CHAPTER 6

Fine-scale pupal abundance and distribution patterns of *Gonometa postica* and *G. rufobrunnea* (Lepidoptera: Lasiocampidae)

INTRODUCTION

The spatial distribution of herbivorous insects is not simply a random phenomenon. A large body of literature has demonstrated that insect herbivores may exhibit oviposition preferences, niche partitioning, utilisation of enemy free space, and microclimate preferences that are likely to result in non-random patterns in their distribution (e.g. Dethier 1959; Strong *et al*. 1984; Bernays & Chapman 1994; Price 1997). At a between-host plant scale, the distribution of insect herbivores may be influenced by host plant density (Dubbert *et al*. 1998; Williams *et al*. 2001; Ohashi & Yahara 2002), distance from the edge of the site (Murchie *et al*. 1999; McGeoch & Gaston 2000), habitat structure (Ellingson & Anderson 2002), direct or plant-mediated interactions between herbivores (Riihimäki *et al.* 2003), avoidance of conspecifics (Stamp 1980) or spatial escape from natural enemies (Williams *et al*. 2001). Alternatively, host selection may be based on host plant size or quality characteristics (Floater 1997; Hodkinson *et al*. 2001), as well as previous levels of attack (Gilbert *et al*. 2001). At a within-host plant scale, spatial distribution may be affected by heterogeneity in plant quality (Orains & Jones 2001), niche partitioning (Dubbert *et al*. 1998; McGeoch & Price 2004), density of conspecifics (Cappuccino 1988; Cappuccino *et al*. 1995) or the presence of, or interactions with, other species (Bernays & Chapman 1994; Faeth & Hammon 1996, 1997), larval behaviour (Anstey *et al*. 2002), thermal regime (Stamp & Bowers 1990; Klok & Chown 1998, 1999) or avoidance of natural enemies (Stamp & Wilkens 1993; Wermelinger 2002). Although several factors therefore clearly influence herbivore insect distribution, some of these are likely to be most important determinants of spatial distribution for specific insect herbivore species. Identifying what these factors are for particular species forms an important component

of understanding the population dynamics of the species, as well as the habitat requirements necessary for their conservation (Ranius 2001).

Species that differ in life history strategy may also be expected to have different distribution patterns (Wallner 1987; Ribeiro *et al*. 2003). For example insects with latent population dynamics have a strong relationship between oviposition site preference and larval performance, and therefore larval distribution will closely track host plant quality (Price *et al*. 1990). In contrast, eruptive insects that show limited oviposition choice may not be able to judge host quality and plant quality is therefore unlikely to determine egg and early instar distribution for such species (Leyva *et al*. 2003). In cases like these larvae are left to locate suitable feeding sites (Dodge & Price 1991), and distance of oviposited eggs from a suitable host plant may determine the number and distribution of surviving larvae (Dethier 1959). Eruptive species are also often poorer dispersers than latent insects (Hunter 1995), and as a result eruptive species tend to have more aggregated distributions with latent species more evenly distributed among plants (Ribeiro *et al*. 2003). Insect herbivores that differ in host specificity, secondary compound tolerance, defence characteristics and microclimate preferences are also expected to have different, non-random distributions (e.g. Strong *et al*. 1984; Holmes & Schultz 1988; Stork *et al*. 2001; Kessler & Baldwin 2002). For example aposematic species are likely to have distributions that differ from those of cryptic species, because they are protected from natural enemies (Brower 1958). Instead, other factors, such as solar radiation, may be major determinants of their distribution (Casey 1993). Monophagous species may be able to utilise chemically defended high quality host plant leaves near the tip of the plant, but polyphagous species may be limited to feeding on older, low quality leaves near the base (Kessler & Baldwin 2002). Polyphagous species are also expected to have a more even distribution across plant species polycultures, while monophagous species are likely to be more aggregated and associated only with stands of their host plant (Strong *et al*. 1984).

Furthermore, different life stages are subject to different mortality factors and the selection imposed by them is likely to result in different behaviours and preferences (Price 1997). For example, early Lepidoptera instars may be unable to move to more nutritious plant parts if dispersal is costly (Kessler & Baldwin 2002) and their distribution thus largely follows female oviposition choice. In contrast, larger instars may move freely to conspecific hosts plants (i.e. upon defoliation of their host plant) depending on available food resources (Floater

1997). Galling-insects and leafminers are a particular group of herbivore insects where increased performance on high quality hosts or host plant parts, results in strong selection for the use of such high quality resources (Price *et al*. 1990; Scheirs *et al*. 2004). Consequently these insect herbivores are often non-randomly distributed as a function of oviposition preference for high host quality (Price *et al*. 1995; Faeth & Hammon 1996, 1997, but see Valladares & Lawton 1991). In contrast, the pupae of insect herbivores may have distributions that maximise their survival, because selection for pupation sites by larvae largely determines pupal survival probability (Ruszczyk 1996). Pupal survival can in turn be influenced by both abiotic (e.g. solar radiation) and biotic factors (e.g. natural enemy attack) (Nowbahari & Thibout 1990; Kukal 1995; Ruszczyk 1996; Irwin & Lee 2003). However, when pupal survival is not affected by the distribution of the pupae, patterns may simply reflect oviposition or larval movement patterns, or track the availability of pupation sites at within or between plant scales (Batzer *et al*. 1995).

Finally, tree size and oviposition load may have marked affects on the distribution of the pupal stage (Batzer *et al*. 1995). At densities where larval mortality is no longer subject to inverse density dependent mortality, the amount of foliage and number of conspecifics determines the degree of defoliation (Floater 2001; Rhainds *et al*. 2002). When the primary host tree is defoliated, a secondary host plant has to be selected or larvae will starve. Although larvae may be able to find secondary hosts, dispersal may be extremely costly when host plants are far apart or co-occur with non-host plants (Floater 2001; Steinbauer *et al*. 2001; Hódar *et al*. 2002). Consequently large host plants have a greater probability of sustaining larger numbers of final instars, while those larvae defoliating small hosts may not find suitable replacements and die of starvation (Dethier 1959). In cases were host defoliation is rare and pupae are not subject to density dependent mortality, most larvae will remain and pupate on plants, especially when these plants are large (Batzer *et al*. 1995). However, if some natural enemy preferentially utilises final instar larvae or pupae found on the host plant (Guildford 1992), one may expect the use of non-host plants, leaf litter, or the soil itself as pupation sites. Thus pupal distributions may be influenced by; defoliation level, use of natural enemy free sites, background colour and microclimate requirements (Batzer *et al*. 1995; Lyon & Cartar 1996; Ruszczyk 1996; Hazel *et al*. 1998).

The pupal cocoons of two wild silk moth species native to southern Africa, *Gonometa postica* Walker and *Gonometa rufobrunnea* Aurivillius (Lepidoptera; Lasiocampidae), have great economic value. Cocoons can be degummed to produce high quality silk, which rivals the silk produced from *Bombyx mori* (Veldtman *et al*. 2002). Currently, the pupal stage is the target of harvesting practices that are totally dependent on the availability of pupae from natural populations (Veldtman *et al*. 2002). These pupae almost exclusively occur on the branches and stems of woody plant species (Hartland-Rowe 1992). Because of the harvesting demand, and poor knowledge of the species biology, there is thus substantial interest in the distribution of pupae among and within trees for both *Gonometa* species. Therefore, this study investigates if between and within-tree pupal distributions in these two species are non-random, and if so, if there are relationships between pupation site use and tree characteristics such as tree size, available pupation space and branch position.

METHODS

Study Area

Gonometa postica and *G. rufobrunnea* populations were examined at six and five sites respectively within the known (historic and recent records) eruptive range of these species, spanning a distance of 400km between the two furthest localities for *G. postica*, and 60km for *G. rufobrunnea*. The localities included Vryburg and Hotazel (North-central South Africa) and Gabane, Kumukwane, and Kopong (South-Eastern Botswana) for *G. postica*, and Shashe and Dumela in North-Eastern Botswana for *G. rufobrunnea* (see Veldtman *et al*. 2002 for further site details). The dominant woody host species utilized by *G. postica* at the first two localities was *Acacia erioloba* Meyer and at the final three, *Acacia tortillis* Hayne (both Mimosaceae). *G. rufobrunnea* only utilizes *Colophospermum mopane* Kirk ex Benth. (Caesalpiniaceae).

Sampling was standardized by delimiting an approximately rectangular area incorporating 100 trees at each site, to compensate for possible tree-density differences between host-plants and localities (see Veldtman *et al*. 2002). An initial minimum of 40 first-generation cocoons per plot was a prerequisite for site selection. At least three sites per host plant were thus selected.

Surveys of plots commenced in winter (June to July, 2000) and were repeated in mid summer (January, 2001). This sampling procedure was repeated the following year, all sites being surveyed four times by the end of January 2002. Newly formed pupae counted in the first, second, third and final survey are referred from here on to as generation one, two, three and four respectively.

Cocoon sampling

For each of the 100 trees per plot, the tree's species, maximum height, number of branches and spatial position were recorded. Tree species used for pupation were divided into three functional groups namely, primary larval host plant species, non-host plant without thorns, and non-host plant with thorns, as the use of each represents a different pupation strategy. Remaining on the host plant to pupate can guarantee that the right host is oviposited on (Bernays & Chapman 1994). On the other hand using non-host plant can disrupt the search image of natural enemies (Guilford 1992). Tree height was measured to the nearest 0.25 m and divided into three categories, i.e. small (< 1.75 m), medium (1.75 – 3.00 m) and large (> 3.00 m). The number of branches per tree was determined by counting the number of tree sub-units (branches). A primary host plant tree of 0.75 m (smallest sampled) was taken to represent one branch. Counting the number of branches in this manner standardises the three-dimensional differences in tree size between different hosts. Consequently, counts of number of branches per tree were only comparable between sites with similar primary host species. The position of each tree within a plot was measured at the main trunk of the tree with a hand held Global Positioning System (GPS: Garmin Etrex). For trees in close proximity to each other the direction and distance between the two trees were noted and assigned to one of three categories (half, quarter and a tenth of the third (last) decimals of a minute), based on hand drawn maps documenting this fine scale distribution of trees within the site. These spatial co-ordinates were used in all spatial analyses.

Every tree was carefully searched and all pupae of the present generation were counted. For each pupa, its sex (see Veldtman *et al*. 2002), cocoon size, height in the tree (to the nearest 5cm), distance from the main tree trunk (to the nearest 10cm), branch position and aspect were recorded. Branch position was divided into seven categories: edge (E) within 15 cm from terminal branch end; edge middle (EM) 15-30 cm from terminal branch end; edge stem (ES)

terminal branch attached directly to stem; middle edge (ME) start of terminal branch 60 cm from edge; middle (M) middle branch; middle stem (MS) start of main branch; and stem (S) on main tree trunk (Fig. 1a, b). Aspect was determined with a compass, dividing measured directions into four sectors, each centred on a cardinal compass direction, i.e. north (N), east (E), south (S) and west (W). At the start of the study, the number of pupae per aspect was not recorded directly in the first generation, but the number of first generation cocoons found in the second survey were counted instead. Consequently, the site sample sizes for which data on aspect use were available could be lower than for other variables, if some pupae became detached and were not resampled in the second survey.

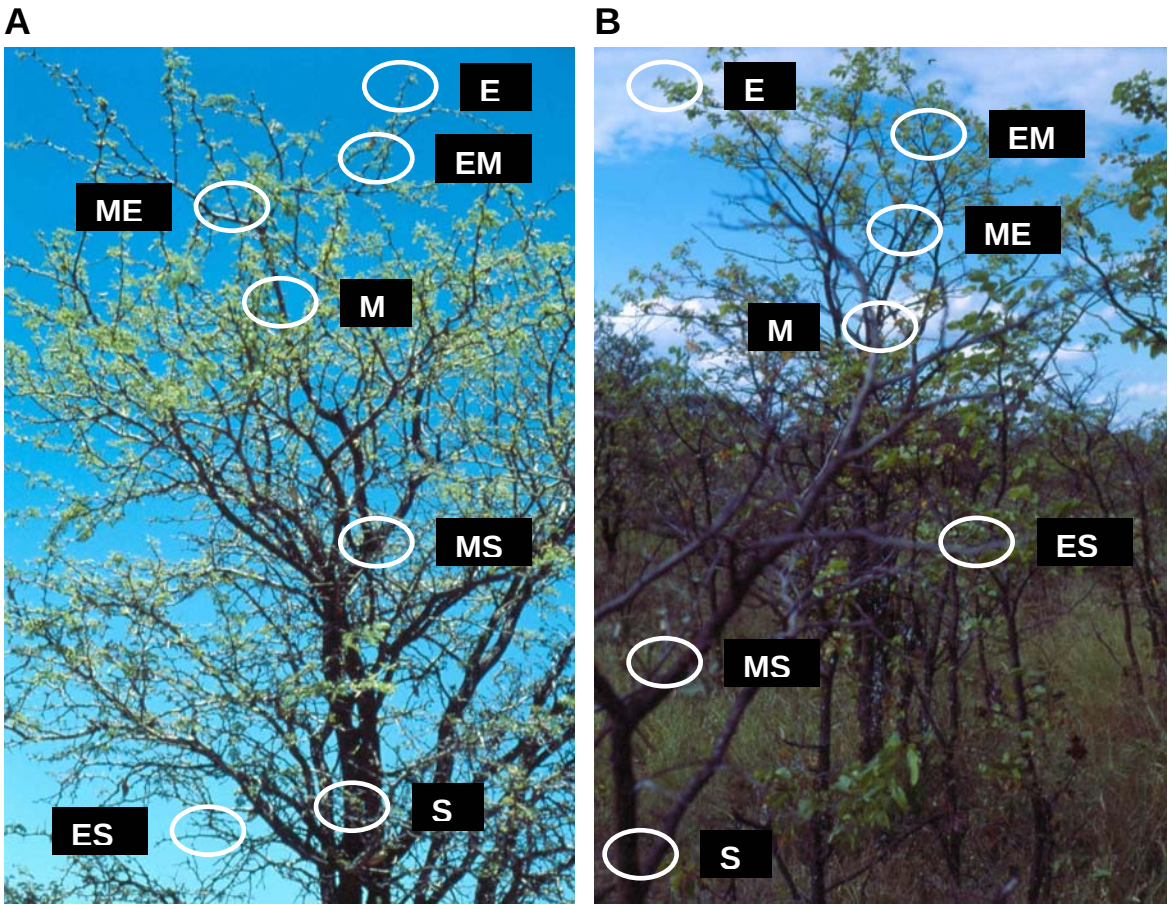

Figure 1. Branch position categories (edge (E) within 15 cm from terminal branch end; edge middle (EM) 15-30 cm from terminal branch end; edge stem (ES) terminal branch

attached directly to stem; middle edge (ME) start of terminal branch 60 cm from edge; middle (M) middle of branch; middle stem (MS) start of main branch; and stem (S) on main tree trunk) assigned to pupae, shown for A) one of *G. postica*'s larval host plants (*Acacia erioloba*) and B) for *G. rufobrunnea*'s larval host plant (*Colophospermum mopane*). Codes shown left or right of encircled area denotes the branch position that will be assigned to cocoons if found within this area.

Data analysis

The relationship between the mean and the variance of the frequency distribution for number of branches per tree counts were quantified by the Poisson index of dispersion (s^2/m) count data (Perry & Hewitt 1991). This index was calculated by dividing the sample variance by the sample mean (Perry & Hewitt 1991). If this index is close to unity the data have a Poisson distribution. When the index is smaller or greater than 1.0 this indicates that the distribution is under- and over dispersed and the data are best fit by a binomial or negative binomial distribution (or another over-dispersed distribution, e.g. gamma distribution) respectively (Bliss & Fisher 1953). Significant departures from randomness were determined by calculating $(n-1)*(s^2/m)$ and comparing them to the X^2_{n-1} distribution (Perry & Hewitt 1991). Alpha level corrections for multiple testing were preformed using the step-up false discovery rate (FDR) procedure shown to be the least over corrective of current alpha level correction methods (García 2004).

Between-tree patterns

The objective was to determine if between-tree variation in pupal abundance could be explained by tree characteristics such as plant functional group (primary host plant, non-host plant, non-host plant with thorns), tree size (for all trees and the primary host plant only), or by across-tree aggregation patterns. First, whether the functional group to which an individual tree belongs influences the number of pupae found was examined. Second, the importance of the frequency of primary larval host-plant trees in different height categories is sufficient to explain the utilisation by pupae, was investigated. To determine if tree functional types or size classes (primary host functional group) had a greater or lower proportion of the pupae than

expected from their recorded frequencies, Chi-square goodness of fit analyses were performed (Zar 1984). If the ratio of observed to expected pupae is greater than one, over utilisation is indicated, while ratios less than one indicate under utilisation. Trees were divided into groups based on functional type (primary larval host plant (H); non-larval host plant (N); non-larval host plant with thorns (T)). Although, there were low numbers of pupae for N and NT categories, as long as expected pupal frequencies were greater than five, the data could be analysed. Primary host plant trees were also divided into three size classes (small (S) < 1.75 m; medium (M) 1.75 - 3.00 m; large (L) > 3.00 m). For both groupings three categories were generally available for comparison. In cases were some groups did not have sufficient pupae to allow analysis a two-way category comparison was done (bias in Chi-square analysis occurs if there are expected frequencies less than one or more than 20% of frequencies below 5, Zar 1984).

Third, it was determined if the number of pupae counted per tree and their location within the site, was significantly different from a pattern expected by chance. Spatial analysis by distance indices (SADIE) methodology (Perry 1995) was used to quantify the degree of departure from spatial randomness for the spatially-referenced (X,Y) branch and pupal count data in this study. Spatial non-randomness is based on the distance to regularity (minimum cumulative distance to achieve a regular distribution of counts, thus when all sample counts are equal to the mean) that can be quantified for the data set as a whole (overall aggregation) or indicate the contribution of each sample point (degree of clustering) to local departures from randomness within the data set (Perry & Dixon 2002). The significance of overall aggregation was tested by dividing the observed distance to regularity by the average distances of randomisations of the sample counts, to give the index of aggregation (I_a) (Perry 1995). This index summarises the spatial arrangement of the counts relative to each other (Perry *et al*. 1999; Perry & Dixon 2002). Although significance is actually tested, values of I_a of approximately 1.5 and greater indicate significant aggregation (Perry *et al*. 1999).

Provided there is evidence of overall aggregation, the degree of clustering in count data can be quantified (Perry & Dixon 2002). The index of clustering, v, provides information on the degree of clustering for each spatially referenced point based on the magnitude of the count and its occurrence in relation to neighbouring counts. Clustering occurs in two forms, namely patches (counts greater than the sample mean, v_i) and gaps (counts smaller than the sample

mean, v_j). For random arrangements of counts, v_i and v_j have expected values of 1 and -1. Values greater than these expected values indicate membership by the count of a patch ($v_i > 1$) or gap ($v_j < -1$). Non-randomness is formally tested by comparing mean v_i and mean v_j values with their expected values of 1 and -1 for random arrangements (Perry *et al*. 1999). If mean v_i and mean v_j are not significant, the lack of overall, strong clustering into patches and gaps is indicated (Perry *et al*. 1999; Perry & Dixon 2002).

For each site-generation combination, I_a, mean v_i and mean v_j were calculated if pupae were found on more than 20% of the trees. At densities lower than this (e.g. mean count per tree < 0.2), it is not possible to quantify overall aggregation and spatial clustering (Winder *et al*. 2001). The maximum ratio of non-zero values to total number of measured values that still allows the detection of significant spatial clustering (sufficient power) has been shown to be 4: 25 (Korie *et al*. 2000). In this study the lowest ratio (1: 4) was well within this limit. Spatial non-randomness was also calculated for tree size, using number of branches per tree as counts. All non-randomness statistics were calculated with SADIEShell v. 1.21, red-blue analysis.

Hereafter spatial matching between the spatial patterns of pupal abundance and number of branches was determined. The degree of matching between two sets of count data sharing a set of spatial references may be determined with spatial association statistics (Winder *et al*. 2001, Perry & Dixon 2002). Spatial association is based on comparing the local clustering indices (described above) of two variables measured at each shared spatially referenced point (Perry & Dixon 2002). A local association value can be calculated based on the matching between the two clustering indices at each of these points. For each set of clustering indices allowance for small-scale spatial autocorrelation has to be made by detrending the data set if necessary with the method of Dutilleul (1993). Failure to do so will inflate the significance of the association (Perry & Dixon 2002). Overall spatial association (X) is then calculated as the mean of these local association values. Significance is determined by comparing an actual overall association value to the critical values of a randomisation distribution of overall association. The randomisation distribution is determined by randomly placing the counts of both data sets and then quantifying the strength of each generated data set's association. Overall spatial association is significant at $p < 0.05$ when larger than the critical value of the 97.5^{th} percentile (see Perry and Dixon 2002). All spatial association analyses between number of pupae and the proportion of parasitised pupae were made using the Association analysis

option of SADIEShell v. 1.21 software. SADIE clustering and association statistics may be affected by the number and spatial position of patches in data sets (Xu & Madden 2003). However, the implications for multi-patch patterns, as found in this study, are limited (Xu & Madden 2003), and the issues these authors raise therefore do not affect the results reported.

Finally, the amount of variation explained by spatial and tree variables when considered collectively were determined and the most important explanatory variables were identified. To determine the amount of variability in pupal abundance explained by spatial and environmental variables (tree variables), trend surface analysis and stepwise model building approaches to analysing spatially referenced biological data were applied (Legendre & Legendre 1998). Trend surface analysis was first applied to determine the best fit of spatial variables that significantly contributed to explaining variation in pupal abundance (significant terms from the 3rd order polynomial of latitude and longitude records of each tree, see Legendre & Legendre 1998). Hereafter a stepwise model building procedure (generalised linear model, Poisson distribution, log link function) was used to determine the additional variation explained by tree variables (number of branches, tree height and tree functional group) after spatial non-independencies were accounted for. A major critique of stepwise regression is that the order in which variables are added influences which variables are included in the final model (Abraham *et al*. 1999; Randic 2001). To counter this problem best subset analyses of only tree variables were done. This allowed likelihood scores to be calculated that were used to rank tree variables in order of importance in explaining variation in pupal abundance. The tree variables were sequentially added to the spatial model according to rank until the percentage of deviance explained was not increased significantly or all tree variables were included. By subtracting the amount of variation explained by the spatial model from the total model, the pure environmental contribution of sequentially added host tree variables was determined (Legendre & Legendre 1998).

Within-tree patterns

The objective was to quantify within-tree patterns in pupal abundance, and to determine how much of the within-tree distribution in pupal abundance is explained by pupal and tree variables, including branch position, aspect, standardised cocoon height, cocoon height and distance from the tree trunk. First, the number of pupae for each branch position and aspect

category was compared within each category. This was done for each site-generation combination separately and for each *Gonometa* species in total. The significance of differences in the numbers of pupae between different branch positions or aspects was determined by Chi-square goodness of fit (Zar 1984). Expected frequencies were calculated as the product of the proportion of trees of a category with the sites' total pupal abundance. For branch position, given the physical space constraints in the number of possible pupation sites in tree shape, all positions farther than 30cm from the tree's outer edge was lumped into one category. Consequently the assumption was made that E, EM and all other categories combined would have equal frequencies of pupae by chance. Different aspects were expected to have equal frequencies of pupae, because there were no noticeable or consistent differences in number of branches between aspects. For both branch position and aspect, the influence of sex was also taken into account with Chi-square analysis of two-way contingency tables (Zar 1984). Equal numbers of female and male pupae were expected for each category of branch position and aspect.

Second, the height frequency distribution of pupae for each primary host plant species was described after controlling for tree height differences between trees. To determine how pupae across sites are distributed in terms of relative tree height, the height recorded for each cocoon was divided by the height of the tree on which it was found. Thus, if pupae are found near the crown of trees, the standardised cocoon height value should be close to one. Distributions were determined for both species, and for *G. postica* populations on different dominant host-plant species separately. The hypothetical crown volume and distribution of each dominant host-plant species (i.e. *Acacia erioloba*, *Acacia tortillis* and *Colophospermum mopane*) was estimated from descriptions and drawings from Palgrave (1977), as well as from observations in the field.

Finally, potential factors responsible for within-tree distribution patterns of pupal abundance of *G. postica* and *G. rufobrunnea* were identified by determining how much of the variation in cocoon height and distance of the cocoon from the tree trunk could be explained by cocoon position attributes or tree characteristics. Functional group and height of tree, as well as branch position of the cocoon and sex were used as explanatory variables for cocoon height. Only tree functional group, tree height, and cocoon sex were used as explanatory variables for distance to trunk because branch position was logically correlated with distance to trunk. For

the analysis of both continuous dependent variables, a generalised linear model assuming a normal distribution (log link function) was used.

RESULTS

Sites differed in the absolute and mean (±SE) number of branches, as well as tree height, between sites and degree of overdispersion (Table 1), and thus offered a range of conditions to investigate pupal abundance patterns. In all but a few cases counts of the number of branches per tree were randomly distributed within sites (Table 1). Mean tree height for sites with *G. postica* or *G. rufobrunnea* was 2.40 ± 4.86 m and 2.19 ± 3.83 m, and significantly different ($t = 3.333$, $P < 0.001$). At all plots, the primary host plant accounted for 60% or more of the trees found (on average 86.3 % for *G. postica* and 82.8 % for *G. rufobrunnea*) (Table 1). Consequently, the number of non-host plant trees per plot was low. Considering only host plant trees, most trees were in the medium height class (Table 1).

Between-tree variability

Significant patterns of over and under utilization were observed, after accounting for differences in the number of trees per site for each functional group (Table 2). For *G. postica* abundance the host plant was frequently significantly over-utilised (ratio of observed to expected number of pupae greater than one) and only under-utilised (ratio of observed to expected number of pupae smaller than one) in one case. In contrast, the host plant of *G. rufobrunnea* was under-utilised, but never over utilised (Table 2). Both non-host functional groups were significantly under-utilised by *G. postica* in most cases (only two cases of over utilisation). In contrast, either non-hosts with or without thorns were always significantly over-utilised by *G. rufobrunnea* (Table 2). Thus, *G. postica* pupated mostly on its primary host plant, while *G. rufobrunnea* tended to pupate on non-host plants, both those with and without thorns. More *G. rufobrunnea* females were found on non-host plants relative to males, and both sexes were significantly larger if occurring on non-host plant species (Table 3). *G. postica* showed similar trends, but both sex ratio and cocoon size were only significantly greater in non-hosts species in one case each.

Table 1. Vegetation characteristics of sites (consisting of a 100 trees each) where *G. postica* and *G. rufobrunnea* were sampled. The frequency of trees according to functional type (primary larval host plant (H); non-larval host plant (N); non-larval host plant with thorns) and primary host plants according to tree size (small (S) < 1.75 m; medium (M) 1.75 - 3.00 m; large (L) > 3.00 m) is given. * and *** denote significant difference at P < 0.05 and 0.001, while ** indicates P > 0.90. s^2/m = variance to mean ratio; I_a = Index of overall aggregation.

	Number of branches				Tree height	Functional group			Primary host size class		
Locality	Total	mean ± SE	s^2/m	I_a	mean ± SE	H	N	NT	S	M	L
G. postica											
Vryburg1	697	7.0 ± 0.6	5.20***	1.03	3.50 ± 0.14	92	4	4	13	20	59
Vryburg2	888	8.9 ± 0.8	6.94***	1.16	2.63 ± 0.13	82	18	0	15	25	42
Hotazel	342	3.4 ± 0.3	2.04***	0.79	1.75 ± 0.12	71	8	21	15	36	20
Gabane	649	6.5 ± 0.9	13.19***	1.10	2.25 ± 0.11	84	15	1	22	43	19
Kumukwane	572	5.7 ± 0.5	3.65***	0.68*	2.25 ± 0.09	90	4	6	22	59	9
Kopong	321	3.2 ± 0.1	0.70**†	1.97***	2.00 ± 0.06	99	0	1	30	68	1
G. rufobrunnea											
Shashe1	1136	11.4 ± 1.3	7.33***	1.12	1.75 ± 0.11	60	39	1	24	21	15
Shashe2	778	7.8 ± 0.4	2.81***	1.03	2.00 ± 0.06	83	13	4	14	63	6
Shashe3	657	6.6 ± 0.3	2.44***	1.10	2.38 ± 0.07	76	21	3	11	57	8
Dumela1	1110	11.1 ± 0.5	2.48***	1.06	2.50 ± 0.08	99	1	0	5	77	17
Dumela2	1175	11.8 ± 0.7	4.83***	1.52*	2.00 ± 0.08	96	0	4	28	60	8

† Variance was significantly less than the mean. Underlined values lost significance after correction with step-up FDR at the 0.05 .α-level.

Table 2. Difference between observed and expected host plant use of trees grouped according to functional type (host plant (H); non-host plant without (N) and with thorns (NT)) for *G. postica* and *G. rufobrunnea*. *, ** and *** denote significant difference at P < 0.05, 0.01 and 0.001. '-' indicates not available; † and ††, denote expected frequencies with more than 20% < 5 and any < 1. Step-up FDR at the 0.05 level, did not change significance.

Locality	Gen	n	Ratio of observed to expected number of pupae			Chi-Square
			H	N	NT	Sum
G. postica						
Vryburg1	1	202	1.07	0.12	0.25	11.71**
	4	157	1.09	0.00	0.00	13.65**
Vryburg2	1	426	1.21	0.03	-	88.70***
	2	91	1.22	0.00	-	19.98***
	4	342	1.22	0.00	-	75.07***
Hotazel	1	288	1.34	0.31	0.12	81.30***
	2	281	1.35	0.22	0.12	83.64***
	3	83	1.37	0.00	0.11	28.56***
	4	587	1.40	0.00	0.02	231.00***
Gabane	1	505	1.03	0.91	0.00	5.98
	2	442	0.96	1.31	0.00	11.60**
	3	76	0.77	2.37	0.00	24.80***
	4	84	1.02	0.96	0.00	0.04
Kumukwane	1	252	1.04	1.19	0.26	8.92*
	2	72	0.97	0.69	1.62	†
	4	67	1.06	0.00	0.75	†
Kopong	1	92	0.98	-	3.26	††
	2	31	0.94	-	6.45	††
G. rufobrunnea						
Shashe1	1	204	0.67	1.52	0.49	34.92***
Shashe2	1	253	0.64	0.33	10.57	968.79***
Shashe3	1	214	0.59	2.51	0.78	130.69***
Dumela1	1	561	0.97	4.10	-	54.45***
	2	36	1.01	0.00	-	††
	4	65	1.01	0.00	-	††
Dumela2	1	281	0.92	-	2.85	39.94***
	4	73	0.98	-	1.37	††

Table 3. Difference between the primary host plant and non-host plants of *G. postica* (*A. erioloba* and *A. tortillis* sites) and *G. rufobrunnea* in the female to male ratio and cocoon size. Underlined values represent sex ratio observed on all plants. ** and *** denote significant difference between groups at P < 0.01 and 0.001. Different letters denote significant differences in cocoon length between groups (†, P < 0.05; ††, P < 0.001).

Species	Sex ratio		Cocoon length (mm)			
Plant site type	N	Expected	Female		Male	
Host plant type	% N	Female/Male	n	Mean ± SE	n	Mean ± SE
G. postica						
A. erioloba (3 sites)	914	1.21/1.00				
Primary	97.9	1.20/1.00 ^{ns}	466	43.77 ± 0.12 ^{a}	394	34.49 ± 0.10 ^{a}
Non-host	2.1	2.17/1.00 ^{ns}	13	44.32 ± 0.58 ^{a}	6	35.98 ± 0.96 ^{a}
A. tortillis (3 sites)	849	1.00/1.02				
Primary	89.6	1.00/1.09 ^{ns}	356	45.26 ± 0.14 ^{a}	393	35.60 ± 0.10 ^{a}
Non-host	10.4	1.75/1.00**	55	46.13 ± 0.34 ^{b†}	32	35.52 ± 0.35 ^{a}
G. rufobrunnea						
C. mopane (5 sites)	1513	1.00/1.56				
Primary	72.7	1.00/1.96***	353	40.02 ± 0.15 ^{a}	719	32.46 ± 0.09 ^{a}
Non-host	27.3	1.12/1.00***	218	41.34 ± 0.18 ^{b††}	195	34.09 ± 0.17 ^{b††}

Categorising tree height of only host plant trees, marked differences in utilisation were found between height classes, even after standardising for frequency differences (Table 4). In all cases large trees were over-utilised while small trees were consistently under-utilised. Where medium sized trees formed the largest category (Kopong), this size class was over-utilised (Table 4). Thus the largest of trees available within the site were over-utilised, independent of the actual size of the plant.

Table 4. Difference between observed and expected host plant use of primary host trees grouped according to tree size (small (S) < 1.75 m; medium (M) 1.75 - 3.00 m; large (L) > 3.00 m) for *G. postica* and *G. rufobrunnea*. ** and *** indicate significant difference between-tree size classes at P < 0.01 and 0.001 respectively. † denote expected frequencies < 1. Column-wide step-up FDR at the 0.05 level, did not change significance.

Locality	Gen	n	Ratio of observed to expected number of pupae			
			S	M	L	Chi-Square
G. postica						
Vryburg1	1	199	0.04	0.21	1.48	82.81***
	4	157	0.00	0.47	1.40	47.96***
Vryburg2	1	424	0.01	0.48	1.66	205.83***
	2	91	0.00	0.43	1.69	48.09***
	4	342	0.02	0.55	1.62	149.62***
Hotazel	1	272	0.00	0.39	2.85	369.40***
	2	269	0.00	0.68	2.32	203.20***
	3	81	0.00	0.29	3.02	131.17***
	4	583	0.01	0.75	2.19	372.89***
Gabane	1	436	0.08	0.64	2.88	474.18***
	2	355	0.06	0.65	2.88	386.55***
	3	49	0.00	0.44	3.43	86.11***
	4	71	0.00	0.91	2.37	48.88***
Kumukwane	1	236	0.02	1.20	2.12	91.17***
	2	63	0.00	1.16	2.38	28.50***
	4	64	0.00	1.26	1.72	21.86***
Kopong	1	89	0.26	1.24	6.67	†
	2	29	0.11	1.36	3.41	†
G. rufobrunnea						
Shashe1	1	82	0.00	0.45	3.37	156.13***
Shashe2	1	135	0.31	0.89	3.79	88.25***
Shashe3	1	96	0.14	1.10	1.48	13.23**
Dumela1	1	538	0.00	0.70	2.66	320.81***
	2	36	0.00	0.82	2.10	10.23**
	4	65	0.00	0.83	2.06	17.29***
Dumela2	1	249	0.10	0.93	4.67	340.22***
	4	69	0.05	1.16	3.13	45.37***

In terms of spatial non-randomness, pupal abundance of both species was normally not aggregated across trees but was rather random (Table 5). Furthermore, with two exceptions the quantified spatial pattern (*sensu* Chapter 4) was not consistent with other generations sampled at the same site. Although there was thus little evidence for overall aggregation in pupal abundance at the site scale, local clustering indices identified certain trees as contributing significantly to the formation of patches of pupal abundance (e.g. at Gabane, Fig 2b-d). Spatial association between number of pupae and number of branches was significant in almost all cases for *G. postica*, while few significant cases were found for *G. rufobrunnea* (Table 5). Local spatial association values were usually significant for only a few single trees (e.g. at Gabane, Fig 3a-d). This suggested that the selection of trees for pupation sites was not for areas of great tree size, but rather showed individual selection of large trees, irrespective of the size of neighbouring trees.

Table 5. Spatial clustering of *Gonometa postica* pupae and association between number of pupae and number of branches of a sample tree. Significant positive association (5% level, two tailed test) was determined using SADIE. I_a, v_i, v_j and X are the overall index of aggregation, mean clustering values of patches and gaps and overall association value. The inflation factor (IF) reports the degree of correction for autocorrelation between data sets. The maximum simulated value (MSV) is the greatest randomised association-value for a data set.

Locality	Gen	N	I_a	v_i	v_j	X	IF	MSV
G. postica								
Vryburg1	1	53	1.62**	1.71**	-1.67**	0.106	1.00	0.300
	4	44	1.00	0.69	-1.01	0.288**	1.00	0.272
Vryburg2	1	55	1.14	1.12	-1.20	0.519***	1.01	0.270
	2	33	0.84	0.83	-0.94	0.556***	1.06	0.273
	4	57	1.12	1.27	-1.31	0.197	1.01	0.336
Hotazel	1	42	1.06	1.17	-1.02	0.288**	1.10	0.302
	2	49	1.19	0.94	-1.17	0.334***	1.09	0.276
	3	23	1.00	0.90	-1.00	0.434***	1.17	0.290
	4	53	0.86	0.93	-0.88	0.396***	1.18	0.263

Table 5. continued

Locality	Gen	N	I_a	v_i	v_j	X	IF	MSV
Gabane	1	60	1.13	1.06	-1.07	0.678***	1.15	0.343
	2	56	0.87	0.91	-0.89	0.492***	1.14	0.292
	3	29	1.06	1.12	-1.07	0.642***	1.26	0.253
	4	38	0.76	0.92	-0.77	0.512***	1.13	0.251
Kumukwane	1	51	0.91	0.69	-0.95	0.294***	1.07	0.206
	2	36	1.03	1.10	-1.08	0.573***	1.19	0.245
	4	36	1.27	1.27	-1.32	0.367***	1.05	0.340
Kopong	1	38	1.09	1.09	-1.17	0.303***	1.02	0.271
	2	27	0.97	0.85	-0.95	0.028	1.07	0.291
G. rufobrunnea								
Shashe1	1	46	1.24	1.15	-1.52*	0.236	1.24	0.212
Shashe2	1	59	1.58**	1.36	-1.54*	0.133	1.08	0.250
Shashe3	1	60	0.84	0.97	-0.88	0.178	1.00	0.305
Dumela1	1	81	0.91	0.94	-0.89	0.194	1.04	0.263
	2	25	0.91	0.89	-0.89	0.198	1.09	0.254
	4	45	1.77**	1.74**	-1.82**	0.206*	1.07	0.267
Dumela2	1	60	0.86	0.92	-0.88	0.390**	1.13	0.440
	4	36	0.96	0.98	-0.97	0.517***	1.05	0.213

Number of pupae for each generation of a locality as specified in Table 2. Underlined values were non-significant after column wide correction with step-up FDR at the 0.05 α-level.

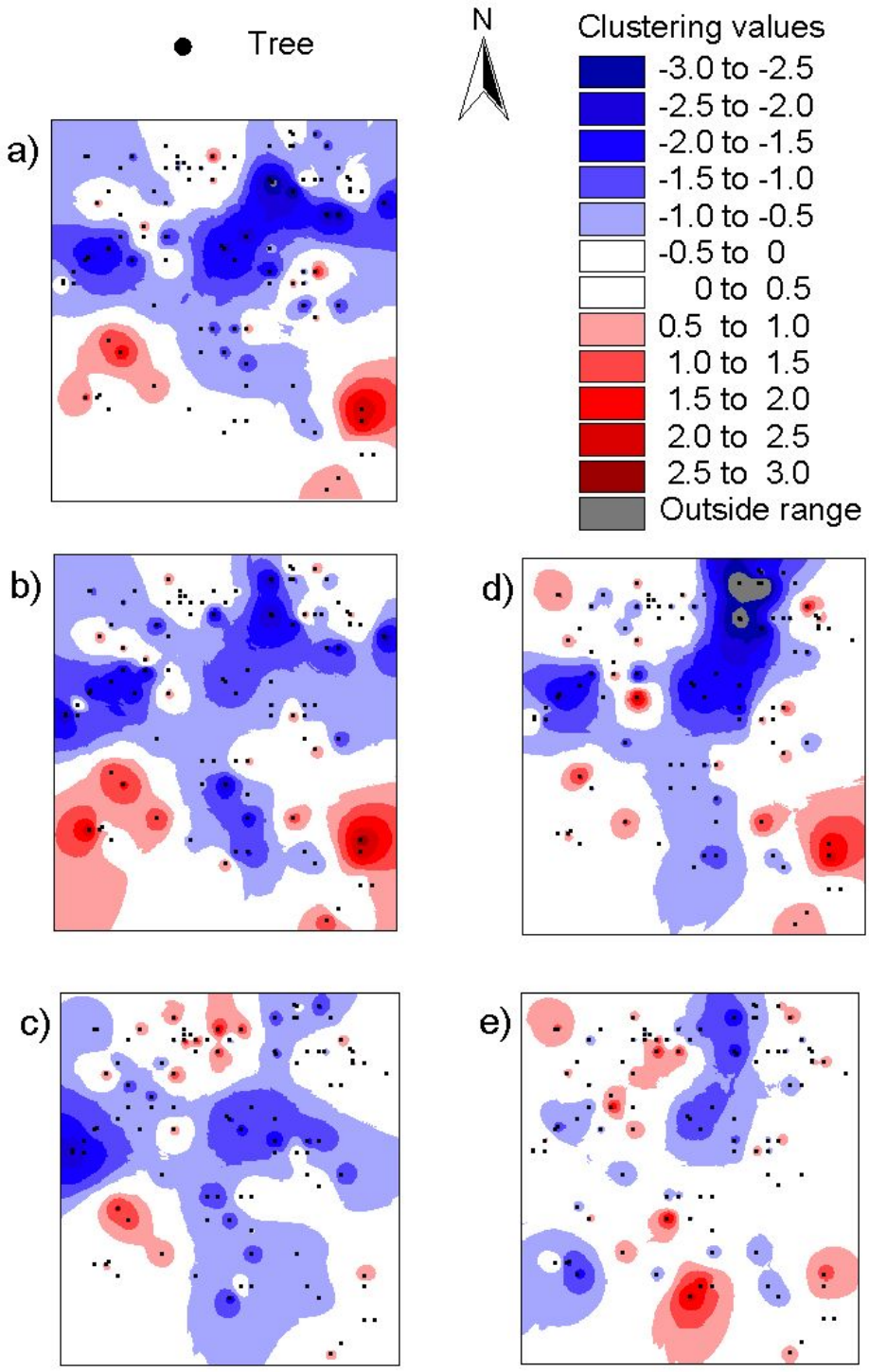

Figure 2. Least distance weighted interpolation of clustering indices of a) number of branches and the number of pupae in the b) first, c) second, d) third and e) fourth generation at Gabane. Areas coded > 1.5 denote areas of significant positive, and areas < -1.5 areas of significant negative, clustering. See Table 5 for specific case statistics.

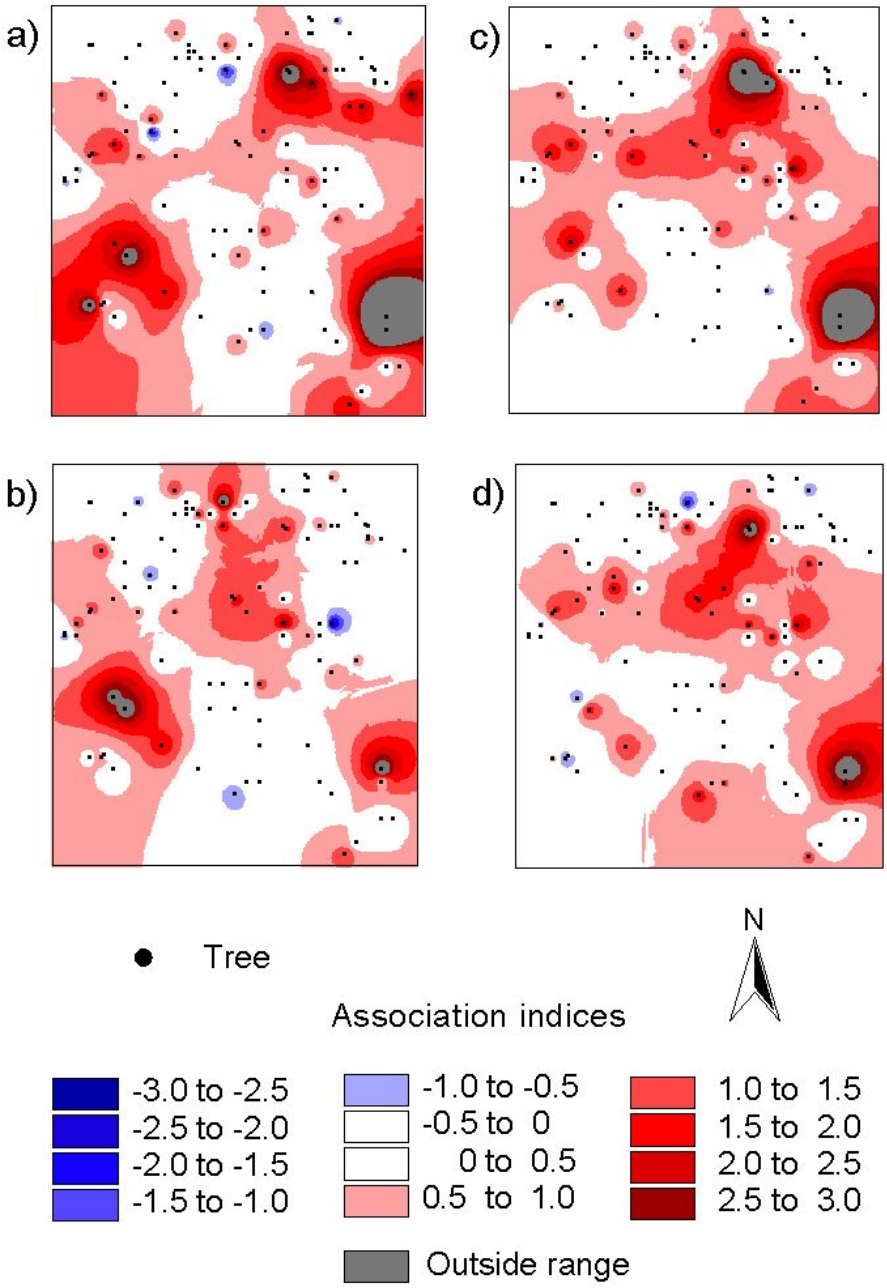

Figure 3. Least distance weighted interpolation of local spatial association indices between number of pupae of the a) first, b) second, c) third and d) fourth generation and number of branches at Gabane. Areas coded as > 0.5 are significantly positively associated at the between-patch scale, while those < -0.5 are significantly negatively associated. See Table 5 for specific case statistics.

The total percentage deviance in pupal abundance explained for *G. postica* and *G. rufobrunnea* ranged between 15-69% and 19-75 % (Table 6). For both species the spatial component contributed little to explaining pupal abundance in most cases, explaining more than 20% of the deviance in only two out of 26 cases. In contrast, generally more than 30% of the deviance was explained by the pure environmental component (spatial non-independence taken into account) (Table 6). For *G. postica* in particular, number of branches added the most to the percentage deviance explained, followed by tree height and tree functional group. Thus, number of branches was the most important variable explaining the pupal abundance of *G. postica* between trees. For *G. rufobrunnea* this pattern was not as general, with functional group and tree height adding greater percentages of explained deviance in several data sets. For both species, number of branches and/or tree height was positively related to pupal abundance in all cases (Table 6). There was, however, a major difference between the species in the relationship between the functional group and pupal abundance. For *G. postica*, pupal abundance was significantly higher on its primary host plant than other groups in both *Acacia* veld types, whereas *G. rufobrunnea* pupal abundance was significantly lower on its host plant (Table 6). In some cases non-host plants and non-host plants with thorns either had higher or lower numbers of *G. postica* pupae than expected. Even though functional group added significantly to the percentage of explained deviance in 10 cases for *G. postica*, in half of these the coefficients were non-significant. In contrast, in four out of five cases functional group coefficients were significant for *G. rufobrunnea* (Table 6). Tree size seems thus to largely explain between-tree variation in pupal abundance for *G. postica*, while functional group was also important for *G. rufobrunnea*.

Table 6. Forward stepwise regression of pupal abundance used to determine the percentage of deviance explained (DE) by spatial and environmental (sample tree) variables. The total %DE by the spatial component (pure spatial and spatially structured environmental; see Legendre & Legendre 1998), as well as the increase %DE by sequentially added significant tree variables (additively the pure environmental component) is shown. The order of adding significant tree variables and their respective coefficients is also shown. BR = number of branches; HGT = tree height; FGRP = functional group (H = host, N = non host, T = non host with thorns).

Locality	Gen	Residual deviance	df	Scaled dev/df	Percentage of explained deviance					Entry sequence of significant biological terms	Coefficients
					Total	Spatial	BR	HGT	FGRP		
G. postica											
Vryburg1	1	226.37	96	0.964	46.4	23.2	18.1	5.1	ns	BR; HGT	+; +
	4	212.38	95	0.833	43.1	9.3	33.8	ns	ns	BR	+
Vryburg2	1	341.24	95	0.909	59.5	8.9	44.0	4.6	2.0	BR; HGT; FGRP	+; +; ns
	2	112.34	96	0.880	56.7	2.5	52.2	2.0	ns	BR; HGT	+; +
	4	375.15	96	0.725	46.1	3.0	39.2	3.9	ns	BR; HGT	+; +
Hotazel	1	272.26	92	0.588	68.0	5.3	49.6	11.7	1.4	BR; HGT; FGRP	+; +; ns
	2	269.66	93	0.829	57.3	7.1	36.7	12.2	1.2	BR; HGT; FGRP	+; +; ns
	3	128.23	95	0.826	58.7	11.1	36.4	9.7	1.5	BR; HGT; FGRP	+; +; ns
	4	446.50	94	0.874	68.6	4.6	49.3	10.5	4.2	BR; HGT; FGRP	+; +; +(H)
Gabane	1	556.95	94	0.594	43.6	5.5	20.4	11.1	6.5	BR; HGT; FGRP	ns; +; +(H)
	2	588.91	92	0.773	38.9	4.3	21.9	8.5	4.2	BR; HGT; FGRP	ns; +; ns
	3	113.16	96	0.736	56.7	5.2	43.7	7.8	ns	BR; HGT	+; +
	4	132.60	95	0.867	30.9	2.1	ns	22.7	6.0	HGT; FGRP	+; -(N)

Table 6. continued

Locality	Gen	Residual deviance	df	Scaled dev/df	Percentage of explained deviance					Entry sequence of significant biological terms	Coefficients
					Total	Spatial	BR	HGT	FGRP		
Kumukwane	1	265.49	93	0.795	48.2	4.6	25.7	ns	17.8	BR; FGRP	+; +(N)-(T)
	2	91.74	94	0.976	49.7	6.6	30.9	ns	12.2	BR; FGRP	+; +(N)-(T)
	4	96.36	95	0.867	38.2	6.3	18.8	ns	13.1	BR; FGRP	+; +(T)
Kopong	1	158.34	97	0.773	27.8	3.9	ns	23.9	ns	HGT	+
	2	70.96	98	0.861	15.2	ns	ns	15.2	ns	HGT	+
G. rufobrunnea											
Shashe1	1	239.59	93	0.905	52.3	5.9	16.3	1.6	28.4	BR; HGT; FGRP	ns; +; -(H)+(N)
Shashe2	1	184.55	94	1.001	74.9	31.0	2.8	11.9	29.2	FGRP; HGT; BR	-(H); +; +
Shashe3	1	385.74	93	0.752	24.0	3.9	16.3	2.2	1.5	BR; HGT; FGRP	+; ns; ns
Dumela1	1	321.94	95	1.036	51.7	9.1	ns	38.7	3.9	HGT; FGRP	+; -(H)
	2	91.14	98	0.930	19.2	ns	19.2	ns	ns	BR	+
	4	79.98	96	1.000	31.5	11.5	ns	20.0	ns	HGT	+
Dumela2	1	210.75	95	1.006	61.9	2.2	40.8	11.7	7.2	BR; HGT; FGRP	+; +; -(H)
	4	98.64	96	0.946	44.4	5.9	32.4	6.1	ns	BR; HGT	+; +

Number of pupae for each generation of a locality is similar as specified in Table 2.

Within-tree variability

For each site-generation combination, the difference between expected and observed numbers of pupae per branch position was significant in most cases, with the E and/or EM categories usually being over-utilised by pupae, while the grouped remaining branch positions were under-utilised (Table 7). *G. postica* had 5 exceptions (28%) which showed the opposite pattern. *G. rufobrunnea*, however, showed no exceptions and, in general, differences between branch positions were stronger (Table 7). There were also significant differences between males and females in the frequencies of branch position occupied. For both species, males usually significantly over-utilised the edges of terminal branches (E), and in a few cases near edges of branches (EM), while females mostly over-utilised the grouped remaining branch positions (Table 7). Sex differences were significant for *G. postica* in 14 cases (61%) and for *G. rufobrunnea* in 3 cases (38%) (Table 7). The same utilisation patterns for *G. postica* and *G. rufobrunnea* were evident when the total number of male and female cocoons per branch position was compared across the entire study. The percentage female cocoons in the 'rest' category was greater than that for males for both *G. postica* (Figure 4a & b) and *G. rufobrunnea* (Figure 5a & b).

Table 7. Observed versus expected within-host plant use in branch position for each *Gonometa* species generation at a site (sample size as in Table 2), quantified for all pupae within a site, and between males and females separately. E, EM and rest (ES, ME, M, MS), and S denote edge, near edge, (stem edge, edge of branch, middle of branch, start of branch) and main stem respectively). 'no diff' indicates non-significant sex differences; *, ** and *** denote $P < 0.05$, 0.01 and 0.001 level. Underlined values were non-significant after step-up FDR at the 0.05 α-level.

Locality	Gen	Ratio of observed to expected number of pupae			Chi-Square	Dominant sex			Chi-Square
		E	EM	Rest	Sum	E	EM	Rest	Sum
G. postica									
Vryburg1	1	1.77	0.74	0.49	61.6***	M	no diff	F	6.58*
	4	0.88	1.38	0.75	11.6**	ns	ns	ns	2.7
Vryburg2	1	2.00	0.77	0.23	233.3***	M	F	F	13.90***
	2	1.25	1.15	0.59	7.7*	M	no diff	F	9.50**
	4	1.10	1.19	0.71	14.9***	M	F	F	19.10***
Hotazel	1	1.87	0.89	0.24	127.7***	ns	ns	ns	4.84
	2	1.38	1.28	0.34	61.3***	M	no diff	F	8.45*
	3	0.54	1.73	0.72	22.9***	ns	ns	ns	2.18
	4	1.20	1.44	0.36	125.0***	M	F	F	28.35***
Gabane	1	1.79	0.81	0.40	171.4***	M	F	F	22.26***
	2	1.22	1.15	0.62	31.5***	M	M	F	13.99***
	3	0.75	0.83	1.42	6.8*	M	M	F	5.58
	4	1.08	1.01	0.90	0.5	ns	ns	ns	4.09
Kumukwane	1	1.13	1.15	0.72	10.5**	M	no diff	F	14.74***
	2	0.63	0.92	1.46	8.6*	ns	ns	ns	4.8
	4	0.54	1.03	1.43	9.0*	M	M	F	10.87**
Kopong	1	0.95	0.59	1.47	12.0**	ns	ns	ns	3.14
	2	0.39	1.16	1.45	6.3*	ns	ns	ns	1.9

Table 7. continued

Locality	Gen	Ratio of observed to expected number of pupae			Chi-Square	Dominant sex			Chi-Square
		E	EM	Rest	Sum			E	EM
G. rufobrunnea									
Shashe1	1	1.64	0.76	0.60	42.3***	M	F	F	12.57**
Shashe2	1	2.03	0.66	0.31	138.9***	ns	ns	ns	1.32
Shashe3	1	2.03	0.73	0.24	122.7***	M	F	F	8.14*
Dumela1	1	1.36	1.37	0.27	150.6***	ns	ns	ns	3.84
	2	1.17	0.92	0.92	0.5	ns	ns	ns	0.9
	4	1.43	0.83	0.74	6.1*	ns	ns	ns	1.79
Dumela2	1	1.88	0.65	0.47	110.1***	M	M	F	32.05***
	4	1.19	1.19	0.62	5.4	ns	ns	ns	1.81

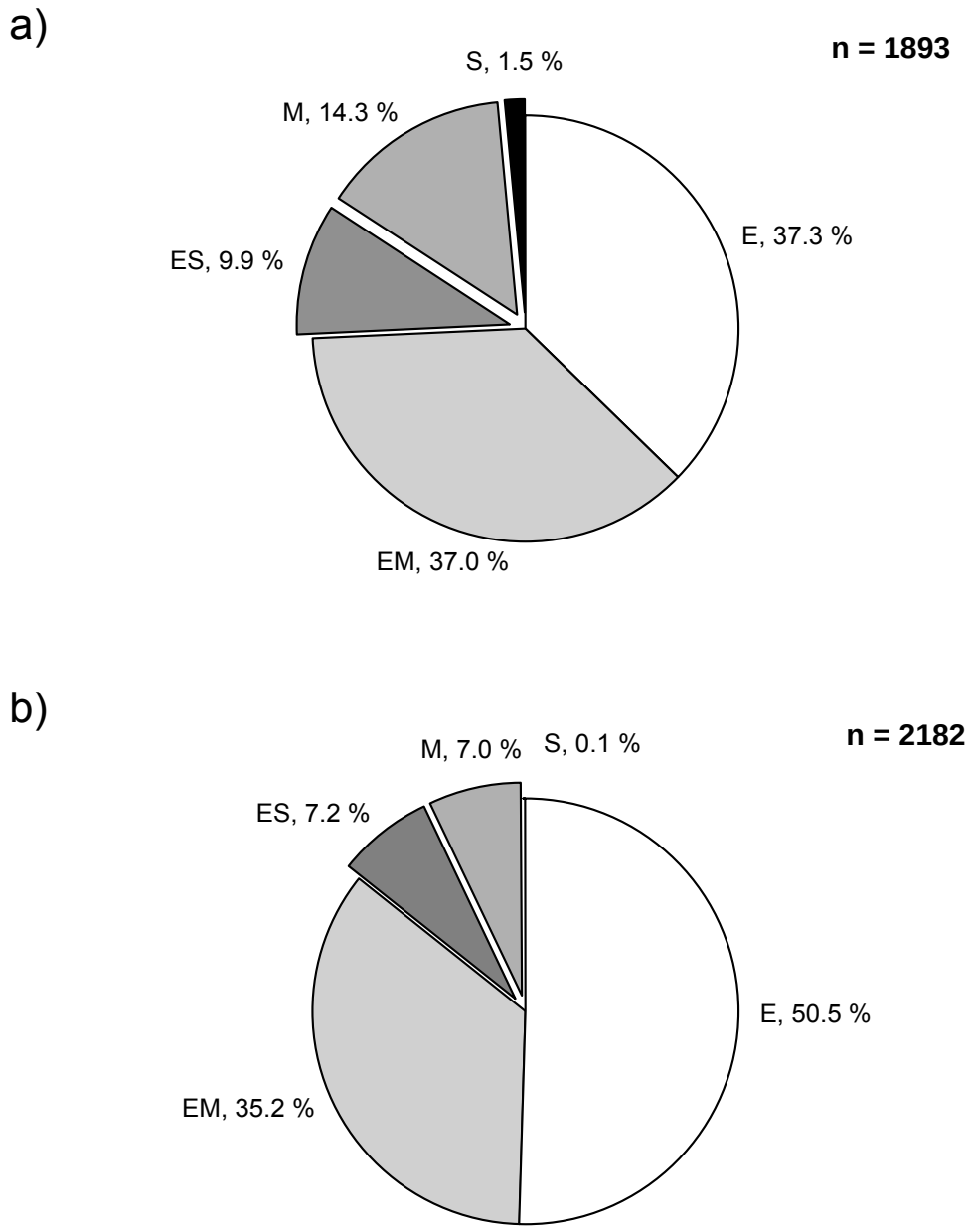

Figure 4. Percentage a) female and b) male cocoons for each branch position for *G. postica* at all sites. E, EM, ES, M (including ME and MS), and S denote edge, near edge, stem edge, middle of branch and main stem respectively.

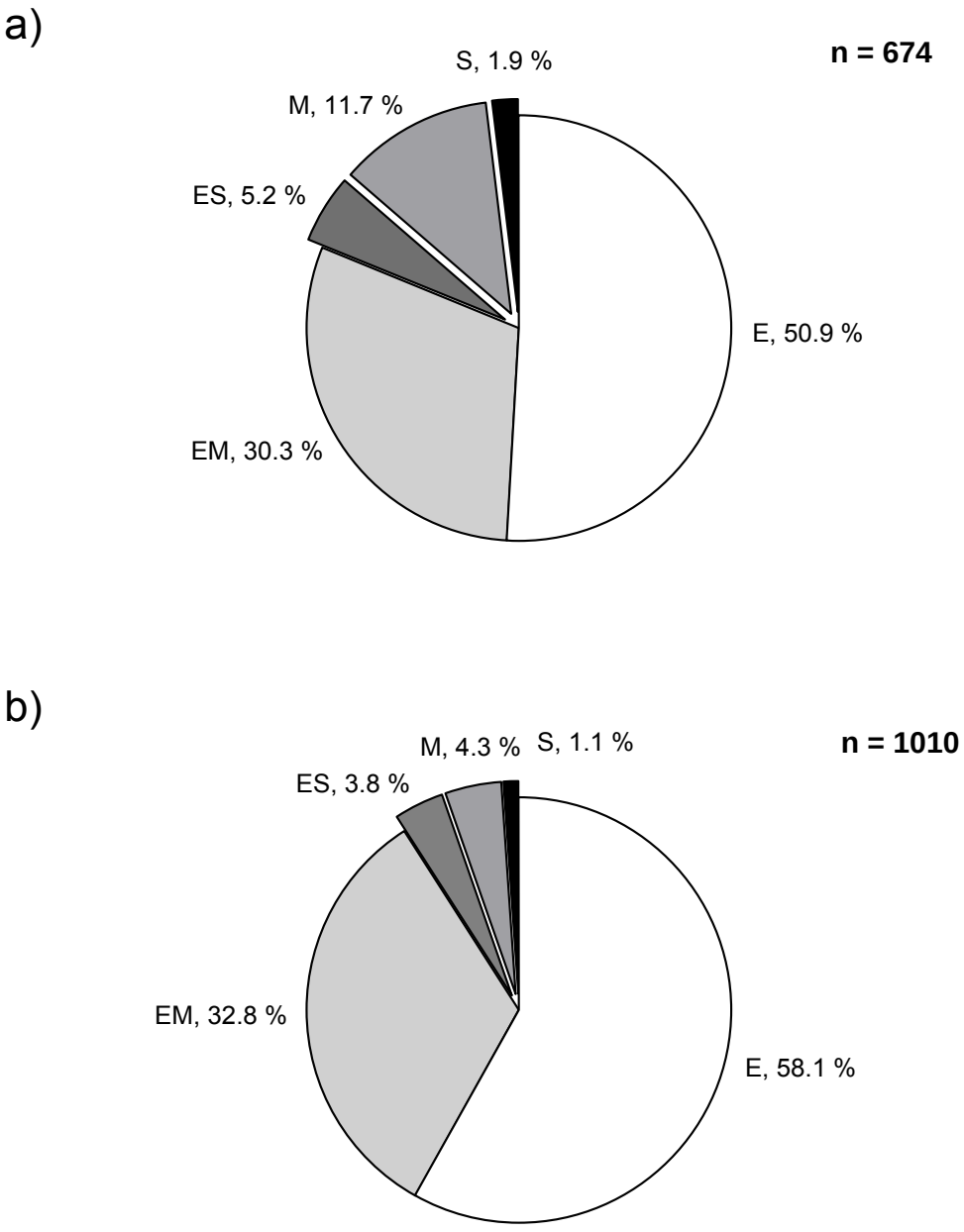

Figure 5. Percentage a) female and b) male cocoons for each branch position for *G. rufobrunnea* at all sites. Notation same as for Figure 4.

The difference between expected and observed numbers of pupae between aspects was significant in most cases for *G. postica* (81%), but not *G. rufobrunnea* (25%) (Table 8). Where such differences were significant, N and/or E aspects were over-utilised, while S and/or W aspects were under-utilised (Table 8). The same pattern was evident for *G. postica* and *G. rufobrunnea* when the total number of male and female cocoons per aspect was considered across the entire study (Figure 6a & b). There were, however, no significant differences in the frequencies of males and females with respect to aspect (Table 8).

Table 8. Observed versus expected within-host plant use according to aspect (N, E, S and W) for all *G. postica* and *G. rufobrunnea* pupae as well as the influence of sex. *, ** and *** denote $p < 0.05$, 0.01 and 0.001 level. '-', not available; † analysis with expected values < 1. Step-up FDR at the 0.05 α-level, did not change significance.

Locality	Gen	n	Ratio of observed to expected number of pupae				Chi-Square Sum statistics	
			N	E	S	W	All pupae	Females vs. males
G. postica								
Vryburg1	1	-					-	-
	4	155	1.47	1.14	0.88	0.52	19.0***	6.84
Vryburg2	1	-					-	-
	2	88	1.23	1.86	0.73	0.18	33.9***	0.02
	4	341	1.09	1.48	0.87	0.56	37.9***	2.05
Hotazel	1	69	0.87	1.74	0.99	0.41	15.8**	1.32
	2	266	1.13	1.25	1.01	0.62	15.0**	5.32
	3	83	1.35	1.01	0.72	0.92	4.3	3.73
	4	580	1.23	1.11	0.80	0.86	18.6***	5.39
Gabane	1	414	1.10	1.49	0.64	0.77	44.6***	0.18
	2	441	1.00	1.45	0.71	0.84	34.6***	6.18
	3	76	1.74	1.47	0.47	0.32	28.7***	1.44
	4	83	1.35	0.96	1.16	0.53	7.7	2.76
Kumukwane	1	159	1.21	1.13	1.18	0.48	14.6**	2.06
	2	70	0.74	1.49	0.57	1.20	9.2*	4.81
	4	65	1.54	1.54	0.49	0.43	18.9***	1.93
Kopong	1	55	0.95	1.82	0.51	0.73	13.6**	0.50
	2	31	0.90	1.29	0.90	0.90	0.9	1.94

Table 8. continued

Locality	Gen	n	Ratio of observed to expected number of pupae				Chi-Square Sum statistics	
			N	E	S	W	All pupae	Females vs. males
G. rufobrunnea								
Shashe1	1	78	1.59	0.87	0.87	0.67	9.6*	6.01
Shashe2	1	30	0.93	1.07	1.20	0.80	0.7	3.82
Shashe3	1	78	1.23	1.18	0.72	0.87	3.5	3.49
Dumela1	1	33	1.21	0.85	0.97	0.97	0.6	3.64
	2	36	1.00	1.00	0.89	1.11	0.2	1.82
	4	65	1.42	1.05	0.80	0.74	4.6	0.16
Dumela2	1	27	1.19	1.19	1.19	0.44	2.8	1.50
	4	72	1.28	1.72	0.67	0.33	20.8***	14.03**†

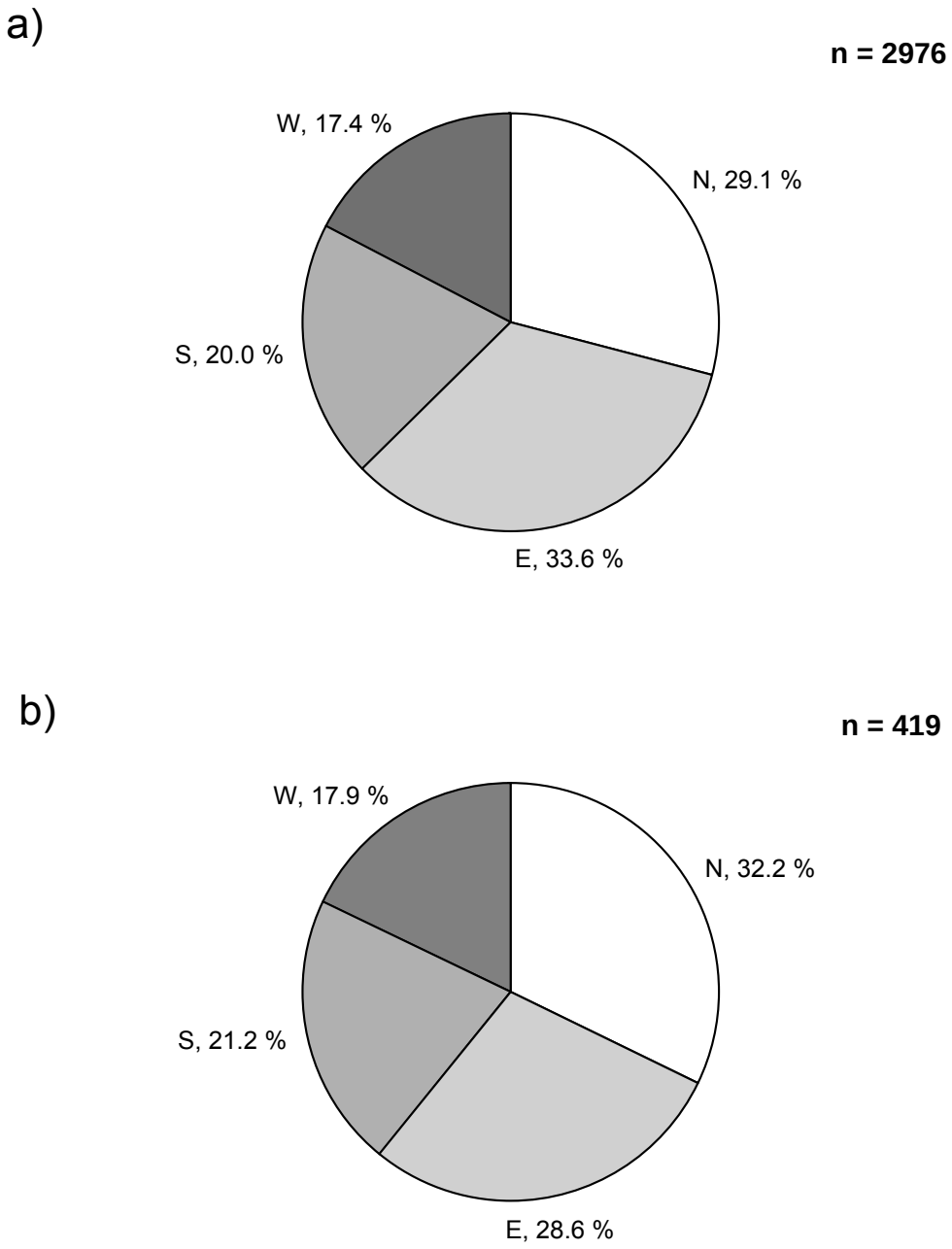

Figure 6. Percentage of cocoons found in each aspect for a) *G. postica* and b) *G. rufobrunnea* at all sites.

The distribution of standardised cocoon height (standardised for tree size) showed marked between-species differences, as well as within-species differences in *G. postica*. *G. postica* at sites with *Acacia erioloba* had a normal cocoon height distribution, with most cocoons just above mid-tree height (Fig 7a). At sites with *Acacia tortillis* cocoon height had a left skewed distribution, but in this case most cocoons were found just below mid-tree height (Fig 7b). In contrast, *G. rufobrunnea* had a right skewed distribution with most individuals at the two-thirds tree height mark (Fig 7c). However, in all cases the height classes at which most pupae was found, were below the height where the greatest available canopy volume of the primary host plant was expected to occur (Fig. 7a-c).

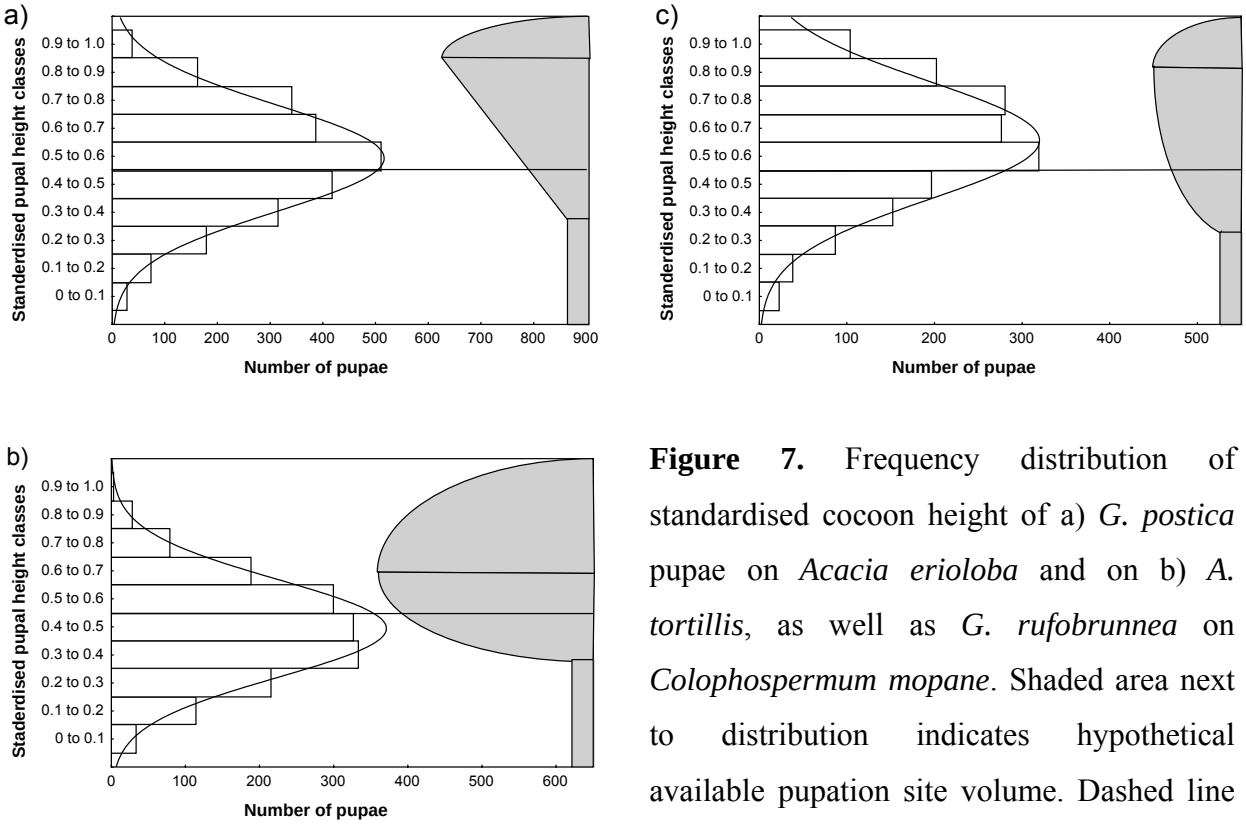

Figure 7. Frequency distribution of standardised cocoon height of a) *G. postica* pupae on *Acacia erioloba* and on b) *A. tortillis*, as well as *G. rufobrunnea* on *Colophospermum mopane*. Shaded area next to distribution indicates hypothetical available pupation site volume. Dashed line indicates mid tree height.

In all cases the relationship between cocoon height and tree height was significantly positive (Table 9). Cocoon height revealed that in all cases branch position, functional group and tree height, but not sex, contributed significantly to the percentage of deviance explained for *G. postica* (on both host plants) and *G. rufobrunnea* (Table 9). Cocoons with branch position category E, EM or ME consistently pupated higher, while cocoons found on S were significantly lower. With respect to functional group, in all three regressions the cocoons on primary host trees were significantly higher than they were on non-hosts (Table 9). For cocoons of *G. postica* on *A. tortillis* and *G. rufobrunnea*, cocoons on undefended non-host plants were significantly lower. This indicates that even when tree height is accounted for, tree functional group may still influence pupation height.

For both *Gonometa* species distance of a cocoon to the tree trunk always had a significant positive relationship with tree height (Table 9). *G. postica* cocoons were significantly further from the tree trunk if on one of its primary host plants, while functional group did not explain distance of *G. rufobrunnea* cocoons from the trunk significantly, although tending to be closer if on a non-host without thorns. *G. postica* on *A. erioloba* and *G. rufobrunnea* were significantly closer to the trunk if cocoons were female, while for *G. postica* on *A. tortillis*, sex had no significant effect (Table 9).

Table 9. Generalised linear regression of the height and distance from the tree trunk where pupation occurred for *G. postica* (for both host plants) and *G. rufobrunnea*. The fit and percentage deviance explained (DE) by the total model as well as the significance of independent variables is shown. Branch position: E, EM, ES, ME, M, MS, and S; denote edge, near edge, stem edge, edge of branch, middle of branch, start of branch, and main stem respectively. Sex: female (F) and male (M); Functional group: primary host (*A.e.* = *A. erioloba*; *A.t.* = *A. tortillis*; *C.m.* = *C. mopane*), non-host no thorns (nhn) and non-host with thorns (nht).

Dependent variable	df	Scaled dev/df	Total % DE	Independent variables	Slope ± SE	Log likelihood	χ^2	P
G. postica* on *A. erioloba								
Cocoon height	2444	1.004	26. 5	Branch position	+ (E, EM, ME, M) – (S)	-13931	232.8	< 0.001
				Functional group	+ (*A.e.*)	-13826	24.04	< 0.001
				Sex	ns	-13815	1.08	0.300
				Tree height	+	-14026	422.71	< 0.001
Distance to trunk	2450	1.002	9.9	Functional group	+(*A.e.*)	-7843.3	37.70	< 0.001
				Sex	– (F)	-7843.6	38.26	< 0.001
				Tree height	+	-7896.4	143.93	< 0.001
G. postica* on *A. tortillis								
Cocoon height	1609	1.007	45.5	Branch position	+ (E, EM, ME)	-8826.3	103.29	< 0.001
				Functional group	+ (*A.t.*) – (nhn)	-8821.1	92.96	< 0.001
				Sex	ns	-8775.1	0.84	0.657
				Tree height	+	-9131.6	713.78	< 0.001
Distance to trunk	1613	1.004	34. 0	Functional group	+ (*A.t.*)	-5770.1	218.36	< 0.001
				Sex	ns	-5674.6	27.32	< 0.001
				Tree height	+	-5974.3	626.80	< 0.001

Table 9. continued

Dependent variable	df	Scaled dev/df	Total % DE	Independent variables	Slope ± SE	Log likelihood	χ^2	P
G. rufobrunnea								
Cocoon height	1673	1.007	52.6	Branch position	+ (E, EM, ME) – (S)	-9349.2	442.49	< 0.001
				Functional group	+ (*C.m.*) – (nhn)	-9181.4	106.98	< 0.001
				Sex	ns	-9128.2	0.65	0.420
				Tree height	+	-9442.7	629.55	< 0.001
Distance to trunk	1682	1.003	12.3	Functional group	– (nhn)	-4216.0	4.48	0.106
				Sex	– (F)	-4218.6	9.61	0.002
				Tree height	+	-4299.7	171.85	< 0.001

DISCUSSION

Between-tree patterns in the pupal abundance of *Gonometa* species were random in terms of absolute spatial position, but markedly non-random in terms of tree characteristics. Most *G. postica* pupae were found on large primary host trees, while *G. rufobrunnea* used large primary host trees as well as non-host trees irrespective of their size. Indeed, very few *G. postica* pupae were found on non-host plants, while almost a third of all *G. rufobrunnea* pupae were found on non-hosts. Also, tree size explained more of the variation in *G. postica* pupal abundance, and had a stronger positive spatial relationship with abundance (i.e. areas with large numbers of branches had high pupal abundance) than *G. rufobrunnea*. Nonetheless, for both species pupal abundance patterns were not explained by the spatial position of trees, but rather specific properties of the tree (i.e. size and functional group). This suggests that trees used as pupation sites are individually selected irrespective of their position relative to other trees (see also Rodeghiero & Battisti 2000). The strong trend in *G. rufobrunnea* towards more females and larger pupae in general on non-host plants is a curious result. It is possible that large larvae are more likely to disperse, or have greater dispersal distances, from the host plant before pupation (see also Gutierrez & Menendez 1997; Etienne & Olff 2004; Ness *et al*. 2004). As a result the pupae found on non-host plants will be larger and have a greater probability of being female. Therefore, at the between-plant scale the two *Gonometa* species differed only in the extent to which non-larval-host plants were used for pupation, as well as the importance of tree size in explaining pupal abundance.

Although several possible mechanisms can lead to more pupae on taller trees, as well as those with more branches, there are two reasons that suggest that oviposition behaviour of *Gonometa* species are responsible for this pattern. First, host plant apparency is known to affect the oviposition patterns of Lepidoptera (Courtney 1982). For example, the oviposition pattern of *Imbrasia belina* (Saturniidae), an ecologically similar species to *G. rufobrunnea*, is related to the apparency of the host plant quantified as tree size and the proximity of neighbouring host plants (Wiggins 1997). During oviposition site selection, location of host plants is partly visual in most butterflies, and if the host plant is conspicuous oviposition is usually limited to host plants (Wiklund 1984). The primary hosts of both *Gonometa* species were highly apparent, generally the largest trees at the site, and most abundant. Large trees

may thus be more apparent to ovipositing females and consequently receive more egg batches (Courtney 1982; Batzer *et al*. 1995; Wiggins 1997). Second, larvae may not survive if the eggs they emerged from are located on small hosts or non-host plants. The first instar larvae of Lepidoptera that often do not oviposit on host plants (generally species that overwinter as eggs or small larvae) use silk threads to 'select' host plants (Bernays & Chapman 1994). Consequently larvae will only have a high probability of survival if a suitable host plant is in close proximity (Leyva *et al*. 2003). *Gonometa postica* early instar larvae have been observed to drop with a silk thread from defoliated branches of potted hosts in a green house. This suggests that if females oviposit on non-hosts, first instars may only be able to disperse to suitable hosts directly next to the host plant. Based on the large distances between the primary host plants of *Gonometa* species, larvae are unlikely to successfully disperse to suitable hosts if oviposited on non-hosts. Furthermore, oviposition on the host plant is typical of southern African Lasiocampidae (Scholtz & Holm 1985).

Pupation patterns of *Gonometa* species are less likely the result of secondary host plant selection by larvae that are still feeding. Although Lepidoptera larvae are more likely to move to an object the bigger it appears to them visually (Bernays & Chapman 1994), dispersal success to alternative hosts is usually low (Floater 2001). The low number of pupae relative to available foliage on host plants suggests that defoliation by *Gonometa* is rare and remaining on the host plant will be less costly than moving to a secondary host (Batzer *et al*. 1995). There is thus little evidence to suggest that density dependent dispersal of larvae to secondary host plants occurs (see Rhainds *et al*. 2002), and oviposition site selection by adult females is therefore thought to be the primary determinant of pupal distributions in *Gonometa* species.

However, the frequent use of non-host plants by *G. rufobrunnea* suggests that a secondary mechanism is required to explain why final instar larvae actively seek out non-host plants. The use of non-host plants by *G. rufobrunnea* pupae, which are very vulnerable to bird predation (Chapter 1), may serve as a form of enemy free space. Predators, especially vertebrates, using visual cues may not only select high-density prey patches, but also form search images of prey against certain backgrounds (Guilford 1992). Using non-host plants may thus be a method of escaping bird predation, by disrupting the search image of the predator (Brower 1958). The distribution of apparent *G. postica* pupae, which appear to be virtually immune to predation (Chapter 1), were seldom found on non-host plants, supporting this

hypothesis. Evidence for selection of crypsis in swallowtail butterfly pupae, which experience lower predation levels when successfully matching their background when pupating high up on their host plant, provides further support (Hazel *et al*. 1998). Furthermore, when host plants have high larval densities, pupating on the same host plant will decrease the effectiveness of cocoon crypsis as an anti-predator defence (Brower 1958). Thus non-host trees may be used especially at medium to high site pupal abundances (i.e. as found for first generation sites). Thus, *G. rufobrunnea* between-tree pupal abundance is not only dependent on oviposition patterns, but may also be a consequence of the selection of enemy free space for pupation by final instars.

At a within-plant scale the pupae of *G. postica* and *G. rufobrunnea* showed similar patterns of branch position and aspect (to a lesser extent) use, as well as cocoon height (non-standardised) and distance from trunk patterns. Most pupae were found on the edge or near the edge of branches, on the eastern and northern sectors of trees, and occurred higher and further away from the stem if on larger trees. The low number of pupae for which aspect data was available for *G. rufobrunnea* in the first generation, may explain the absence of significant differences between aspects, compared with the significant differences commonly found for *G. postica*. Nonetheless, for both *Gonometa* species across study within-tree aspect use was similar. Thus, similarities in within-tree use for *Gonometa* species suggest that these patterns have a common explanation. Although there are more pupation sites on terminal branches, within-tree pupation patterns were not simply a matter of resource size, as more exposed branch positions were used than expected. Differences in solar radiation possibly explain these patterns. The shade provided by trees reduces the solar radiation and long wave radiation from the ground (Kotzen 2003). Branch positions near the trunk will receive the least solar radiation because of maximum shading by tree branches, while terminal branch positions will receive minimum shading (Kotzen 2003). Within their host plants caterpillars may expose themselves to maximum radiation at low temperatures, and move to more shaded areas as the temperatures increases (Casey 1993). Therefore, it is possible that the cooler microclimate of more heavily shaded branch positions near the tree trunk are less favourable for the development of a pupa into an adult, compared to those on the edge of branches that are most likely to receive oblique, early morning radiation (see Bryant *et al*. 2002). Differential aspect use within trees may also be explained by differences in thermal microclimate properties (Stork *et al*. 2001). In the

Southern Hemisphere, northern and eastern aspects of trees will receive more solar radiation in the morning than southern and western aspects, while the reverse is the case in the afternoon (see Kotzen 2003). Therefore, pupae positioned to receive maximum morning radiation may warm up more quickly, while decreased exposure to afternoon radiation could prevent pupae experiencing maximum temperatures potentially detrimental to their survival. Because pupal metabolic rate is positively related to temperature, avoidance of high midday temperatures may also be a strategy to conserve energy usage in overwintering pupae (e.g. Bennett *et al.* 2003; Irwin & Lee 2003).

These explanations for these within-tree pupation tree patterns were further supported by standardised cocoon height patterns. Differences between *Gonometa* species in cocoon height standardised for tree height corresponded with differences in the shape of the primary host plants. The difference between *G. postica* populations on different host plants may also be explained by tree shape. Large *Acacia tortillis* trees are typically umbrella shaped and *A. erioloba* trees have a wide spreading crown, while *C. mopane* typically occurs as upright shrubs or trees, widening only close to its crown (Palgrave 1977). Although tree shape is a measure of the three-dimensional space available for pupation, the maximum frequency height classes of *G. postica* and *G. rufobrunnea* corresponded to regions below the maximum canopy volume of their host species. Thus pupation site availability itself was not a major determinant of the relative height of pupae within trees. Alternatively, using the shaded pupation sites just below the maximum canopy volume may provide a more buffered and cooler microclimate, particularly at midday (see Kotzen 2003). Therefore, at the within-tree scale branch position, aspect and tree shape may influence pupation site choice by providing microclimate conditions for which pupating *Gonometa* larvae have a particular preference, and which optimises pupal survival, energy usage, or adult development rate.

However, sex differences in pupation site use suggest alternative explanations for within-tree pupation patterns. Branch position categories and distance to trunk were significantly different between males and females. In contrast, aspect and cocoon height did not show significant sex differences. The causes of these sex differences are unknown, but appear to be less important than the broad trend of more pupae on the edge of branches. It has been observed (pers. obs.) that males usually emerge at midday while females emerge at dusk. Males are stronger fliers (Chapter 1) and may be less vulnerable to predators than females that

fly mostly at night. Males typically start wing fluttering upon emergence compared to females that remain inactive for extended periods after emergence. Therefore, using terminal branch edges is possibly advantageous for the rapid, post-eclosion dispersal in males, while more sheltered branch positions allow cover until nightfall in females. Nonetheless, the stronger patterns in within-tree pupation site use suggest that microclimate differences with respect to received solar radiation is the major factor explaining within-tree pupal distribution.

This study highlights the value of documenting between tree and within tree patterns as a first step to explaining pupation site selection, as well as identifying possible evolutionarily selective factors in the species, and generating testable hypotheses from these. Subsequent experiments on female oviposition choice, larval dispersal, and pupal survival under different levels of natural enemy attack at the between-tree scale, and microclimatic conditions at the within-tree scale, may now be conducted to test the proposed hypotheses. The marked differences between *Gonometa* species at a between-tree scale, but strong similarities at a within-tree scale, emphasises the fact that factors influencing herbivorous insect distributions are scale dependent (see also Hamid *et al*. 1999). Therefore, studying the distribution of herbivorous insects at more than one scale provides more information when comparing species, and reduces the risk of missing possible mechanistic explanations for the patterns observed (e.g. McGeoch & Price 2004).

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