Chap. 5: Space - Small scale distribution in the field

5.1. Introduction

Spatial patterns of herbivorous insects exist on different spatial scales. Within one habitat different microclimatic conditions might cause different population densities (Bach 1993) or different levels of herbivory can be found on the same host plant in sun and shade (Lincoln & Mooney 1984, Louda et al. 1987, Niesenbaum 1992, Louda & Rodman 1996). Within one plant individual, there can be a vertical stratification (Rowe II & Potter 1996, Brown et al. 1997), a preference of sheltered microsites like furled leaftips (Willmer et al. 1996) or of a distinct leaf side (Tahvanainen 1972) by the phytophagous insect species.

The reasons for such small scale distributions are various. A specific microhabitat can simply meet the physiological needs of the organism in terms of food and microclimatic requirements best (fundamental niche). Insect species can differ in these requirements. One place can be better protected from predators or parasitoids than another (Berdegue et al. 1996, Hopkins & Dixon 1997). Other biotic interactions, like competition, might be responsible that species do not live under optimal but suboptimal conditions (realized niche)(Denno 1995). Sommaggio et al. (1995) defined the term "microhabitat" with the factors microclimate, nutrient conditions and interactions with the arthropod community. As possible causes for a vertical stratification of a leaf mining moth within a tree, Brown et al. (1997) tested foliage quality, natural enemies, plant phenology, microclimatic gradients and interspecific competition. None of the factors tested, however, could explain the observed stratification.

One of the most fascinating things about the study of herbivorous insects is the way the abiotic environment, the host plant and the insect interact with each other. One situation where abiotic factors have a direct influence on insect performance (temperature and humidity) as well as an indirect one via host plant quality, is differential shading. It occurs for example in a sun-shade-mosaic created by a forest edge or single trees or shrubs within an open habitat.

Most often the availability of nitrogen in the food limits the growth and fecundity of insects (McNeill & Southwood 1978, Mattson 1980, White 1993). It has been shown that low leaf nitrogen and water content causes a prolonged developmental time, low relative growth rate (RGR) and a low food conversion index (ECI = efficiency of the conversion of food in growth) in chrysomelid larvae (Obermaier & Zwölfer 1999) as well as in other herbivorous insect orders (Scriber 1977, McNeill & Southwood 1978, Loader & Damman 1991).

Both, leaf nitrogen and leaf water content differ, together with other plant traits, when a plant is growing either in full sun or in shade. A prediction supported by numerous studies is that shade adapted plant species have low nitrogen concentrations in their leaves (Chapin III et al. 1987). In a single vine plant, climbing into the canopy, the lower shaded leaves show a lower nitrogen concentration than the sun exposed leaves on top because of a higher concentration of Rubisco (enzyme in photosynthesis) there (Hikosaka et al. 1994, Hikosaka 1996). Often in these studies, however, nitrogen content is given per unit leaf area. When, however, expressed on a weight basis, average N contents were higher in the subdominant (more shaded) plants(Anten & Werger 1996). Similar results for shaded vs. unshaded plants for five plant species of three different families are reported by Heilmeier (1988) and Steinlein (1991) probably caused by an accumulation due to carbon (light) limitation. With regard to nitrogen availability herbivorous insects should, in that case, prefer to feed in the shade.

There are also direct effects of the microclimate, mainly of temperature and humidity, on insect performance. Insects are especially vulnerable to abiotic conditions because of their small size and relatively large surface area. Some microclimatic analyses of leaves have shown that higher humidities are to be expected close to the transpiring surface, in particular at the lower side; and in some cases these surfaces are also measurably cooler (see review in Willmer 1981). The direct effect of microclimate can be important for insect movements and locations on the host plant (Willmer 1982, Willmer et al. 1996, Alonso 1997), relative growth rates of caterpillars (Stamp & Bowers 1990) and geographical distribution of butterfly species (Bryant et al 1997), to give some examples.

In this study a community of seven West African tortoise beetle species (Fam. Chrysomelidae), living on the same host plant family (Fam. Convolvulaceae), was examined for their resource use and patterns of coexistence. A separation of the beetle community in space and related factors possibly responsible for this, was already briefly discussed in chapter 4. The factor which explained most of the distribution of the five beetle species on *M. hederacea* in river side habitats in an ordination analysis, was the factor "microhabitat". Different microhabitats were found along different light intensities. The host plants, vines of the genus *Merremia* and *Ipomoea*, grew there under a broad spectrum of light intensities. In the present chapter, small scale distribution in the tortoise beetle community and its underlying factors are examined on two spatial scales, a within-habitat and a within-plant scale. I used similar factors as Brown et al. (1997) to define the microhabitat: In this chapter I present data on two of these factors, plant quality and microclimate. Interspecific competition is discussed

here and additionally in chap. 3. The influence of predation and parasitism on the spatial separation of the beetle species is examined in chap. 7.

Questions investigated in this chapter, were: (1) Do different beetle species use different microhabitats (=Is there a differentiation of the beetle guild on a small spatial scale)? Is there a seasonal shift between the microhabitats? (2) How do food quality and microclimate change at different light intensities? (3) Do effects of plant quality and microclimate on larval development differ between sun and shade microhabitats? (4) Are different species differently distributed within a host plant?

5.2. Material and methods

5.2.1. Sun- and shade microhabitats

Microhabitat use in the field

Whether different beetle species use different microhabitats in the field, was investigated by abundance estimates. In May/June and Nov./Dec. 1995, all individuals of all beetle species encountered during the regular abundance estimates in the field (every 14 days on 6 sites), were categorized with regard to the microhabitat inhabited. (The abundance estimates and sites were described in detail in the material and method-section in chap. 3.) All stages of development (eggs, larvae and adults) were pooled for the classification since some of the species were quite rare. Seven classes of microhabitats were distinguished visually by the light intensity in different (vegetation) structures under which the host plants grew: Rock-sun, open sun, grass sun, shrub sun, tree sun, shrub shade and tree shade. The leaf shape of the host plant, *M. hederacea*, changed from deeply lobed to simple cordate within the light gradient (Lee & Richards 1991) and could therefore be used as an additional indicator for the quantity of light received in a certain microhabitat.

A resource matrix (Krebs 1989) was constructed of all data by assigning species to rows and microhabitats to the columns. The data were also used to calculate niche breadth (Levin`s B) and niche overlap (Morisita´s index of similarity, Krebs 1989) for all seven species.

Microhabitat availability and use at different times in the season

To compare the availability of host plants in different microsites with their use by the beetles throughout the year, microhabitat use of the beetle species was recorded during abundance estimates from March to June and in November/December 1995 every two weeks on three

sites at the river side (see m+m, chap. 3). Light conditions, here, were qualified in three classes: ”sun”, ”light shade” and ”shade”. Additionally, in three river side habitats, along transects, the host plants were characterized with the same three classes (transects, see chap.3). Every step along each transect was characterized for host plant presence or absence and the microhabitat. The method gives an idea of the proportional availability of vines in sun and shade habitats on a site and their change over time. It does, however, only partly reveal the real quantities of the host plant, because leaf mass of vertically growing plants, which grew up to 10m high in the trees over the season, got under- and leaf mass of horizontally growing plants overestimated. The leaf mass of vertically growing plants increased over the course of the season.

Plant quality in sun and shade

Additionally to the abundance of the beetles and the availability of the host plant in the field, the plant quality in different microhabitats was investigated. *Merremia hederacea* plants from the field as well as plants grown for experiments were analyzed for leaf water and leaf nitrogen content. For methodological reasons only two microhabitat-classes, sun and shade, were used for further analysis and experimentation.

In the field 15 plants of *M. hederacea* were harvested completely in the shade habitat and 15 plants in the sun habitat at the river side (site:Vofapl.2)(5/16 till 5/19 1995). Stem length of plants was measured. Fresh and dry weight of leaves was taken and leaf water content per mg dry weight per plant calculated. The dried leaves were grounded in a mill and analyzed for total leaf nitrogen content in a CHN analyzer (see also m+m, chap. 3). Only 10 of 15 plants per group were analyzed for nitrogen content.

Ten control plants for each treatment group, sun and shade, were grown additionally to the plants used for field experiments (see below). They were harvested after the experiments were finished, (6/15 and 6/17 in 1995) and were treated similar as the field plants above. Leaves were additionally divided into three age classes of young, mature and senescent leaves and analyzed separately for nitrogen, carbon and water-content of the leaves.

Microclimate in sun and shade habitats

From March till June and in November/December 1995 at three river side sites and at total of six microsites, temperature was measured for six consecutive days. For this, two data loggers (squirrel 1200, grant instruments, Cambridge, UK) were placed in turn at the different sites

(places). The temperature was measured on living *M. hederacea* leaves. The thermal sensors were fixed on the underside of the leaves by a piece of tape. Each time one pair of leaves, consisting of one leaf in the full sun and one leaf in shrub shade, was measured. The time span from the first day, 6.00 p.m. until the sixth day, 11.00 a.m. of each run, was taken to calculate a temperature mean. Several runs were rejected, either because the thermal sensors were removed from the leaves by wind or sudden rains made it necessary to save the data loggers. Of the 13 intervals with correct measurements, the means over the six day periods were calculated and the sun-shade pairs were tested with a Wilcoxon matched-pairs signed rank test.

5.2.2. Field experiments on the influence of microclimate and plant quality on larval development

To investigate the effects of the microhabitat factors microclimate and plant quality on larval development combined and separately, three different field experiments were conducted: (1) In the **shading experiment** the larvae were reared in the sun and under experimental shading on sun and on shade plants, respectively, to test the combined effects of the **factors microclimate and plant quality**. (2) In **the box experiment** the larvae were reared under identical climatic conditions in boxes but fed with leaves of either sun or shade plants, to investigate the effect of the **factor plant quality**. (3) In the **exposure experiment** the larvae were reared on plants in pots which were exposed in natural sun and shade microsites in the field. The plants had been cultivated in pots under the same conditions in light shade prior to the experiment. Here the effect of the **factor microclimate** alone was tested. For the first two experiments, the beetles host plant, *Merremia hederacea*, was sown on May 12-13th in 1995 in a germination bed. After May 27th the seedlings were replanted in pots with three seedlings in each pot. Pots were supplied with sticks to facilitate the climbing of the plants. Half of the pots were kept for the rest of the experiments beneath a double layer of a special shading cloth, simulating shade conditions of the microhabitat ”shrub-shade” (3500 Lux)(open sun: ~40000Lux). The plants beneath the artificial shading were rotated every 3 days to avoid edge effects by the light. The other half of the pots, the ”sun-plants” were positioned in the savanna (microhabitat: ”open sun”). All pots were surrounded with a ring of glue (tangle-food) to prevent larvae from leaving the plants and predators from the ground from entering. The plants were watered every day and plants with little leaf mass remaining were exchanged by new plants on which

the larvae were transfered. 5 L1 larvae (newly hatched within the last 24h) were placed on each pot.

(1) For the first experiment the species *Acrocassis roseomarginata* (14 pots per treatment group), *Aspidimorpha quinquefasciata* (10 pots per group) and *Aspidimorpha confinis* (5 and 6 pots per group) were used. 10 pots of each treatment group (sun/shade) were left without larvae as control. They were harvested and analyzed for plant quality afterwards, as described above. The experiments lasted from 5/27/95-7/1/95.

(2) The second experiment, the ”box experiment”, was conducted with only two of the species, *A. roseomarginata* and *A. quinquefasciata,* at the same time as the first experiment. This time the larvae were not placed on the plants, but the plants were harvested and fed to the larvae in boxes. Five plastic boxes (10,5x10,5x6 cm), per species and per treatment group (sun and shade plants), were equipped with newly hatched larvae. Each box contained 10 *A. roseomarginata* or 6 *A. quinquefasciata* larvae. The larvae were provided with newly cut plants every 2-3 days, which were put in water filled cups to prevent desiccation of the leaves. Plants, treated in the same way as those for the first experiment (cultivated under artificial shading/in open sun), were used in this experiment. All boxes with larvae were kept under the same microclimatic conditions in the shade under the roof of my hut.

(3) In the third experiment, the ”exposure experiment”, plants were grown from cuttings in pots (see chap. 7, predation) and cultivated under identical microclimatic conditions in light shade. After growing sufficient leaf mass, plants were exposed in the field in natural sun and shade microhabitats. Six L1 larvae were transferred onto each plant and stayed on the plant till pupation. The experiment was conducted in May/June 1995 and repeated in June/July 1997 with two species, *A. roseomarginata* and *A. quinquefasciata*. For a more detailed description of the third experiment see chap. 7 (predation).

In all three experiments the larvae stayed on the plants until pupation. Duration of development until the day of pupation and dry weight of pupae were taken as measures of the microhabitat-quality.

5.2.3. Preference of leaf sides in three species

On May 29th in 1995 during the ”shading experiment” (method see above) the use of upper and lower leaf side by the larvae of three beetle species, *A. roseomarginata*, *A. quinquefasciata* and *A. confinis*, in relation to shading and time of the day, was observed. Two groups, larvae on host plants in the sun and larvae under an artificial shading were examined.

At lunch time, in the sun there was a light intensity of 40000 Lux and under the artifical shading, of 3500 Lux. At 9.00 a.m., 12.00 a.m., 3.00 p.m. and 6.00 p.m., I checked upper and lower leaf sides of each plant for the number of larvae, sitting there. Additionally the leaf temperature on upper and lower leaf side was measured with an infrared thermometer (Cyclops 330S, Minolta, Japan).

5.2.4. Statistics

The Chi^2-tests which compared the resource matrices of different species in terms of their microhabitat use were corrected by the Bonferoni correction (each species was compared with each other).

5.3. Results

5.3.1. Within habitat distribution: Sun- and shade microhabitats

5.3.1.1. Microhabitat use in the field

The distribution of the five beetle species differed significantly among the seven microhabitat classes at the river side (Fig. 5.1.a). Fresh eggs, larvae and adults found in Mai/June and in November/December 1995 were categorized for the microhabitat and therefore light climate on their host plant. The distribution of *A. roseomarginata* differed significantly from all other species. It could be found on its host plant in all seven microhabitat classes but had its highest abundance in the sun (rock-sun, open sun, grass sun, shrub sun). The remaining four species could be found in different proportions in the shaded parts of the river side, but never in the most exposed microhabitats, rock sun and open sun. Of those ”shade” species only *A. quinquefasciata* and *A. submutata* differed significantly from each other, with *A. quinquefasciata* having its highest abundances in shrub sun and tree sun whereas *A. submutata* reached its highest densities in shrub shade and tree shade.

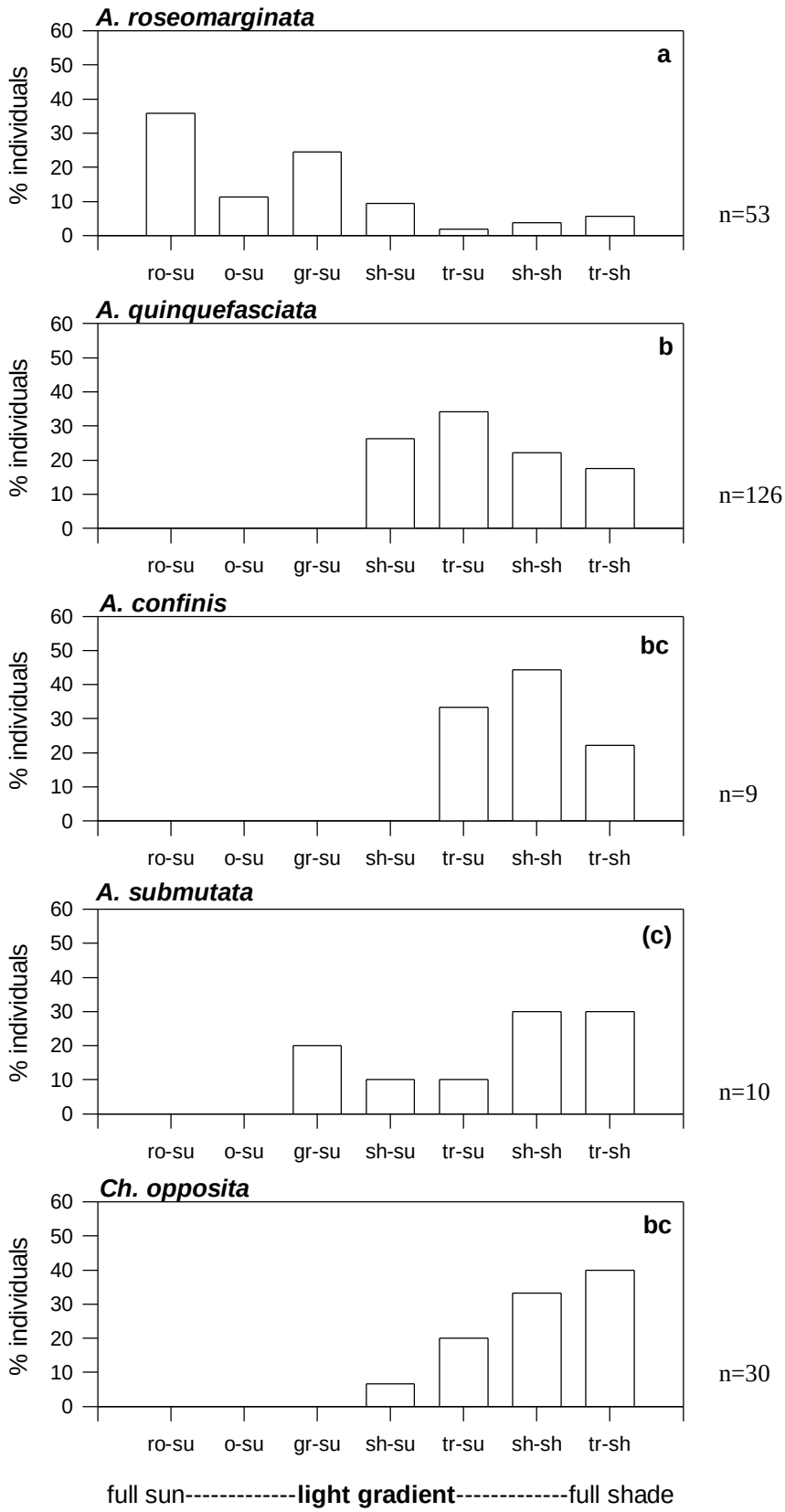

Fig. 5.1.a: Resource matrices (Krebs 1989) for the five species living in the river side habitat. The habitat was divided in seven classes of light intensity. Tests between distributions with chi^2-test and Bonferroni correction. Different letters indicate significant differences at $p<0,05$.

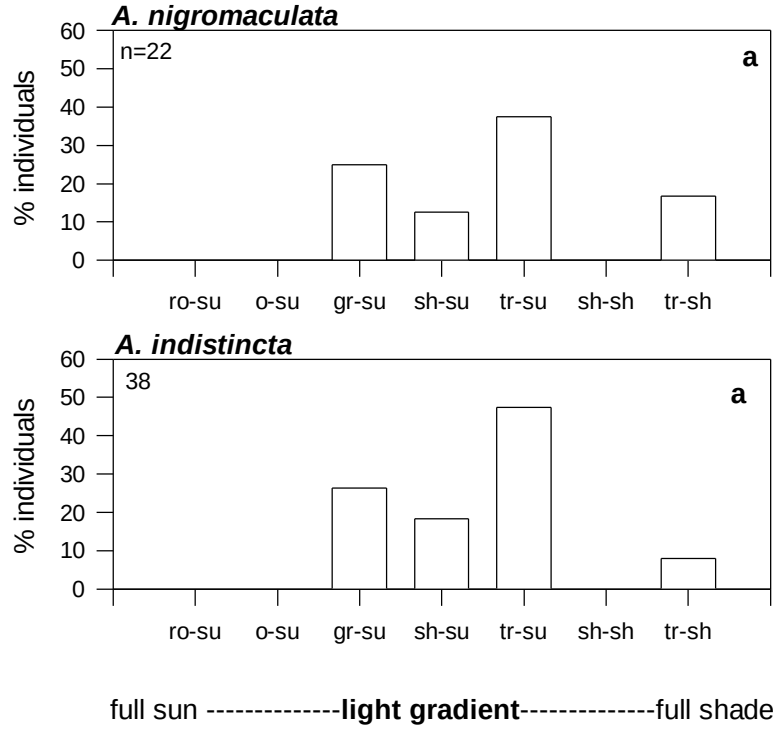

Fig. 5.1.b: Resource matrices (Krebs 1989) for two species living exclusively in the savanna habitat. The microhabitat was divided in seven classes of light intensity. Tests between distributions with chi^2-test (Mehrfelder) and Bonferroni correction. Different letters indicate significant differences at $p<0,05$.

In the savanna (Fig.5.1.b) *A. nigromaculata* and *A. indistincta* did not differ significantly in their microhabitat use. Both species occurred mainly in grass sun, shrub sun and tree sun. The river side habitat offered in general a broader spectrum of microhabitats, in terms of light intensities, than the savanna.

A. quinquefasciata occurred from the beginning of the rainy season (April) till the beginning of the dry season (Dec.). Since sample size was large enough, I tested whether microhabitat preferences in this species were constant throughout the season. This was not the case in this species (Fig 5.2). The resource matrix in June 1995 differed significantly from Nov./Dec. ($X^2=51,097$, $p<0,001$) and microhabitat use shifted from deep shade (shrub-shade, tree-shade) in June to light shade (shrub sun, tree sun) in Nov./Dec.

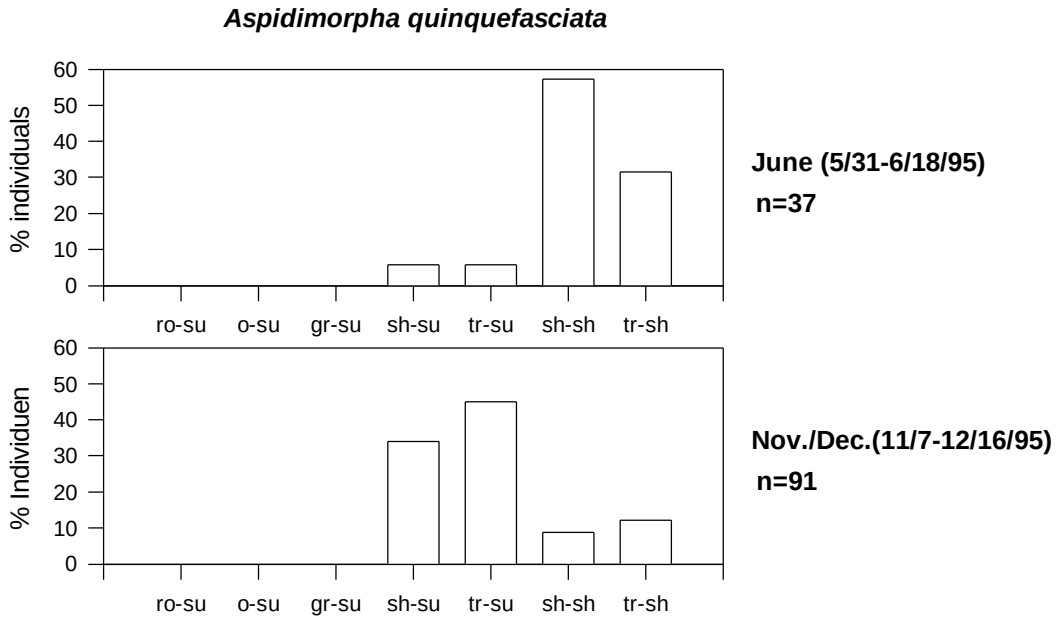

Fig. 5.2: Resource matrices for *A. quinquefasciata* at the beginning (May/June) and at the end of the rainy season (Nov./Dec.). Tests between distributions with chi^2-test (Mehrfelder). Distributions differed significantly ($p<0,05$).

Niche breadth and niche overlap were calculated as standardized measures of the use of space. Of several indices introduced, Krebs (1989) suggested Levin´s B for the calculation of niche breadth, and Morisita´s index of similarity for niche overlap. In terms of microhabitat use *A. roseomarginata* and *A. submutata* showed a wider niche breadth and could therefore be regarded as relative generalists whereas *A. confinis* and *A. indistincta* were the most specialized among the beetle species (Tab. 5.1). For comparison: the highest theoretical value for Levin´s B for an even distribution within 7 resource classes is 7.
Regarding niche overlap (Tab. 5.2) of the river side species, the "shade species" *A. quinquefasciata*, *A. confinis*, *A. submutata* and *Ch. opposita* showed, as expected, high values in the similarity index (the latter three even higher) and therefore a broad overlap with each others niche, whereas *A. roseomarginata* had a relatively small similarity index with all other species. The two savanna species, *A. indistincta* and *A. nigromaculata* had the highest index of similarity in this comparison.

Tab. 5.1: Resource matrices for the microhabitat use of 7 Cassidinae species. Numbers represent percentage of use of each habitat by the species in question. The niche width (Levin`s B) was calculated after Krebs (1989). Habitat classification follows the gradient from the most exposed to the most shaded microhabitats: ro-su=rock sun; o-su=open sun; gr-su= grass sun; sh-su= shrub sun; tr-su=tree sun; gr-sh=grass shade; sh-sh=shrub shade; tr-sh=tree shade; Lev. B=Levin´s B; n=number of individuals.

	ro-su	**o-su**	**gr-su**	**sh-su**	**tr-su**	**sh-sh**	**tr-sh**	**n**	**Lev. B**
A. roseomarginata	35,8	11,3	24,5	17,0	1,9	3,8	5,7	53	4,26
A. quinquefasciata	-	-	-	26,2	34,1	22,2	17,5	126	3,78
A. confinis	-	-	-	-	33,3	44,4	22,2	9	2,80
A. submutata	-	-	20	10	10	30	30	10	4,17
Ch. Opposita	-	-	-	6,7	20	33,3	40	30	3,17
A. nigromaculata	-	-	27,3	13,6	40,9	-	18,2	22	3,41
A. indistincta	-	-	26,3	18,4	47,4	-	7,9	38	2,99

Tab. 5.2: Niche overlap in the microhabitat use of 7 Cassidinae species (Morisita´s index of similarity, Krebs 1989). Grey shade highlights species with a high overlap. Numbers in brackets describe species which in the field normally do not occur at the same location. *A.r.=Acrocassis roseomarginata, A.q.=Aspidimorpha quinquefasciata, A.c.=Aspidimorpha confinis, A.s.=Aspidimorpha submutata, Ch.o.=Chiridopsis opposita, A.n.=Aspidimorpha nigromaculata* and *A.i.=Aspidimorpha indistincta.*

	A.r.	**A.q.**	**A.c.**	**A.s.**	**Ch.o.**	**A.n.**	**A.i.**
A.r.	-	0,290	0,144	0,513	0,198	0,450	0,407
A.q.	0,290	-	0,936	0,865	0,834	(0,798)	(0.778)
A.c.	0,144	0,936	-	1,077	1,065	(0,657)	(0,591)
A.s.	0,513	0,865	1,077	-	1,102	(0,788)	(0,603)
Ch.o.	0,198	0,834	1,065	1,102	-	(0,594)	(0,457)
A.n.	0,450	(0,798)	(0,657)	(0,788)	(0,594)	-	1,059
A.i.	0,407	(0,778)	(0,591)	(0,603)	(0,457)	1,059	-

5.3.1.2. Host plant availability and use in different microhabitats at different times in the season

The food plant of the beetles at river side habitats, *Merremia hederacea*, had a distinct seasonal phenology. This could eventually cause seasonal differences in the microhabitat use of the beetles. It germinated with the first rainfalls at the beginning of the rainy season in almost any microhabitat where seeds were available. Later on plants died out at dry places and gained huge biomass at more humid locations where they could climb vertically and found the appropriate microclimate. To quantify the resource availability in different microhabitats at different times of the season I censured 3 heterogeneous river side habitats (Lola, Badeplatz, Vogelfangplatz) every 14 days (Fig. 5.3) and classified the plants´ microhabitat in 3 classes (sun, light shade, shade). In the first three months at the beginning of the rainy season, March, April and May, the highest percentage of the vines (64,2-76,9%) could be found in the microhabitat ”sun”. In June, proportions had already changed and in light shade and shade together, 65% of the plant mass could be found. In December, which is the middle of the dry season and the end of the vegetation period, the microhabitat shade had the highest *M.hederacea*-density. In November relations were different compared to June and Dec. This could be due to a flooding of site 3 in November which was inaccessible at that time. Due to the method the growing leaf mass in the shade, which was increasing mainly vertically during the season, was not considered (only presence/absence was registered for every step); the leaf mass in the shade was therefore underestimated, compared to the sun, later in the season.

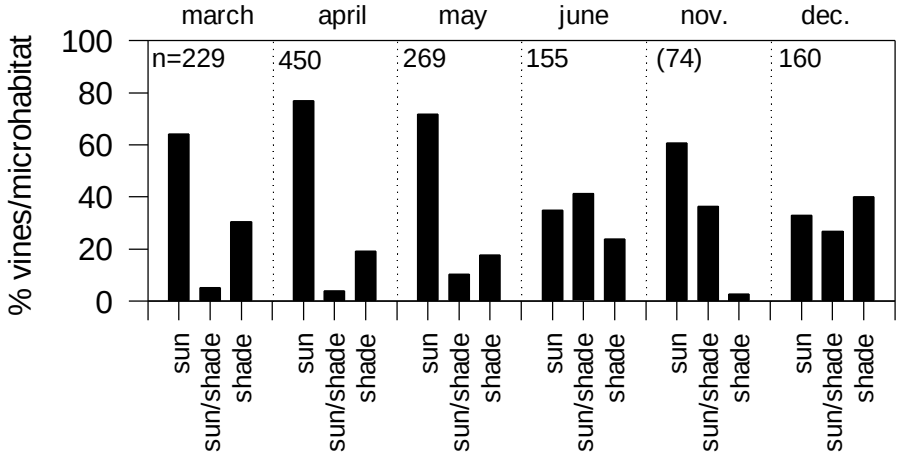

Fig. 5.3: Distribution of *Merremia hederacea* in different microhabitats over the rainy season in 1995. Shown is the percentage of food plants available in sun, light shade and shade in relation for each month.

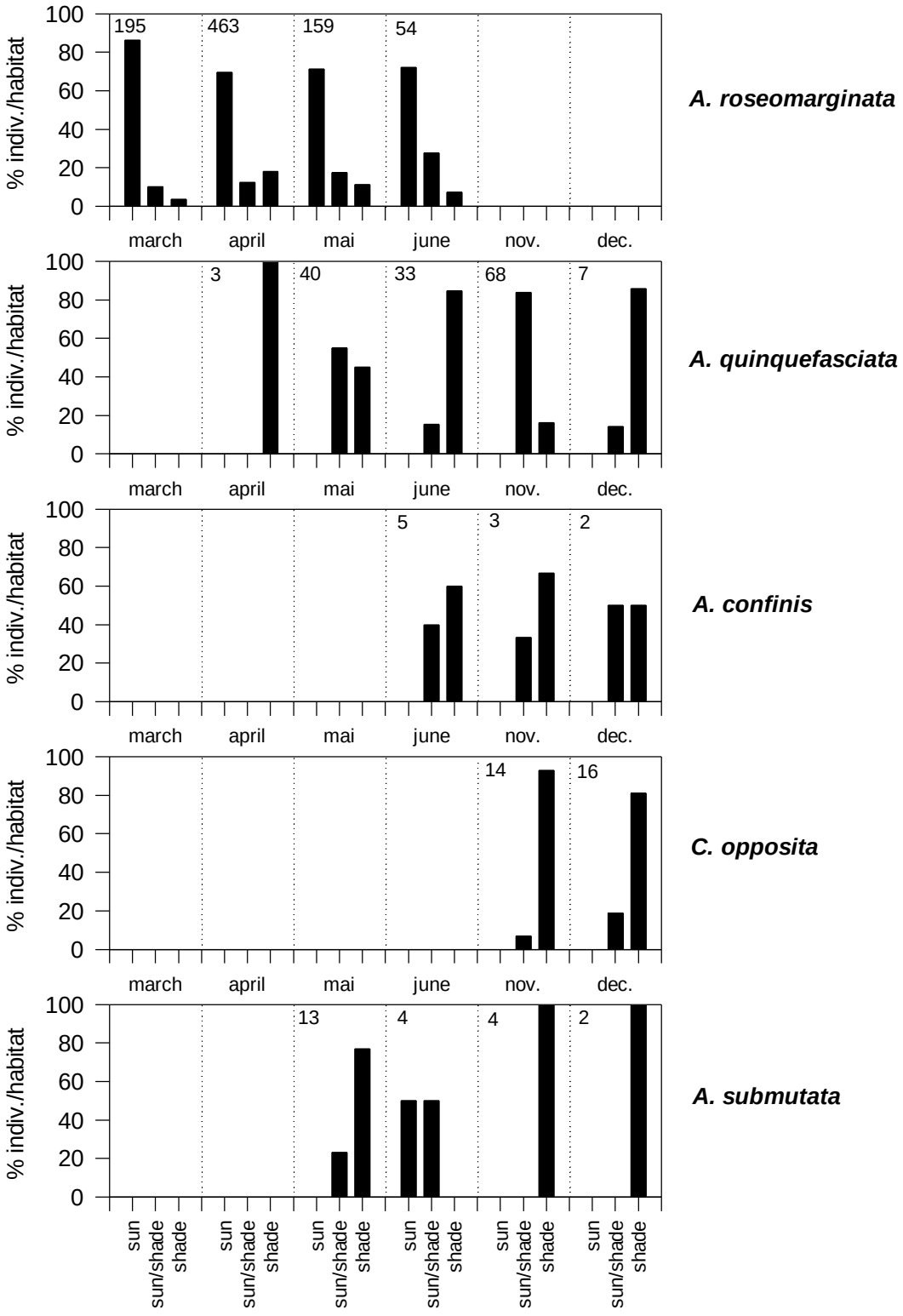

Fig. 5.4: Microhabitat use of the five river side species over the rainy season in 1995. Shown is the percentage of beetle individuals found in the sun, light shade and shade for each month.

The microhabitat use of the beetle species was examined in the same time period in 1995 (Fig. 5.4). In one of the five species investigated, *A. submutata*, some evidence could be found for a seasonal shift in microhabitat use with this method. In May and June all three microhabitat classes were used by this species, whereas in November and December individuals could be found exclusively in the microhabitat "shade". Because of a small sample size the shift has, however, to be seen critically. *A. roseomarginata* could be found only at the beginning of the rainy season, but had during that time span a high abundance. It was most abundant in the sun during its whole occurrence. *A. quinquefasciata* did, in contrast to the data in chap.1.1 where the microhabitat was categorized in seven classes, show no change in use during the season. Only between November and December there was a switch between light shade and shade. *A. confinis* did not switch microsites. *Ch. opposita* was exclusively found at the end of the rainy season in November and December. When evaluating each month separately, sample sizes become smaller. Thus data should be interpreted with caution.

5.3.1.3. Plant quality in sun and shade microhabitats

Quality of plants in the field

The microhabitat is composed of different factors which represent together the spatial niche of a beetle species. One of these factors is host plant quality. I analyzed host plants from the field as well as plants cultivated for the field experiments.

Sun and shade plants from the field were harvested as whole plants in typical sun and shade microhabitats at one site. Leaves were classified according to age in three categories (young, mature and senescent leaves) and analyzed. Young and mature leaves of sun plants showed a significantly lower nitrogen and water content compared to shade plants (Tab. 5.3). All other plant parameters measured did not differ significantly between sun and shade plants.

Quality of cultivated plants

The plants for the shading and for the box experiment were cultivated in full sun or under artificial shading (similar to shrub shade). Like in the field plants, the leaf-N was significantly lower in sun plants than in shade plants (Tab. 5.4). The leaf water content in cultivated sun plants was even only half of that found in shade plants. The carbon content, in contrast, was elevated in sun plants. Among the morphometric parameters, stem length and leaf dry weight differed significantly. The total leaf dry weight was higher in sun plants whereas the stem length in the shade was 7 times longer as in the sun.

Tab. 5.3: Parameters of sun and shade plants in the field (*Merremia hederacea*; harvest 6/15/95). t-test; *Mann-Whitney-U-test;

	Leaf age	sun plants	shade plants		
		x ± SE	x ± SE	n	p
N-content [mg/g DW]	young	22,93 ± 1,38	34,31 ± 2,01	10	0,001
	mature	19,65 ± 1,48	29,42 ± 1,86	10	0,001
	senesc.	15,34 ± 1,34	19,53 ± 1,52	5/9	n.s.
C-content [mg/g DW]	young	424,18 ± 4,60	425,32 ± 2,82	10	n.s.
	mature	413,53 ± 4,91	420,21 ± 3,07	10	n.s.
	senesc.	370,27 ± 16,19	361,83 ± 9,25	5/9	n.s.
H_2O-content [g/g DW]	young	3,44 ± 0,22	4,60 ± 0,28	15	0,01
	mature	3,34 ± 0,23	4,37 ± 0,23	15	0,01
	senesc.	3,41 ± 0,34	3,38 ± 0,18	11/13	n.s.
	total	3,39 ± 0,21	4,33 ± 0,21	15	0,01
Stem length [m]		4,61 ± 0,65	4,95 ± 0,86	15	n.s.
Leaf number/plant	young	61,60 ± 12,29	41,53 ± 7,15	15	n.s.*
	mature	45,80 ± 8,23	33,53 ± 6,09	15	n.s.*
	senesc.	7,33 ± 1,92	8,47 ± 1,75	15	n.s.*
	total	114,73 ± 19,92	83,53 ± 13,16	15	n.s.*
Leaf fresh weight per plant [g]	young	2,25 ± 0,40	2,14 ± 0,47	15	n.s.
	mature	2,92 ± 0,59	3,32 ± 0,77	15	n.s.
	senesc.	0,33 ± 0,08	0,51 ± 0,13	15	n.s.
	total	5,49 ± 0,96	5,97 ± 1,18	15	n.s.
leaf dry weight per plant [g]	young	0,51 ± 0,09	0,36 ± 0,06	15	n.s.
	mature	0,64 ± 0,11	0,61 ± 0,13	15	n.s.
	senesc.	0,08 ± 0,02	0,11 ± 0,03	15	n.s.
	total	1,22 ± 0,19	1,08 ± 0,18	15	n.s.

Tab. 5.4: Parameters of plants cultivated for the shading experiment (*Merremia hederacea*).

	sun plants	**shade plants**	
	x ± SE	**x ± SE**	**p**
Leaf-N content [mg/g DW]	22,35 ± 0,34	29,49 ± 0,80	0,001
Leaf-C content [mg/g DW]	408,13 ± 3,28	359,28 ± 4,05	0,001
Leaf-H_2O content [g/g DW]	2,5 ± 0,09	5,4 ± 0,20	0,001
Stem length [cm]	6,1 ± 0,46	42,8 ± 4,42	0,001
Leaf number per plant	8,9 ± 0,38	10,5 ± 0,92	n.s.*
Leaf fresh weight per plant [g]	0,28 ± 0,019	0,31 ± 0,034	n.s.
Leaf dry weight per plant [g]	0,08 ± 0,005	0,05 ± 0,005	0,001

t-test; *Mann-Whitney-U-test; n=10;

Quality of different leaf age classes

The use of different leaf age classes could be another possibility for the beetle species to separate spatially within the same habitat. In sun plants the leaf age classes differed significantly in leaf-N content and leaf-C content but not in leaf water content (Tab. 5.5). In shade plants additionally to the N- and C-content the leaf water content differed highly significantly between the age classes. Young leaves showed in all parameters measured the highest values and therefore the highest leaf quality.

Tab.5.5: Comparison of leaf chemistry of different leaf age classes of sun and shade plants in the field (*Merremia hederacea*; harvested 6/15/95)

sun plants:

	Young	mature	senescent	n	p
	x ± SE	x ± SE	x ± SE		
N-content [mg/g DW]	22,93 ± 1,38	19,65 ± 1,48	15,34 ± 1,34	10/10/5	0,05
C-content [mg/g DW]	424,18 ± 4,60	413,53 ± 4,91	370,27 ± 16,19	10/10/5	0,05
H_2O-content [g/g DW]	3,44 ± 0,22	3,34 ± 0,23	3,41 ± 0,34	15/15 /11	n.s.

shade plants:

	Young	mature	senescent	n	p
	x ± SE	x ± SE	x ± SE		
N-content [mg/g DW]	34,31 ± 2,01	29,42 ± 1,86	19,53 ± 1,52	10/10/5	0,001
C-content [mg/g DW]	425,32 ± 2,82	420,21 ± 3,07	361,83 ± 9,25	10/10/9	0,001
H_2O-content [g/g DW]	4,60 ± 0,28	4,37 ± 0,23	3,38 ± 0,18	15/15 /13	0,001

Friedman two-way ANOVA;

5.3.1.4. Microclimate in sun and shade habitats

Microclimate is another factor which should differ in different light climates (microhabitats). Fig. 5.5 shows a sequence of seven 5-day temperature measurements on the underside of sun- and shade-leaves during the rainy season 1995. Whereas at night there was almost no difference between the two microhabitats, during daytime temperature differences between the sun and the shade leaf of one leaf pair were as high as 10° (at noon), although the measurement was taken on the lower side of the (fresh) leaves. All measurements in this figure were taken on one site (Badeplatz).

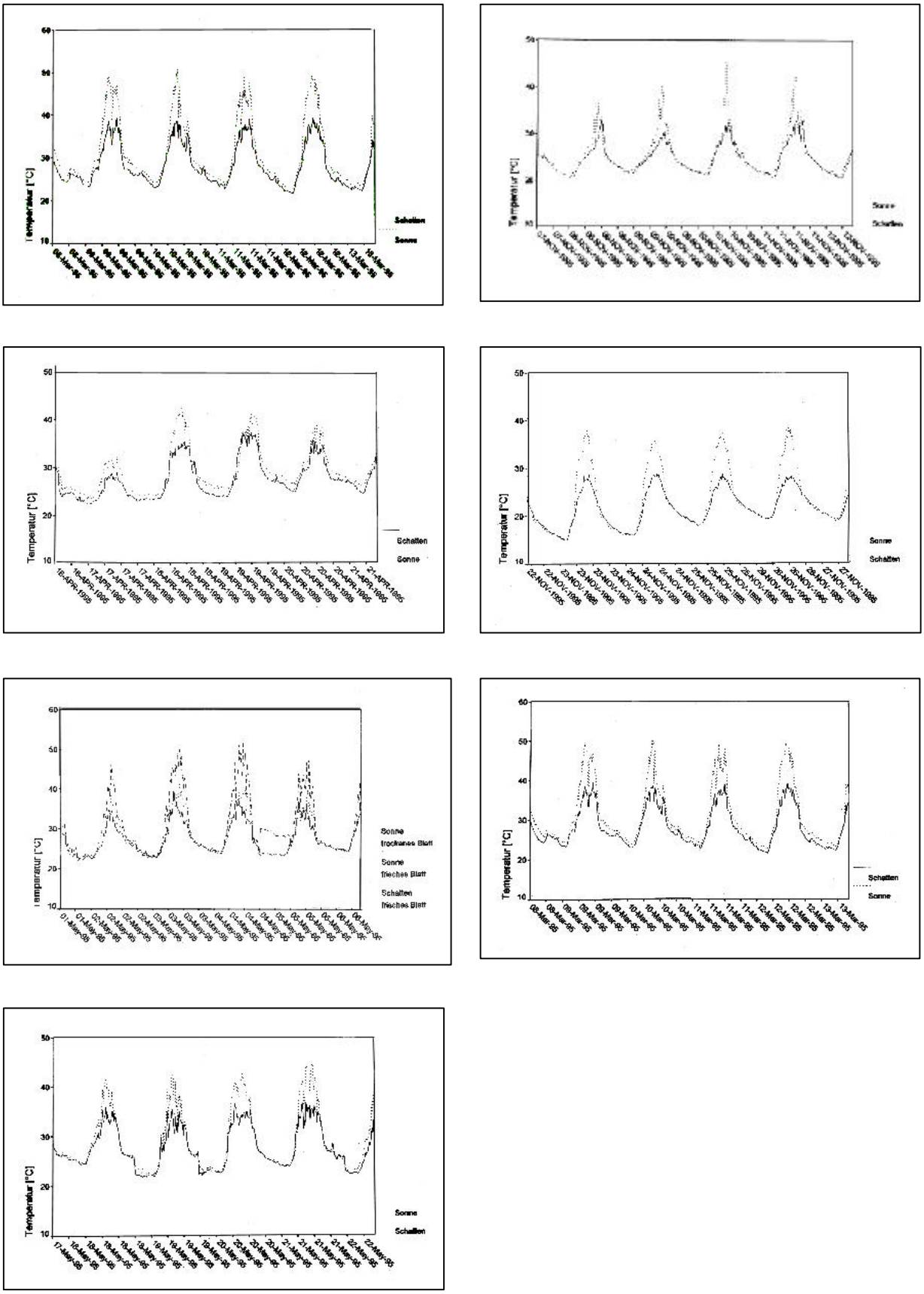

Fig. 5.5: 5-day intervals of measurement of temperature in sun (dotted line) and shade microhabitats (solid line) at different times of the year in 1995. The lower side of a fresh leaf was measured (site "Badeplatz").

Mean maximum temperatures on the lower side of sun leaves were 40-49°C (Mar.-June) and 38-41°C (Nov./Dec.), under shade leaves 36-39°C (Mar.-June) and 28-34°C (Nov./Dec.). In one of the graphs in fig. 5.5, (1^{st}-6^{th} of May), an additional measurement was taken on the lower side of a dry leaf in the sun. The temperature on the lower side of a dry leaf was much higher than under the fresh leaf in the sun (up to 50°C in the sun!). The lower temperatures under the fresh leaf were probably due to leaf transpiration.

Fig. 5.6 summarizes the temperature-data as means for each 5-day interval in the sun and in the shade (measurements taken on the lower side of leaves). The temperature in the sun was higher than in the shade in every month. There was a profound decrease in temperature during the rainy season from June to Nov./Dec. Means of sun-shade pairs (5-day intervals) from three sites were tested in a Wilcoxon matched pairs signed ranks test. There was a significant difference in the temperature of sun and shade microhabitats (p=0,0024) for all three sites and for all intervals measured in 1995 (n=13). Humidity was not recorded due to methodical difficulties.

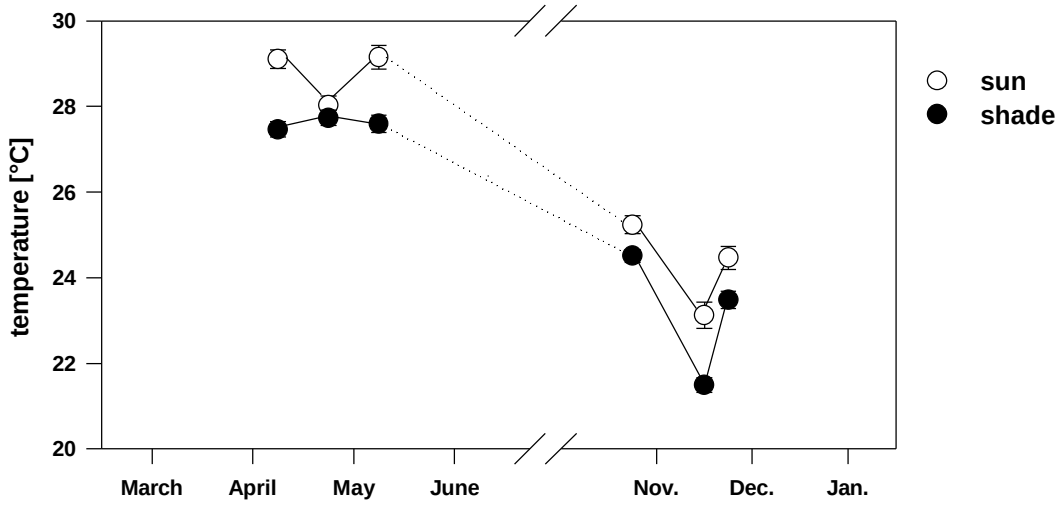

Fig. 5.6: Means of temperature intervals in sun and shade microhabitats during the year. Means were calculated for each sun-shade pair on the site ”Badeplatz”.

5.3.1.5. Effect and interaction of microclimate and plant quality on larval development

So far the distribution of the beetle species in different microhabitats in the field and two factors defining this environment (food quality and temperature) have been discussed. Field experiments now should reveal how the species perform in microhabitats where they naturally do not (or only rarely) occur, under which conditions (sun or shade) they perform better and what effects the factors microclimate and plant quality, alone or combined, have on larval development. If it would have turned out that a species did not live in optimal but in suboptimal microhabitats in the field, this could have been evidence for the occurrence of interspecific competition leading to niche separation within the beetle community.

The microclimate and plant quality differed significantly between sun- and shade microhabitats (see 1.3 and 1.4). To evaluate the separate and combined impact of these two factors on larval performance I tested larval development under three different experimental designs in the field. (1) In the ”shading experiment” larvae fed on sun and shade plants, cultivated in pots and without or with artificial shading respectively (factors microclimate and plant quality). (2) In the ”box experiment” larvae were fed with sun and shade plants from the shading experiment, but were kept in boxes in an identical environment (factor plant quality). (3) In the ”exposure experiment”, finally, larvae were exposed on potted plants of the same quality in natural sun and shade microhabitats (factor microclimate).

(1) Shading experiment: The period of larval development was significantly shorter in the shade for all three beetle species investigated and pupal weight was significantly higher for *A. quinquefasciata* and *A. confinis* (Fig. 5.7 and 5.8). (2) Box experiment: Duration of development of the larvae was again significantly shorter on shade plants; pupal weight was significantly higher under the shade than under the sun treatment for *A. roseomarginata* (Fig. 5.7 and 5.8). (3) Exposure experiment: For *A. quinquefasciata* duration of development was again significantly shorter in the shade than in the sun (Fig. 5.9). *A. roseomarginata*-larvae, however, showed an inverse trend and therefore a significantly longer developmental period in the shade than in the sun in 1995 and a trend for a shorter developmental time in the sun in 1997. Combined probabilities (Sokal & Rholf 1995) of both years were significant for both species between sun and shade treatments *(A. roseomarginata*: X^2=11,84985, p<0,05; *A. quinquefasciata*: X^2=27,63102, p<0,001).

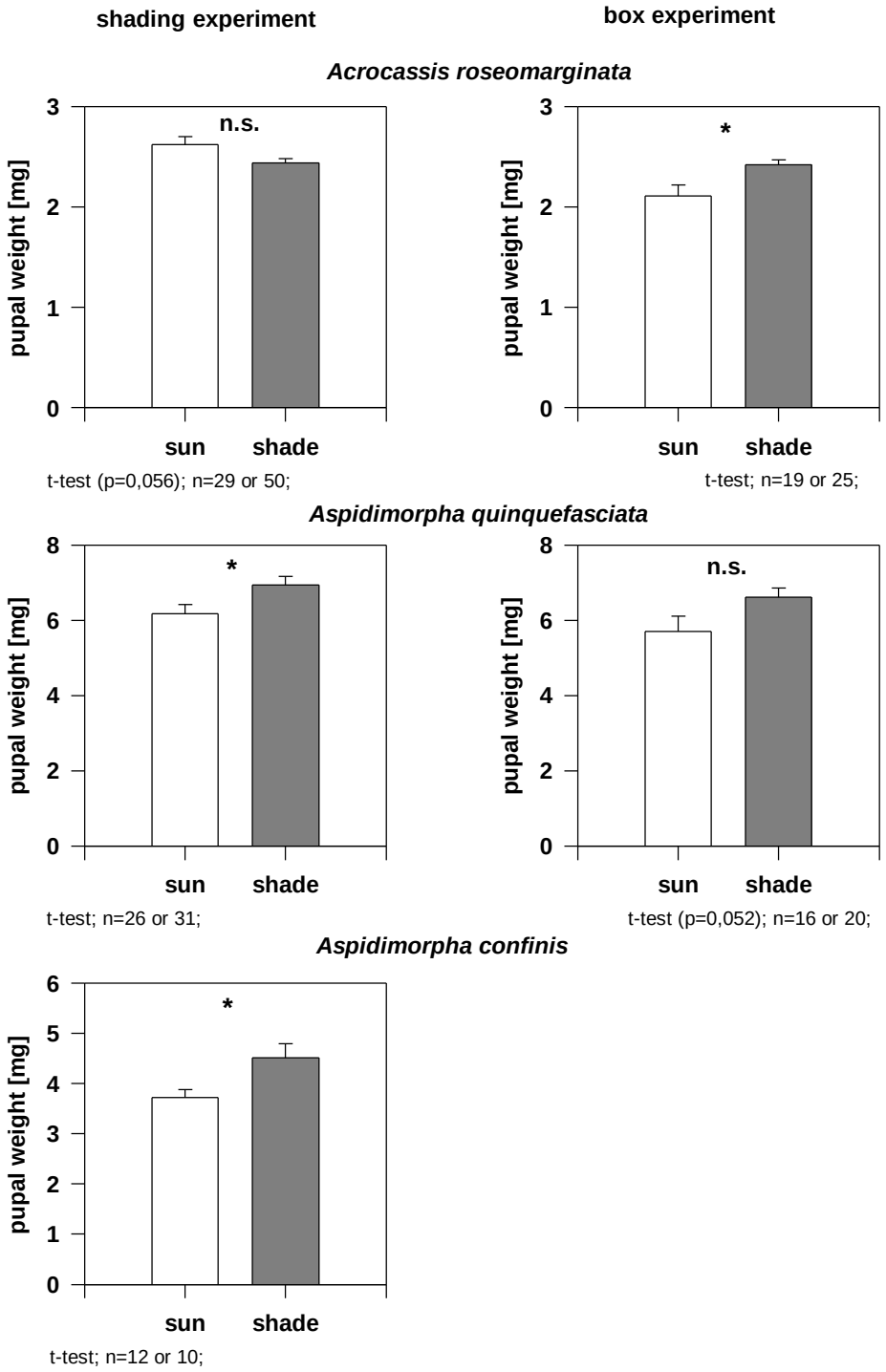

Fig. 5.7: Pupal weight (mg dry weight) of pupae of three beetle species in two experimental settings: (1) fed with sun and shade plants in the respective microclimate (shading experiment) and (2) fed with sun and shade plants under the same microclimatic conditions (box experiment). White columns: larvae which had fed on sun plants; filled: larvae on shade plants; t-test, * $p<0,05$;

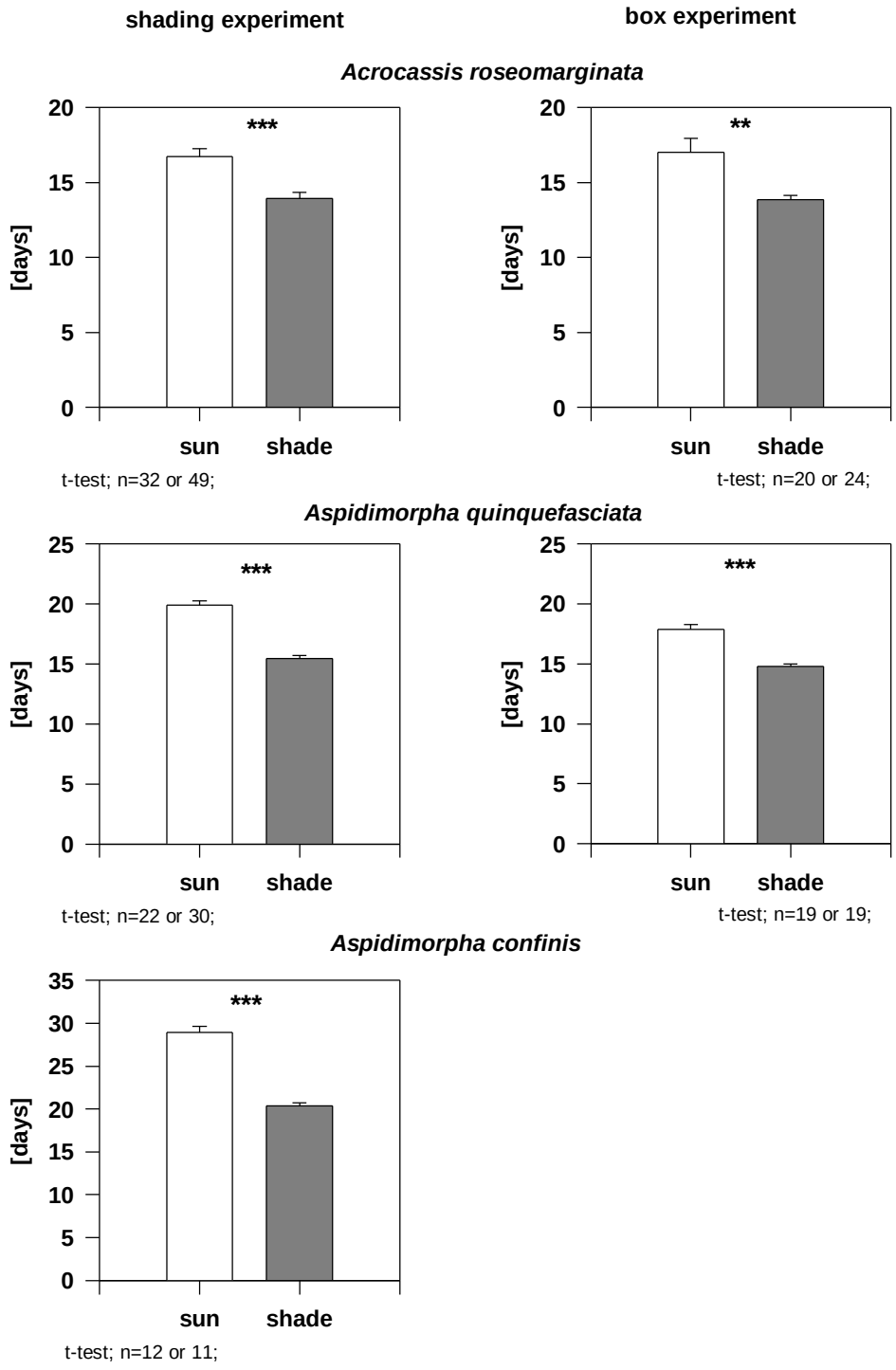

Fig. 5.8: Developmental time (days) of larvae of three beetle species from hatching to pupation in two experimental settings: (1) fed with sun and shade plants in the respective microclimate (shading experiment) and (2) fed with sun and shade plants under the same microclimatic conditions (box experiment). White columns: larvae fed on sun plants; filled: larvae on shade plants; t-test, *** p<0,001; ** p<0,01;

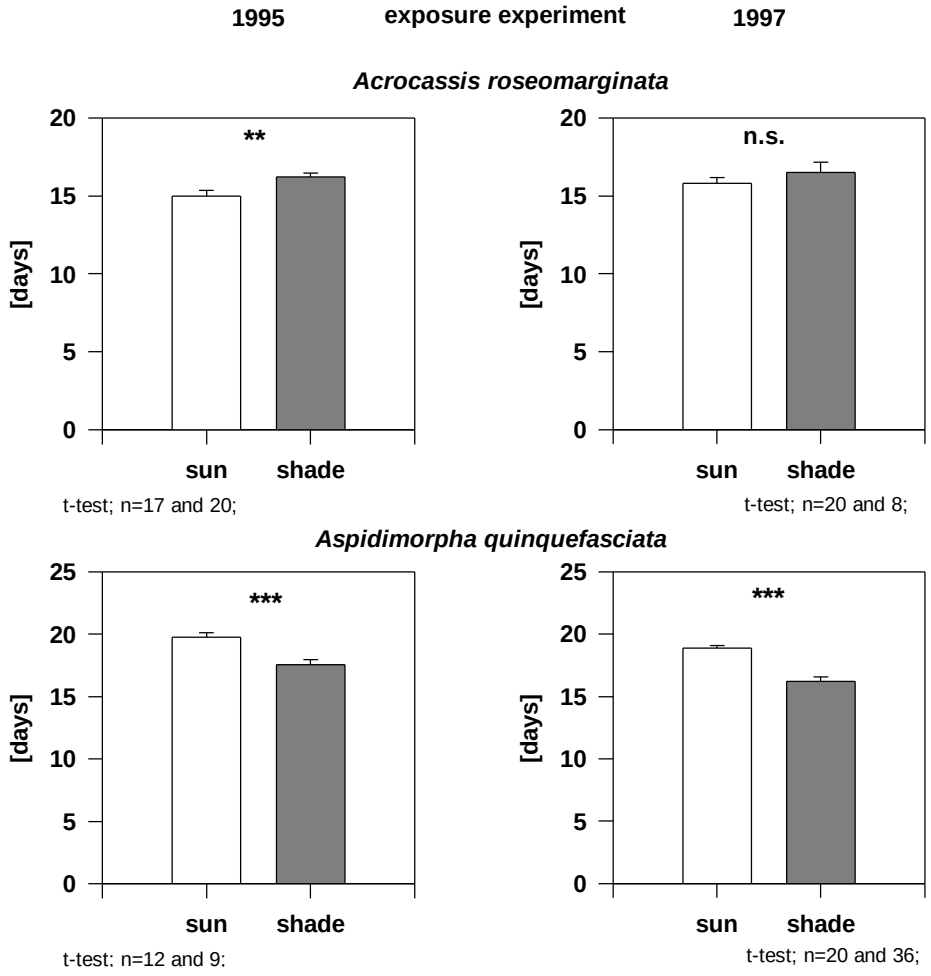

Fig. 5.9: Developmental time (days) of larvae of two beetle species exposed in sun and shade microhabitats (exposure experiment) in 1995 and in 1997. White columns: larvae fed on sun plants; filled: larvae on shade plants; t-test, *** $p<0,001$; ** $p<0,01$; * $p<0,05$;

In summary, in the first two experiments where either plant quality and microclimate combined (shading experiment) or plant quality alone (box experiment) was tested, the larvae of all three beetle species showed a significantly faster development on shade plants than on sun plants (Fig. 5.8). In the third experimental setting (exposure experiment), where the influence of the microclimate alone was tested, only *A. quinquefasciata* developed again significantly faster in the shade treatment than in the sun in both years (Fig. 5.9), *A. roseomarginata*, however, showed the reverse trend. *A. quinquefasciata* seemed to be better adapted to the microclimate under shady conditions, *A. roseomarginata* under sunny conditions.

5.3.2. Within plant distribution: Preference of leaf sides of larvae depending on degree of shade and time of the day

The hypothesis was tested that larvae chose actively an appropriate microclimate by moving around the leaf and that species differ in their requirements. During abundance estimates in the field the larvae of three beetle species had shown different preferences of leaf side in their natural microhabitats. Of the species which prefered shade microhabitats, *A. quinquefasciata* stayed on the lower leaf side and *A. confinis* on the upper leaf side. *A. roseomarginata* which inhabited mostly sunny microsites, was found on both sides of the leaves (Obermaier, unpubl. data).

Fig. 5.10 shows the leaf side preferences of larvae of three beetle species depending on exposure to sun (treatment groups: sun and shade) and the time of the day. In *A. roseomarginata* there was a highly significant difference in the preferred leaf side at all times of the day between larvae on plants which were placed in the sun vs. plants under artificial shading ($p<0,001$). In the sun nearly all larvae sat on the lower leaf side. In the shade half of the larvae sat on the upper and the other half on the lower leaf side. In the morning at 9 a.m. in the sun some more larvae sat on the upper leaf side than later during the day.

For *A. quinquefasciata* larvae at any time of the day no significant difference existed in the preferred leaf side between the sun and the shade. Almost all larvae sat on the lower leaf side.

In *A. confinis* there was again a significant difference between sun and shade in the choice of the leaf side for all times of the day measured ($p<0,01$). For larvae of this species an obvious pattern in the course of the day existed. In the morning (9.00 a.m.) and in the evening (6.00 p.m.) part of the larvae in the sun could be found on the upper leaf side. At around noon (12.00 a.m. and 3.00 p.m.), however, (almost) all larvae of plants in the sun stayed on the lower leaf side. The larvae on the plants in the shade, in contrast, stayed on the upper leaf side during the whole day as the larvae do in their natural habitat.

The larvae of all species searched actively for a suitable place to stay. Although all species preferred the lower leaf side on the plants in the sun during noon hours, they differed in the way they used the leaf sides during less extreme conditions. This pattern seemed to correspond to that found in the natural microhabitat.

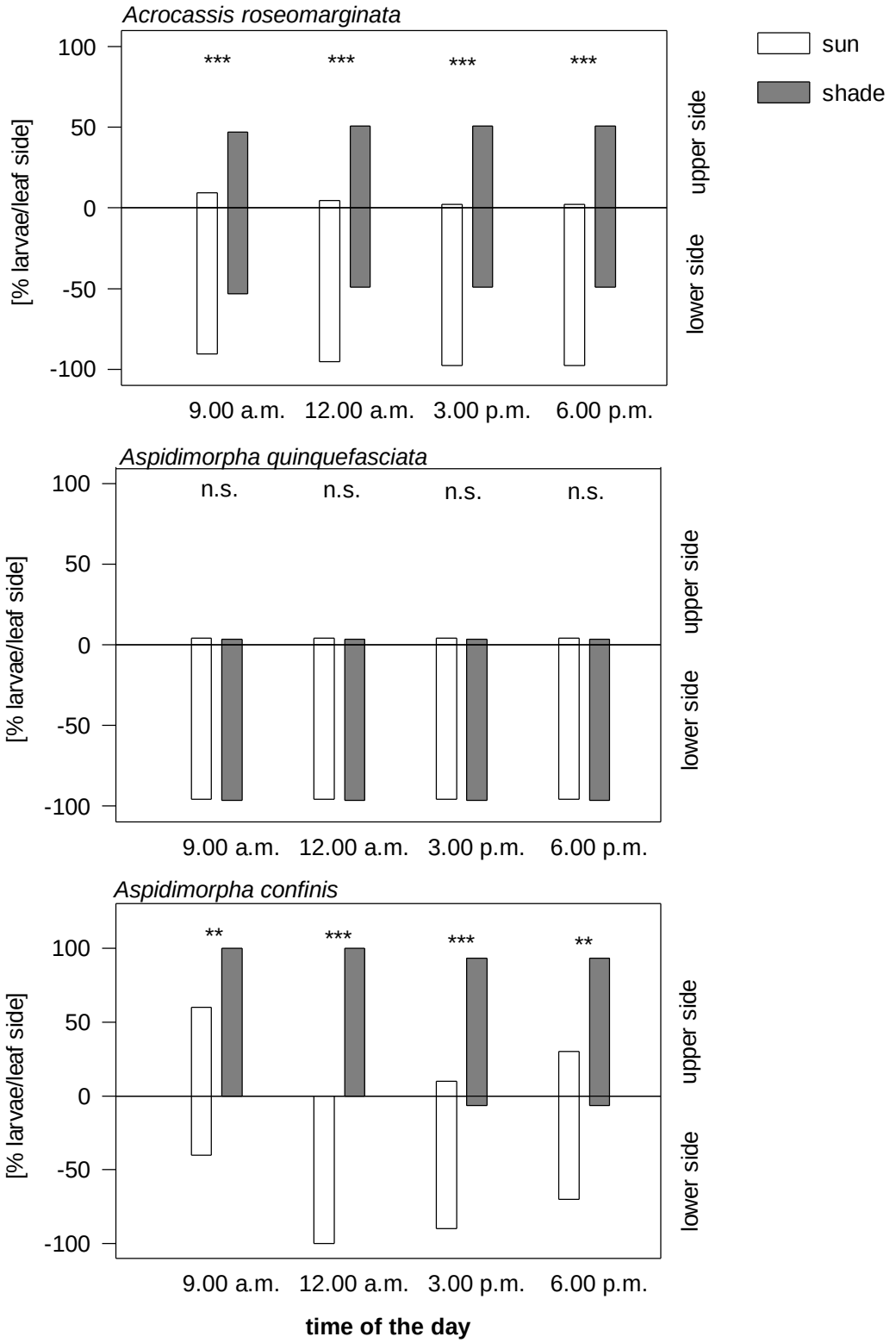

Fig. 5.10: Preference of the leaf side of larvae in the sun and in the shade at different times of the day. Larvae of *A. roseomarginata*, *A. quinquefasciata* and *A. confinis* were examined. Sun was tested against shade (Chi^2-test, ** $p<0,01$, ***$p<0,001$).

Along with the observations of the larvae, temperatures on upper and lower leaf sides were measured with an infrared thermometer at different times of the day (12 a.m., 3 p.m., 6 p.m.)(Fig. 5.11). Tested were the upper leaf sides in sun vs. shade (circles) and lower leaf sides in the sun vs. shade (squares). At 12.00 a.m. and 3.00 p.m. there was a highly significant difference between sun and shade for the upper as well as the lower side of the leaf (t-test, p<0,001, n=10). At 6.00 p.m. there was no longer a significant difference for either leaf side. In general after 12.00 a.m. temperatures declined along the course of the day.

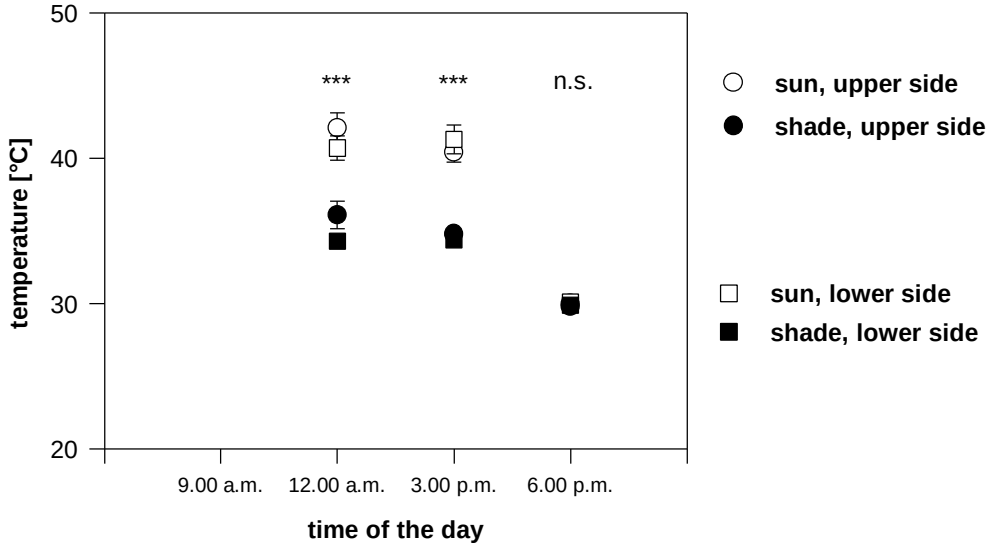

Fig. 5.11: Temperature of upper and lower leaf side during the course of the day. Sun-leaves were tested against shade-leaves (t-test, ***p<0,001).

5.4. Discussion

5.4.1. Within habitat distribution

5.4.1.1. Beetle distribution and seasonal shift, niche breadth and overlap in microhabitat use

There were distinct differences in the microhabitat use between the five beetle species, living at the river side. *A. roseomarginata* differed significantly from all other species as it was most abundant in open and sunny microhabitats. *A. quinquefasciata* differed significantly from *A. submutata* and had its abundance maximum in light shade; *A. submutata* was most abundant in shade habitats. Due to low abundances, however, significance of differences between the four beetle species, living in the shade, could not be shown or were not as strong as with *A.*

roseomarginata. In the following I shall refer to species, which preferred microhabitats in the light gradient between shrub-sun and tree-shade, as “shade-species”. The results of the χ^2-tests (see above) were confirmed by the calculated values of niche overlap. *A. confinis*, *A. submutata* and *Ch. opposita* had the highest indices of overlap (indices >1) with each other, with *A. quinquefasciata* they had still an index of similarity between 0.9 and 0.8. With *A. roseomarginata*, however, the index of similarity was much lower and fluctuated between 0,1 and 0,5. The two species living exclusively in the savanna, *A. indistincta* and *A. nigromaculata*, also had a high overlap (>1) with each other. I did not calculate the overlap with *A. roseomarginata* because of missing data of microhabitat use in the savanna in May/June.

Niche breadth shows how far the species are restricted to certain microhabitats. *A. roseomarginata* had the largest value (Levins B=4,26) of the beetle community, using virtually all microhabitats where the host plant was available. This species was also the most abundant at the time of its occurrence in both habitat types (river side and savanna) (Obermaier, unpubl. data, chap. 3). Among the beetle community investigated, *A. roseomarginata* can be regarded as a generalist in terms of habitat requirements (although it had a preference for sunny microhabitats).

A seasonal shift in the availability of the host plant in different microhabitats, due to growth and climbing of the seedlings into the canopy over the course of the season, could cause a shift in microhabitat use of the beetle species. The host plant at the river side, *Merremia hederacea*, was proportionally most abundant in the sun, at the beginning of the rainy season (March-May). Until June proportions had changed and in June and December abundance was equally high in sun, sun/shade and shade. However, no beetle species showed an obvious shift between the 3 different microhabitat categories (fig. 5.4). There was a trend that the ”sun-species”, *A. roseomarginata*, appeared early in the year, when there was the proportionately largest food supply in the sun, and the four ”shade-species” at the river side later, when host plant biomass in the shade had grown.

Although, the distribution of *A. quinquefasciata* did not show a significant seasonal shift between the 3 microhabitat categories, when observed monthly (Fig. 5.4), it differed significantly when all 7 microhabitat classes were used for the comparison and several months were combined (Fig. 5.2). Then the distributions of May/June compared with Nov./Dec. 1995 differed significantly from each other (Fig. 5.2). In June this species had its maximum abundance in the shade, in Nov./Dec its maximum abundance was in light shade, a change in

distribution which was opposite to the trend in resource availability. The proportions of *A. quinquefasciata* in both figures were consistent in June, but not in Nov./Dec. Different sample sizes in Nov. (n= 68) and Dec. (n=7) suggested different distributions when both months are regarded separately. If distributions were combined (Fig. 5.2), they were, however, similar to the distribution in Nov. in Fig. 4 (large sample size!). A niche shift of *A. quinquefasciata* during the season therefore seems realistic, in spite of the discrepancy between the distributions in Fig. 5.2 and 5.4.

The observed patterns of microhabitat use of the tortoise beetle community in the field rises some new questions: 1. Which factor is responsible for a different microhabitat use of *A. roseomarginata* compared to the other four species on *M. hederacea* at the river side? In which microhabitat along the light gradient (sun, shade) do the beetle species perform best? 2. How do the four "shade-species" at the river side coexist in spite of similar niches? The rest of the chapter will mainly address the first question. In the subchapter "within plant distribution" one aspect of the second question will be discussed.

5.4.1.2. Plant quality and microclimate

Beetle species differed in their distribution over sun and shade microhabitats. Similar as Brown et al. (1997) I used the factors host plant quality, microclimate, interspecific competition and predation/parasitism to define the term "microhabitat" and tested them as potential causes for a spatial stratification of the beetle community along the horizontal light gradient. In this chapter, two of these factors, plant quality and microclimate, were examined further.

Leaves of *Merremia hederacea*-plants in the shade had a significantly higher nitrogen and water content per mg dry weight than leaves of sun plants. That was the case in plants, harvested in the field, as well as in plants, cultivated for experiments. These results correspond to two studies on the influence of shade on herbivorous insects (Collinge & Louda 1988, Rossi & Stiling 1998) and plant ecological studies (Heilmeier 1988, Steinlein 1991), where also higher levels of total nitrogen in shade plants were found.

A general opinion in plant ecology (Chapin III et al 1987), however, supported by numerous studies, predicts a low concentration of nitrogen in leaves of shade adapted plants compared to sun adapted. Additionally, studies of nitrogen partitioning within single plants have shown that it was more profitable for the plant to have a higher Rubisco concentration in the upper sun leaves than in the lower shade leaves (Chapin III et al 1987). This was also the

result of a study on *Ipomoea tricolor* Cav., a close relative to the host plants in this study. The most shaded leaves in the lowest leaf position, had the lowest nitrogen concentrations. When the gradient of shading was inverted, an inverted gradient of leaf nitrogen was formed, with young leaves having the least nitrogen (Hikosaka et al. 1994, Hikosaka 1996). One reason for the contradicting results might be a different unit of measurement of leaf nitrogen in the different studies. Anten and Werger (1996) found average N contents per unit leaf area to be higher in sun exposed plants in the canopy. When expressed on a weight basis, however, average N contents were higher in the subdominant (shade) plants. Hikosaka et al. (1994) and Chapin III (1987) measured nitrogen per unit leaf area, in Rossi and Stiling (1998) and in this study it was measured as mg N per g dry weight.

Nitrogen is quite often the limiting nutrient in insect nutrition and important for growth of larvae and fecundity of adults (McNeill & Southwood 1978, Slansky & Rodriguez 1987, White 1993, Obermaier & Zwölfer 1999). However, also a low leaf water content can reduce larval growth (Scriber 1977).

Sun and shade plants differed not only in their chemical composition, but also in their visual aspect. Vines have some of the most extreme heteroblastic changes in the plant kingdom (Lee & Richards 1991). For example *Ipomoea caerulea*, which climbs by twining into the canopy, exhibited a transition of leaf morphology from simply cordate to deeply lobed, due to different light intensities. Plants grown in 72-78% shade did not longer produce mature leaves (Lee & Richards 1991). Light climate influenced not only leaf morphology (leaf form) but also leaf anatomy of shade leaves. Leaves, in the lower part of the canopy or generally in the shade were thinner, with lower specific weight and fewer cell layers, which in general is a trait of young leaves (Lee & Richards 1991). Shade leaves should therefore be softer and easier to chew than sun leaves. Effects of the different leaf anatomy of sun and shade leaves on the feeding of a specialist leafminer was investigated by Kimmerer and Potter (1987).

GC-MS-analyses of leaves of *M. hederacea* and *Ipomoea sp*. showed only very small amounts of alkaloids in the leaves (Obermaier and Proksch, unpubl. data). Therefore, I do not expect secondary chemicals to have altered plant quality in sun and shade, as it was the case with plants in other plant families (Dudt & Shure 1994).

Microclimate was the second factor which was examined in the different microhabitats. Temperature was measured directly under leaves of sun- and of shade-plants of *M. hederacea* in five-day intervals, several times during the season. On the lower side of shade leaves,

temperature was significantly cooler than on the lower side of sun leaves. In one five-day interval temperature additionally was measured on the lower side of a dry leaf in the sun. Temperature was cooler on the lower side of the fresh leaf than on the lower side of the dry leaf in the sun. There was a profound decrease in temperature over the growing season of the vines, from March till December.

Because of their small size and proportionally large surface area, insects are especially dependent on climatic conditions (Willmer 1981). Microclimatic analyses of leaves have shown that higher humidities are expected close to the transpiring surface and particularly on the lower side; in some cases these surfaces were also measurably cooler (see review in Willmer 1981), as it was also indicated by my measurements under fresh and dry leaves. Whereas beetle larvae would have overheated and desiccated very quickly, on the lower side of dry leaves in extreme microhabitats like rocks in the open sun, they were obviously able to survive under fresh leaves of their host plant at the same place. The critical upper temperature for survival of insects varies widely, but is commonly in the range of 40-45°C. Some insects, however can survive up to 50-55°C (Willmer 1981). The mean maximal temperatures on the lower side of fresh (!) leaves in the sun at the river side ranged between 38°C and 49°C. Because of these very high maximum temperatures (and a probably low humidity) under leaves in the open sun at noon, which could be above lethal limits of the larvae, I expected leaves in the shade to offer a more suitable microclimate for larval development than leaves in the sun (see also “larval development at different temperatures”, chap. 6).

Vine-plants growing in mosaic like shaded habitats as well as vines growing vertically high in the canopy, offer a diverse spectrum of microhabitats to herbivores. Leaves represent unique resource units, with specific nitrogen and water contents, as well as specific microclimates, both related to their specific position in the canopy. A single habitat can, therefore, harbor a number of diverse resource units within a single plant species. Among those, the beetle individuals of the different species should choose their optimal resource for feeding and oviposition. In the beetle community investigated in this study I found interspecific differences in the use of sun and shade plants, but not between leaves at different heights above ground or between different leaf ages (chap. 4).

5.4.1.3. Interactive effects of plant quality and microclimate on larval development under experimental conditions

Both microhabitat parameters, plant quality and microclimate had a significant impact on larval performance. Only the factor microclimate, however, explained the distribution of *A. roseomarginata* and *A. quinquefasciata* in different microhabitats in the field.

The influence of microclimate on the local distribution of insect species was examined and confirmed in several field studies (mainly in temperate regions) (Bach 1993, Willmer et al 1996, Alonso 1997). Even more interesting, however, for a comparison here, are studies which tested several factors, possibly responsible for the spatial distribution of insect species.

In three recent studies on within-plant distribution of phytophagous insects in a natural vertical light gradient, the factor plant quality could not explain the vertical stratification of the respective insect species (Rowe II & Potter 1996, Willmer et al. 1996, Brown et al. 1997). In one of these studies, microclimatic constraints, instead of plant chemistry or food quality, influenced the distribution of raspberry beetles on its host plant *Rubus idaeus* (Willmer et al. 1996). The vertical stratification of *Cameraria*, a leaf-mining moth, in contrast, could neither be explained by plant quality nor microclimate (Brown et al 1997).

Also, a lot of the studies which investigated the distribution of herbivore species along a horizontal light gradient were not consistent with the results of my study or showed no effect of the light environment at all. A noctuid moth preferred small, shaded host plant patches instead of large, sun-exposed ones for oviposition, but neither mortality, larval growth rate nor pupal size differed for different exposure to the sun (Förare & Engqvist 1996). Oviposition preferences were interpreted as „insurance against bad weather“. Also no differences in larval growth rates of three butterfly species could be found between a sun and a shade habitat (Rausher 1979), egg laying preferences of the adults, however, differed. The population of a herbivorous mite was significantly lower on stinging nettles located near a hedge than in the open field, despite their higher nitrogen content (Sommaggio et al. 1995), probably because of predator density. There was no effect at all of light supply on the number of ovipunctures or surviving larvae of a gallmaking herbivore on *Solidago* (Horner & Abrahamson 1992). In a study on the abundance of leaf miners on artificially shaded Emory oak, two species preferred the shade trees and two other species had higher densities in the sun (Bultman & Faeth 1988). Bittercress was even significantly more infested by a leaf-mining fly in the sun than in the shade. In my study, however, when artificial shade was offered, the shade plants were preferred over all other treatments. Like the host plants in this study, shade plants contained

significantly higher nitrogen concentrations (Collinge & Louda 1988). Plant phenology was found to be the responsible factor for a preference of sun over shade plants by a leafminer in the natural habitat, in spite of a lower plant quality (Collinge & Louda 1989). A very recent experimental study of Rossi and Stiling (1998) observed similar effects. All four clones of a sea daisy in South Florida developed more galls of a gall-making cecidomyiid, when the plants were placed in the shade at all four sites examined, compared to those in the sun. Shade and fertilization caused an additive increase in plant nitrogen content.

The interaction of food quality and microclimate (temperature) was investigated in a laboratory study on caterpillars. Whether food quality had an impact on relative growth rate depended on daytime temperature. At 20°C (cool weather) there was no impact, at 30°C larvae fed with young leaves grew significantly faster than larvae fed with mature leaves (Stamp & Bowers 1990).

The confusing body of literature on sun-shade systems has in common, that there is, in most cases, a significant effect of sun and shade on the distribution of herbivorous insects. The outcome for the single species, however, differed due to factors like plant quality, plant phenology, predation pressure or unknown causes. The combined and separate effects of two important factors, plant quality and microclimate, on larval development and their implication for the distribution of the phytophagous insects in the field have not been shown before. Plant quality of shade plants enhanced the development of all beetle species examined, which resulted in a shorter developmental time, probably because of a higher nitrogen and water content of shade plants. The response of the beetle species to microclimate differed and point to a physiological adaptation of *A. roseomarginata* to sunny and of *A. quinquefasciata* to shady conditions. This might explain the observed distributions of the beetle species in different microhabitats in the field.

The hypothesis that *A. roseomarginata* performed a niche shift from optimal microhabitats (shade) to suboptimal microhabitats (sun) due to interspecific competition could be rejected by the experiments: Both beetle species live in their microclimatically optimal microhabitat.

5.4.2. Within plant distribution: preference of leaf side

During abundance estimates in the field, a preference for a certain leaf side was observed for the different beetle species (Obermaier, pers. observation). A quantification of larvae of three beetle species on upper and lower leaf side on sun- and on shade-plants, at different times of the day, showed that all three beetle species stayed on the lower leaf side during the whole day, when exposed to full sun. Only *A. roseomarginata* was found in full sun in the field. In the shade, larvae of the beetle species differed in their preferences: *A. roseomarginata* were found on the upper as well as on the lower leaf side, *A. quinquefasciata* stayed, like in the sun, only on the lower leaf side and *A. confinis* stayed on the upper leaf side. Within limits, the beetle larvae could regulate their body temperature by moving actively around the leaf and therefore experienced different microclimates. The preferred leaf side for a certain microhabitat (sun, shade) and a certain time of the day was species specific. Two of the beetle species, which used the same microhabitat (shade) naturally, differed in their preference of the leaf side there (*A. quinquefasciata*: lower leaf side; *A. confinis*: upper leaf side) which can be interpreted as a difference in this niche dimension of the shade species community.

Different reasons might explain the different use of leaf sides by the beetle larvae. Most important are microclimate, predation/parasitism and competition. Although I did not test each factor per se, the distribution patterns observed, correspond quite well with the temperature data of upper and lower leaf sides of sun and shade plants during the course of the day. Of the three species only *A. confinis* showed a distinct diurnal pattern, with resting on the lower leaf side during the hot hours at noon and returning to the upper side of the leaf in the afternoon. It showed this behavior only on sun plants, a fact which supports the temperature hypothesis further.

Higher humidities close to the transpiring surface of a leaf and therefore cooler temperatures, especially on the lower leaf side, are also known from the literature (Willmer 1981). Tahvanaien (1972) studied flea beetles on collards which distributed themselves in accordance with microclimate. The preferred leaf side differed for the two species studied. The timing of activity of different species of flies on water-lily leaves, differed according to species and in relation to microclimatic conditions at the leaf surface (Willmer 1982). Finally the seasonal and diurnal distribution patterns of the raspberry beetle on their host plant differed according to microclimatic constraints (Willmer et al. 1996).