refer to the effects of plant traits on the distribution of herbivores within and among host plants (Cornelissen & Stiling 2006). It is obvious that host plant trait differences have a great impact on herbivore dynamics (Underwood & Rausher 2000, McIntyre & Whitham 2003), distribution (Lawrence et al. 2003, Gripenberg & Roslin 2005, Crawford et al. 2007) and abundance (Rand & Louda 2006, Lara et al. 2008). Thus, recently the study of host plant variation effect on insect herbivore population dynamics became a priority regarding the need to incorporate results into applied integrated pest management (Price 2000).

Gall wasps are obligate parasites of plants. The effect of host's spatial distribution on parasitism may show positive and negative density dependence or density independence (Altizer et al. 2003, Hails & Crawley 1992, Rózsa et al. 1996). The distribution pattern of parasites on their hosts is determined by their prevalence (ratio of parasitized individuals in the sample), intensity (indi-vidual level of parasitism in the sample), and the host's spatial distribution and density (Stiling & Strong 1982, Rékási et al. 1997, Sandin & Pacala 2005, Cronin & Strong 1999). When host plants are spread on equal distances from each other (uniform spatial distribution), from the view of the parasite there is a higher effort on the search of hosts, opposite to the case when the host plants are spread on unequal distances (aggregated spatial distribution) even if parasites do not search randomly in general (Cronin & Strong 1999). There are a series of plant characteristics which may contribute to the host search of the parasites. But the relationship between patchy occurrence of plants and their fitness may affect searching effort of parasites. There exist evidences that plant distribution indeed has a significant effect on herbivore searching behavior (e.g. Visser 1988). Accordingly galls may be distributed uniformly on aggregated hosts.

Recognizing that intra-plant heterogeneity affects both the distribution and the performance of herbivorous insects, a variety of hypothesis were suggested to explain herbivore distribution on hosts: the plant stress (White 1984), plant vigor (Price 1991), plant architecture (Lawton 1983, Strong et al. 1984) and resource availability (Grime 1979, Coley et al. 1985) hypotheses.

In the case of galling insects, intra-plant heterogeneity effects are more frequently studied compared with the spatial density-dependence on host plants (plant stress hypothesis: review includ-

ing gall makers by Koricheva et al. (1998); plant vigor hypothesis (Price 1991, 2003)). Negative density dependence or density-independence was found for cynipid gall inducers (Hails & Crawley 1992, Schönrogge et al. 1995).

We studied the parthenogenetic gall wasp *Diplolepis rosae* which induces multi-chambered galls on rose shrubs (*Rosa spp.*). *D. rosae* usually parasitizes *R. canina*, but galls also occur on *R. dumalis*, *R. rubiginosa*, *R. villosa*, *R. sherardi* and *R. rubrifolia* (Stille 1984). Females of *D. rosae* emerge from galls in early spring and lay their clutches in new rose buds within one or two months. The new gall finishes its development in late summer and pupae overwinter within the gall.

In this research we (i) investigated the pattern of occurrence of galls on every host individual, (ii) analyzed the effect of the host spatial pattern and density on the gall distribution on hosts, and (iii) supplemented the analysis with the effects of architectural characteristics of shrubs.

Our study hypothesis was that the increase in host plant density infers aggregated per host distribution of galls which may be also related with plant trait variation. Our first prediction involved the change in spatial distribution of rose host-plant with its change in density. Our second prediction was that the density and prevalence of galls decreased with increasing rose shrub density. Our last prediction involved the antagonistic relationship of host shrub and gall density with host shrub architecture.

We aimed to find supporting evidences of plant architecture hypothesis by means of plant size in the case of the galling system compounded by the Bedeguar gall and its wild rose host shrubs.

Material and methods

There were eight sampling sites observed for two years (2004, 2005). Sampling sites were dry pastures or the forested edges of these pastures. Sampling sites were: (a) Târgu-Mureș, Mureș county, Romania, elevation: 452 m, one site with 3 (2004, 2005) quadrates – 46.5126N / 24.5771E; (b) Cluj-Napoca, Cluj county, Romania, elevation: 472 m, four sites, with 2 or 3 quadrates (2004: site2 with 2, site3 with 2, site4 with 2, and site5 with 3 quadrates; respectively 2005: site2 with 2, site3 with 3, site4 with 3, and site5 with 3 quadrates) – 46.8018N / 23.6131E; 46.8317N / 23.6315E; 46.7328N / 23.5780E; 46.7672N / 23.4937E; (c) Berettyóújfalu, Hajdú-Bihar county, Hungary, elevation: 105 m, one site with 1 (2004), and 3 (2005) quadrates – 47.2476N / 21.5377E; (d) Tépe, Hajdú-Bihar county, Hungary, elevation: 95 m, one site with 2 (2004) and 2 (2005) quadrates – 47.3301N / 21.5605E; (e) Emőd,

Borsod-Abaúj-Zemplén county, Hungary, elevation: 125 m, one site with 2 (2005) quadrates – 47.9522N / 20.8047E.

Sites (a) and (b) were neighbouring oak-hornbeam forests; where the following species were abundant: *Rubus spp.*, *Hippophae rhamnoides*, *Prunus spinosa*. On sites (d) and (e) among the *Rosa spp.* shrubs there were scattered *Prunus spinosa* shrubs, and on the lower watery parts there were patches of *Phragmites australis*. On these latter two quadrates two sites were taken on young sessile oak (*Quercus petraea*) plantations. On site (e) besides rose shrubs there were scattered *Prunus spinosa* shrubs too.

In each of the randomly chosen 50×50 meter quadrates we recorded the coordinates of each rose shrub with a GPS unit, also measured the height, the diameter, and counted the number of *D. rosae* galls on them. From the recorded height and diameter of shrubs we calculated a mean shrub size which we consider as an architectural component of shrubs. To determine the spatial density of rose shrubs and galls the 50×50 meter quadrates were divided into smaller 10×10 meter quadrates; herewith we refer the 50×50 meter quadrates as quadrates and the 10×10 meter quadrates as small quadrates.

The spatial pattern of *Rosa spp.* individuals was determined on every quadrate by counting the small quadrates with shrubs in them, the number of shrubs on these small quadrates and the small quadrates with same shrub intensity class.

The pattern of occurrence of galls on individual host was determined on every quadrate by counting infected hosts from all occurring hosts, determining the intensity class of every infected host and counting the hosts belonging to the same intensity class.

Based on these counts we calculated the Poulin's index of discrepancy (PID) (Poulin 1993), and in the case of galls we also calculated their prevalence. Values of PID range from 0 to 1, the lower values show uniform, while those closer to one show aggregate distributions.

Rose shrub's coordinates were processed using GPS TrackMaker (Ferreira 2008) and GRASS GIS (GRASS Development Team 2010). Statistical analyses of spatial distribution and prevalence were calculated with QP 3.0 (Rózsa et al. 2000) software. The R language and environment for statistical computing was used for other statistical analyses (R Development Core Team 2010).

To demonstrate that PID values do indeed differ from random distributions, we simulated Poisson distributed point-patterns for different densities (d = 10, 20, …, 200); i.e. the simulated point patterns were Completely Spatially Random (CSR) (Cressie 1993). The range for density values was based on the field data. The 'spatstat' package was used during the simulation (Baddeley & Turner 2005).

Distributions of PID values, prevalence and density were continuous right-skewed (gamma distribution). These derived variables were based upon negative binomial distributed count data. Comparisons of simulated and field data, and the relationships between variables were tested using a gamma error distributed generalized linear model (GLM) framework. Logarithmic transformations were used to achieve normality of variables where needed. The variability of samples was characterized by

the interquartile range, IQR.

Results

On the analyzed quadrates there were 994 shrubs, from which on 332 shrubs (32.5%) we found 975 *D. rosae* galls. Aggregations for the field data were significantly higher than for the simulated Poisson distributed point patterns (GLM: gamma dispersion parameter = 0.11, coefficient estimate = 0.78, deviance = 10.91, $F_{1,70}$ = 94.58, p < 0.0001) (Fig. 1). For the field data the median of PID was 0.66 (IQR = 0.22), while for the simulated data the median of PID was 0.24 (IQR = 0.09).

The density of shrubs showed significant variability (median = 0.92, IQR = 1.1) depending on the sampling sites (GLM: gamma dispersion parameter = 0.46, deviance = 9.58, $F_{7,28}$ = 2.94, p = 0.01), e.g. shrub density was dependent on sites. At site2 (GLM: estimated coefficient = –1.36, standard error = 0.48, p = 0.008) and site4 (GLM: estimated coefficient = –1.66, standard error = 0.45, p

= 0.001) densities were significantly smaller than the site1, whereas there was no other significant difference. Aggregation of the rose host shrubs was strongly negative density-dependent (linear regression; t = – 9.33, p < 0.0001, equation = 0.61 – 0.13 * log(shrub density)) (Fig. 2). The aggregation of shrubs based on their density can be estimated with a 71.1% precision (linear regression; adjusted R^2 = 0.71, $F_{1,36}$ = 87.22, p < 0.0001). Furthermore, shrub diameter and height was not significantly affected by per site shrub density (Table 1).

The density of galls showed no significant variability (median = 1.11, IQR = 0.74) depending on sampling sites (GLM: gamma dispersion parameter = 0.53, deviance = 5.27, $F_{7,28}$ = 1.40, p = 0.24), e.g. there were no consistent differences between sites.

The density and prevalence of galls showed a negative host shrub density-dependence, while the aggregation of *D. rosae* galls on shrubs showed a positive density-dependence (Table 2). This latter relationship means that the aggregation of *D.*
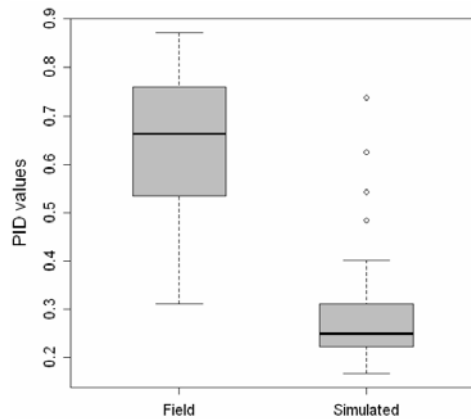

Figure 1. The difference between Poulin's index of discrepancy (PID) values of field (N = 36) and simulated (N = 36) data. Field data were significantly more aggregated than the point patterns generated by a Poisson process.
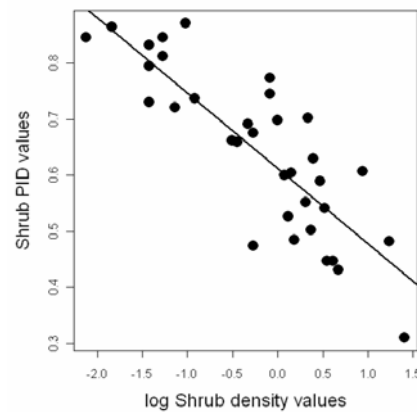

Figure 2. The relationship between the log density and PID values of rose shrubs on N = 36 quadrates. As shrub density grows their spatial pattern becomes uniform.

Table 1. Results of a generalized linear model (gamma family with log link) fitting variation on the shrub height and diameter by shrub (N=36).

Per site		
Shrub density vs.	Shrub height (cm)	Shrub diameter (cm)
dispersion parameter	0.04	0.12
coefficient estimate	–0.05	–0.12
deviance	0.10	0.47
$F_{1,34}$	2.40	3.75
p	0.13	0.06

Table 2. Generalized linear models (gamma family with log link) on per rose host shrub gall density, prevalence and aggregation with shrub density and aggregation. Spatial pattern is characterized by the Poulin's index of discrepancy (PID) (N=36).

Per shrub individual			
Shrub density vs.	Gall density	Gall prevalence	Gall aggregation
dispersion parameter	0.37	0.21	0.05
coefficient estimate	–0.45	–0.32	0.21
deviance	6.32	3.16	1.14
$F_{1,34}$	16.78	14.73	19.25
p	0.0002	0.0005	0.0001
Shrub aggregation vs.			
dispersion parameter	0.28	0.16	0.05
coefficient estimate	3.32	2.40	–1.55
deviance	8.33	4.26	1.61
$F_{1,34}$	29.66	25.44	29.36
p	<0.0001	<0.0001	<0.0001

Table 3. Results of generalized linear models (gamma family with log link) fitting variation on per rose host shrub gall density and aggregation with shrub height and diameter. Spatial pattern is characterized by the Poulin's index of discrepancy (PID) (N=36).

Per host individual		
Gall density vs.	Shrub height (cm)	Shrub diameter (cm)
dispersion parameter	0.68	0.64
coefficient estimate	0.002	0.002
deviance	0.29	1.56
$F_{1,34}$	0.42	2.42
p	0.51	0.12
Gall aggregation vs.		
dispersion parameter	0.07	0.07
coefficient estimate	–0.001	–0.001
deviance	0.25	0.31
$F_{1,34}$	3.42	4.41
p	0.07	0.04

rosae galls on host shrubs increases with the increase of shrub density.

Regarding the relationships between host shrub aggregation and gall density and prevalence there are significant positive effects, while the gall aggregation showed a significant negative effect (Table 2).

The height and diameter of shrubs showed no significant effects on density of galls per host shrub (Table 3). Aggregation of galls per host shrub was not affected by shrub diameter, while shrub height showed no significant effect (Table 3).

Discussion

We found that the spatial pattern of rose shrubs affected the distribution pattern and parasitism of *D. rosae*. But the height and diameter of shrubs (considered as plant architectural indicators) had no effect on the gall's distribution pattern and parasitism. Our recent findings regarding the relationships of density and aggregation of rose host shrubs with the density, prevalence and aggregation of *D. rosae* galls confirm our earlier results (László & Tótmérész 2007).

Regarding the density of *D. rosae* galls, as the density of rose host shrubs increased the former decreased. The more rose shrubs found, the less *D. rosae* galls occured, and at lower gall density they faced an aggregated distribution, which mean that most galls appeared only on a few hosts. This inverse density dependence was also found in the case of the gall wasp *Andricus quercuscalicis* (Hails & Crawley 1992), although they found density dependence, the inverse density dependence was preponderant. Additionally, in the case of herbivorous insects, density dependence was found to be more likely due to a source acting from

lower trophic level (as plant trait) than from above (Stiling 1988). The prevalence of galls showed the same effects of rose host shrub density and aggregation as their density. As the density of host shrubs decreased the prevalence of galls increased. Positively related gall survival with plant growth may increase the prevalence of galls (Price et al., 1987, Craig et al. 1989, Abrahamson & Weis 1997).

When the host shrub is abundant, gall wasps can choose between host shrubs with different architectures, and may use with more advantage the simpler ones. If the host shrubs are rare, the parasites have no opportunity to choose between them; therefore, all available hosts are used, even in that case when the probability of failure is greater. These former predictions fit well to our results that at high rose host density, galls are scarce and aggregated; and that at low rose host density, galls are plenty and evenly distributed. These predictions involve the plant architecture hypothesis which is not supported here.

When the habitat is optimal for rose shrubs (resource availability hypothesis) their abundance increases and their spatial distribution becomes uniform. The uniform distribution may be the consequence of the adjustment to an optimal distance between rose shrubs. The exceptions from the uniform spatial distribution could form the disadvantageous islands (patches) in the combat against gall wasps. This is supported by the result of Abrahamson & Weis (1997), who confirmed that gall-makers show active host selection in high density patches of hosts, while in case of low host abundance there is no host selection. This is why at low host abundance the distribution of rose galls is uniform. If the habitat is characterized by suboptimal parameters from the view of rose shrubs the mean abundance of shrubs is low and their distribution is aggregate; therefore, their architecture is simple and the spatial distribution of galls is uniform.

In a former paper (László & Tóthmérész 2007) we made a prediction for the host-choice of the gall wasps *D. rosae* based on the plant architecture hypothesis linked with host plant fitness. We stated that the relationship between gall and host distribution pattern and host architecture stands if the mean fitness of shrubs linked with architecture is higher at low density habitats, where they appear aggregated, and lower at high density habitats, where they appear uniformly distributed. This statement is contradictory with the findings of Stoll & Prati (2001) and Raventós et al. (2010),

but it is based on the significant negative correlation between shrub density and shrub size (László & Tóthmérész 2007). However, this latter statement is not supported by the present study, as neither was supported the relationship between density of galls and shrub size. Thus, we can't support the prediction of Stoll & Prati (2001) and Raventós et al. (2010).

This means that a fitness component of the relationship between rose host shrub spatial distribution pattern and *D. rosae* gall density, and distribution pattern on hosts may not be measured by the size of shrubs. Other characteristics that could be measured easily on rose shrubs under field conditions could be the mean diameter, number of shoots, or the number of rosehips, mean number of seeds in rosehips. Until other characteristics, which could describe in an appropriate manner the fitness of rose shrubs, were investigated; we can not conclude that the fitness of host shrubs does not represent as a contributing factor to the distribution of galls on host plants. Therefore, it can be stated that the diameter and height of rose shrubs are not appropriate characteristics for assessing fitness. Hence we retain the hypothesis that *D. rosae* has a higher preference of shrubs with a simpler architecture.

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