

Chap. 3: Time - Seasonal phenology of the beetle species and resource availability.

3.1. Introduction

Seasonal change in weather profoundly influences the growth and development of plants and by this also affect the growth and species composition of insects. Plant parts like leaves are not one uniform resource for herbivores, but a continual series of temporally overlapping resources, from new buds, through young leaves, to senescent leaves, shoots and stems (Strong et al. 1984). Plant quality, too, is variable both in time and space (Simpson & Simpson 1990). In temperate regions highest nutrient concentrations occur during early growth in spring and gradually decline during the course of the growing season until tissue senescence (Mattson 1980, Bernays & Chapman 1994). Many phytophagous insect species differ in their phenology due to their use of different parts of their host plant or due to specialization on tissues of different quality. A widely used strategy of phytophages to overcome the problem of decreasing nutrient nitrogen is a synchronization of the life cycle with high nutrient contents in the host plant (Slansky & Rodriguez 1987), e.g. “early season feeders” (Strong et al 1984) or “flush-feeders” (White 1993). There are, however, also disadvantages of early occurrence, such as a high unpredictability of food, low spring-temperatures (in temperate climate) or unfavorable microclimatic conditions on the small plants. Of three Chrysomelidae species examined for their host exploitation strategies, only one species exploited the spring nitrogen peak of its host plant (Obermaier & Zwölfer 1999). Of 59 European and North American chrysomelid species, the majority of the folivorous species had their main larval feeding period not before June (Heikertinger et al 1954). Besides abiotic and host plant conditions, also biotic interactions between coexisting species were found to be responsible for a temporal niche separation (Inbar & Wool 1995).

Although competition was generally considered to be of minor importance in herbivorous insect communities (Strong et al 1984), conclusive evidence from field experiments still is rare (Underwood 1986). In recent studies about phytophagous insects, competition has been documented for several cases (Belovsky 1986, Denno et al. 1995, Stewart 1996). The competitive exclusion principle (Gause`s principle) predicts that if two species compete for a limited common resource, one of the species should be displaced (Begon et al. 1986). Although it can be very difficult to demonstrate competition in the field, it is relatively easy to quantify available food resources and to test for a limitation of resources at different times in the year in the field.

This chapter examines the seasonal phenology of the seven Cassidinae species and their host plants in a tropical seasonal climate with a distinct dry and wet season. I asked the following questions: (1) Do the beetle species investigated differ in their phenology or is there a complete temporal overlap of the niches? (2) Does the availability and quality of the host plant species change over the season? (3) What kind of stochastic events do occur over the season and what is their possible effect on beetle populations? (4) How high is the leaf damage of the host plants and does food become a limited resource at any time of the year?

3.2. Methods

3.2.1. Abundance and species composition during the season

Abundance censuses were conducted during 6 months, March-June and November-December 1995 in a 14-day routine at each of 6 sites (3 savanna and 3 river side sites). Additionally, during May-Aug. 1994, Feb.-June and Nov.-Dec. 1995 and Jan.-Nov. 1996 presence of the beetle species was ascertained at 2 sites (1 savanna and 1 river side site). The time chosen for the investigations, coincided with the beginning and the end of the main vegetation period in the Comoé-Park. At the beginning of March, after the first rains, the host plants started to germinate or to sprout from rhizomes. The censuses at the end of December '95 were stopped when host plants had finally dried out or were burned by early savanna fires at the beginning of the dry season. Thus, in 1995, the time period of the abundance censuses represented the whole activity period of the beetle species in that year. In 1996 the observations were not done by myself, but by an African assistant. Records were therefore not as complete as in 1995 and the absence of a species does not necessarily imply its absence in the field at that time (it might have been rare). However, I could confirm records of the species found, because all individuals found during the censuses were preserved in alcohol in 1996.

At the river side sites I examined 1000 leaves and at the savanna sites 300 leaves per site for eggs, larvae, pupae and adults of the different species. At all sites I used "number of individuals/100 leaves" as unit of measurement. Unknown stages I took to the camp and reared them to adulthood, till I knew all stages by appearance. All developmental stages are included in the figures of total population (Varley et al 1980). For *A. quinquefasciata*, which oviposits in clutches, the lowest number of eggs per clutch (6 eggs) was used for calculation. There was always only one host plant species per site. For all river side sites this was *Merremia hederacea*, for two of the savanna sites *Ipomoea heterotricha* (Buschgruppen, G-K-Piste) and for the third savanna site (Felsplateau) it was *Ipomoea eriocarpa*. For the

estimates of abundance only data of the standardized abundance censuses were used, for the phenology of the beetle community all observations were used. (Observations in 1994 and 1996 were also made with the leaf-counting method. However, leaf number examined was not standardized in 1994).

3.2.2. *Leaf damage analysis*

Leaf damage was analyzed at the same time as the abundance censuses on the 6 research sites in 1995 were accomplished. I started with the analysis in the beginning of April. In the months April and May I took measurements every 14 days, later only once a month. The degree of leaf damage was recorded for all leaves for each of 10 plants per site (randomly chosen). It was calculated per plant and averaged over the 10 plants. Leaf damage was classified in 5 classes and estimated per view. Class 0=0% leaf damage; class 1=0-5% leaf damage; class 2=5-30% leaf damage; class 3=30-100% leaf damage; class 4=100% leaf damage. After the last censuses in Nov. or Dec. 1995 the savanna-sites were burned or the leaves of the fruiting plants at the river side-sites were wilting.

3.2.3. *Resource availability: Plant abundance*

Together with the abundance censuses transects were examined at the 6 study sites. They were used to determine the availability and quantity of the host plant at different times in the season. The river side sites were each walked in full length. In two of three savanna plots 2 parallel transects were established, which measured 130 steps each. The savanna site “Felsplateau” measured only 14 steps in diameter and only one transect was established.

At each step presence or absence of the host plant was controlled in an area about 1m to the right and to the left of the transect. Of the total number of steps and the number of steps with a host plant the percentage of steps with vines (%) for one site and one sample date was calculated. In March-May the recordings took place every 14 days, in June, Nov. and Dec. once a month.

3.2.4. *Resource availability: leaf age classes and leaf chemistry*

On one of the research sites (river side site “Lola”) I harvested 10 host plant individuals of *Merremia hederacea* every 14 days (in Nov./Dec. once a month) at the same time as the abundance censuses. In the beginning the plants were harvested completely, later a representative part of each plant was harvested. The leaves of each plant were divided into 3 leaf age classes (young, mature, senescent) based on their position at the branch, on size,

toughness and color. The fresh weight of the different age classes was determined. (Leaf fresh weight was recorded only from the beginning of May on.) Afterwards leaves were dried completely. In the laboratory in Germany leaves were dried again for 24h at 70°C and their dry weight was determined. Of leaf fresh weight and leaf dry weight leaf water content was calculated as the difference between fresh and dry weight and the average for the 10 plants per sampling date was calculated.

For the analysis of total carbon and total nitrogen content leaves of the plants of one sampling date were thoroughly mixed, ground in a mill (Fa. Retsch GmbH & Co.KG, Haan) and analyzed for total leaf nitrogen content in a CHN analyzer (Elementaranalysator CHN-O-Rapid, Fa. elementar, Hanau).

Because of the number and length of the side branches of the vine-plants it was not always possible to harvest whole plants(plants also climbed in the surrounding vegetation). Effort would have exceeded expected results. Therefore, instead, for each plant percent of young, mature and senescent leaves was calculated and averaged over the 10 plants per sampling date.

3.3. Results

3.3.1. Seasonality

In the Comoé Park there is a seasonal climate with a distinct rainy season and a dry season. Most host plant individuals, in the savanna as well as at the river side, were recruited from seedlings, which germinated after the first rains in March (first seedlings found 3/8/1995). With the ongoing rainy season, vines grew up high into trees, flowered in November and set seed in December. Leaves wilted in mid till end of December, depending on the site examined. Beetle species appeared early in March or April, some starting immediately to oviposit on the seedlings (*A. roseomarginata*), some waiting till plants were a little larger. All beetle species, except *A. roseomarginata*, could be found on their host plants till leaves have wilted in December. Only of the more abundant beetle species abundance could be recorded continuously over the season. Among those were *A. roseomarginata*, which had its maximum abundance in April after which numbers decreased continuously, *C. opposita*, which was found only in November/December in 1995 and finally *A. quinquefasciata*, *A. nigromaculata* and *A. indistincta* which were represented in rather constant numbers over the whole growing season. The abundance of two of the beetle species (*A. confinis* and *A. submutata*) could not be recorded continuously, because they were too rare.

3.3.2. Phenology of the beetle species

The main questions of this chapter are the seasonal activity periods of the beetle species investigated and their degree of overlap. Fig. 3.1 presents the phenology of the Cassidinae species on vines in three consecutive years (1994-1996). All observations of beetle species and their developmental stages during the marked periods of field work (black bars) are included in the table. In the Comoé-Park there was a rainy season from approximately March till October and a dry season from approximately November till February. The beginning and the end of each period, however, varied strongly from year to year and can only roughly be specified. Host plants were available only after the beginning of the first rains in March and persisted till December, when the last plants dried out after fruiting or were burned. Most beetle species could be found from April till December, which was best documented in 1995 but also was shown in 1996. Two species differed from that scheme: *A. roseomarginata* occurred already in March in 1995 and disappeared not later than August (in 1994: August; in 1995: June; in 1996: July). *C. opposita* was found only in November/December in 1995. In 1996, however, it was sampled also from March till July. Additionally, *A. quinquefasciata* was documented also already in March in 1996. There was substantial overlap in the seasonal phenology of all beetle species of the community.

1994	dry season			rainy season						dry season		
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>A. roseomarg.</i>					■	■	■	■	■			
<i>A. quinquefasc.</i>					■	■	■	■	■			
<i>A. submutata</i>						■	■					
<i>A. confinis</i>						■	■	■				
<i>C. opposita</i>												
<i>A. nigromaculata</i>							■	■				
<i>A. indistincta</i>												
Field work					■	■	■	■	■			

1995	dry season			rainy season						dry season		
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>A. roseomarg.</i>			■	■	■	■	■	■	■			
<i>A. quinquefasc.</i>				■	■	■	■	■	■	■	■	■
<i>A. submutata</i>				■	■	■	■	■	■	■	■	■
<i>A. confinis</i>				■	■	■	■	■	■	■	■	■
<i>C. opposita</i>											■	■
<i>A. nigromaculata</i>				■	■	■	■	■	■	■	■	■
<i>A. indistincta</i>				■	■	■	■	■	■	■	■	■
Field work		■	■	■	■	■	■	■	■		■	■

1996	dry season			rainy season						dry season		
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>A. roseomarg.</i>					■	■	■	■	■			
<i>A. quinquefasc.</i>			■	■	■	■	■	■	■	■	■	■
<i>A. submutata</i>						■	■					
<i>A. confinis</i>						■	■	■				
<i>C. opposita</i>			■	■	■	■	■	■	■	■	■	■
<i>A. nigromaculata</i>						■	■	■	■	■	■	■
<i>A. indistincta</i>					■	■	■	■	■			
Field work	■	■	■	■	■	■	■	■	■	■	■	■

■ Observed occurrence □ Supposed occurrence

Fig. 3.1: Seasonal phenology of the Cassidinae species on vines in the southern part of the Comoé-Park in three consecutive years: 1994, 1995 and 1996. Periods of field work during which observations took place are marked with black bars.

3.3.3. Species abundance and composition at different sites

The three river side sites (Fig. 3.2a) showed different species compositions. *A. roseomarginata* was the most abundant species on all three sites (host plant: *Merremia hederacea*). It occurred, however, only in the first half of the rainy period from March till June (in 1995). From the second half of April on the total population curve of this species already declined. In 1995, *C. opposita* was found only at the end of the rainy period in Nov./Dec., however, quite regularly on two sites. Additionally, *A. quinquefasciata* was quite abundant on three sites from April till December. The other three species were found only rarely during the abundance censuses.

Among the savanna sites (host plant: *Ipomoea spp.*) species composition and abundance of species during the season were more similar than at the river side habitats (Fig. 3.2b). The species composition differed only for the site “Felsplateau” (host plant: *Ipomoea eriocarpa*) because here also *A. quinquefasciata* occurred which was otherwise known only from the river side sites. Concerning the species abundance: *A. roseomarginata* again was the most abundant species on all three savanna sites. It occurred there only from March till the end of May at the latest. The two other species (*A. nigromaculata* and *A. indeterminata*) were present in similar abundance during the whole rainy period. These two species were very rare at the river side sites. The populations declined continually from the beginning of the dry season in Nov./Dec. till the end of December. When all savanna plots had been burned beetles were no longer documented active.

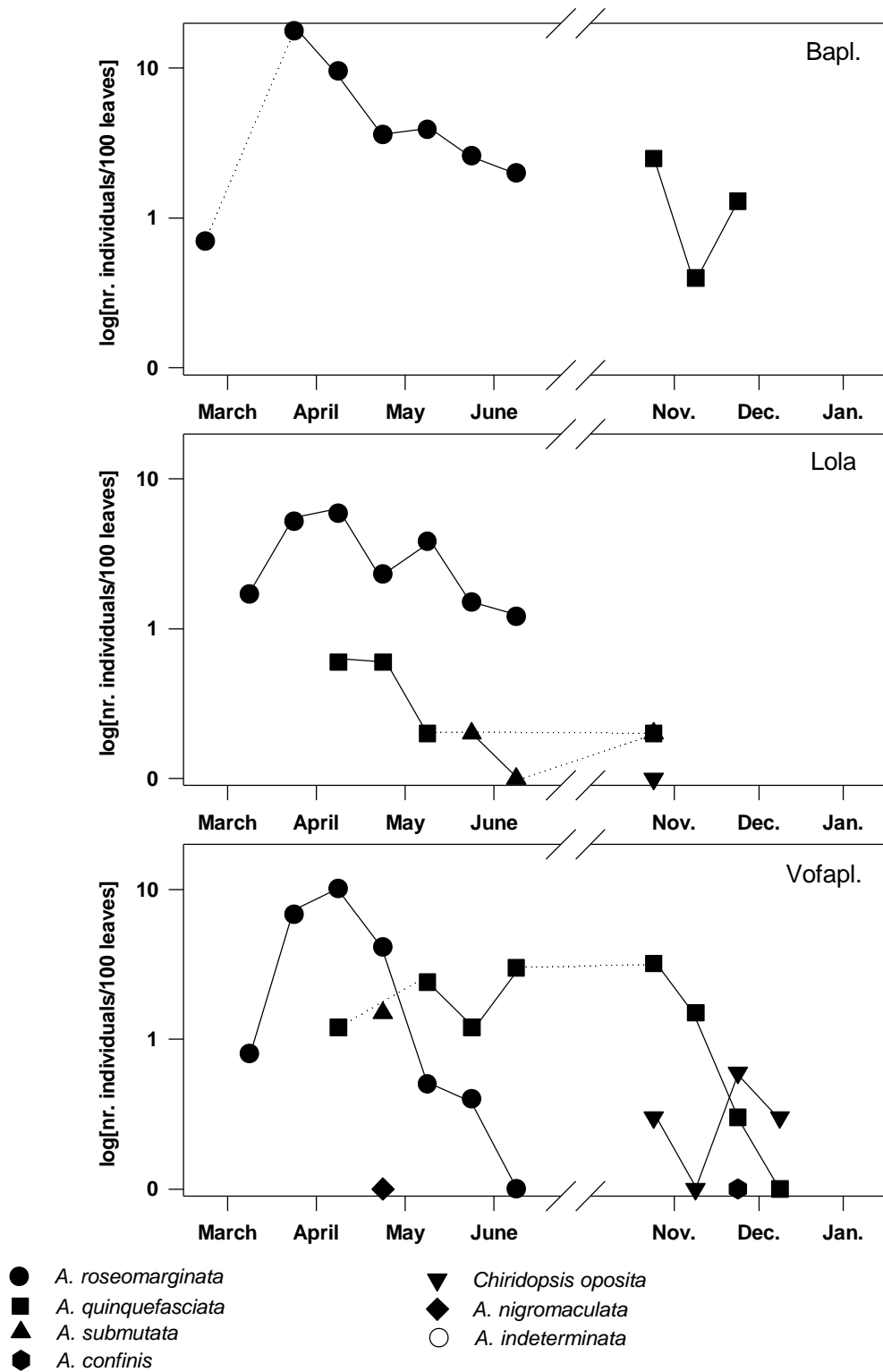


Fig. 3.2.a: Total population curves of all species on river side sites. Y-axis is on a log-scale. Abundance censuses every 14 days March-June and Nov.-Dec. 1995. Dotted lines are exploitations.

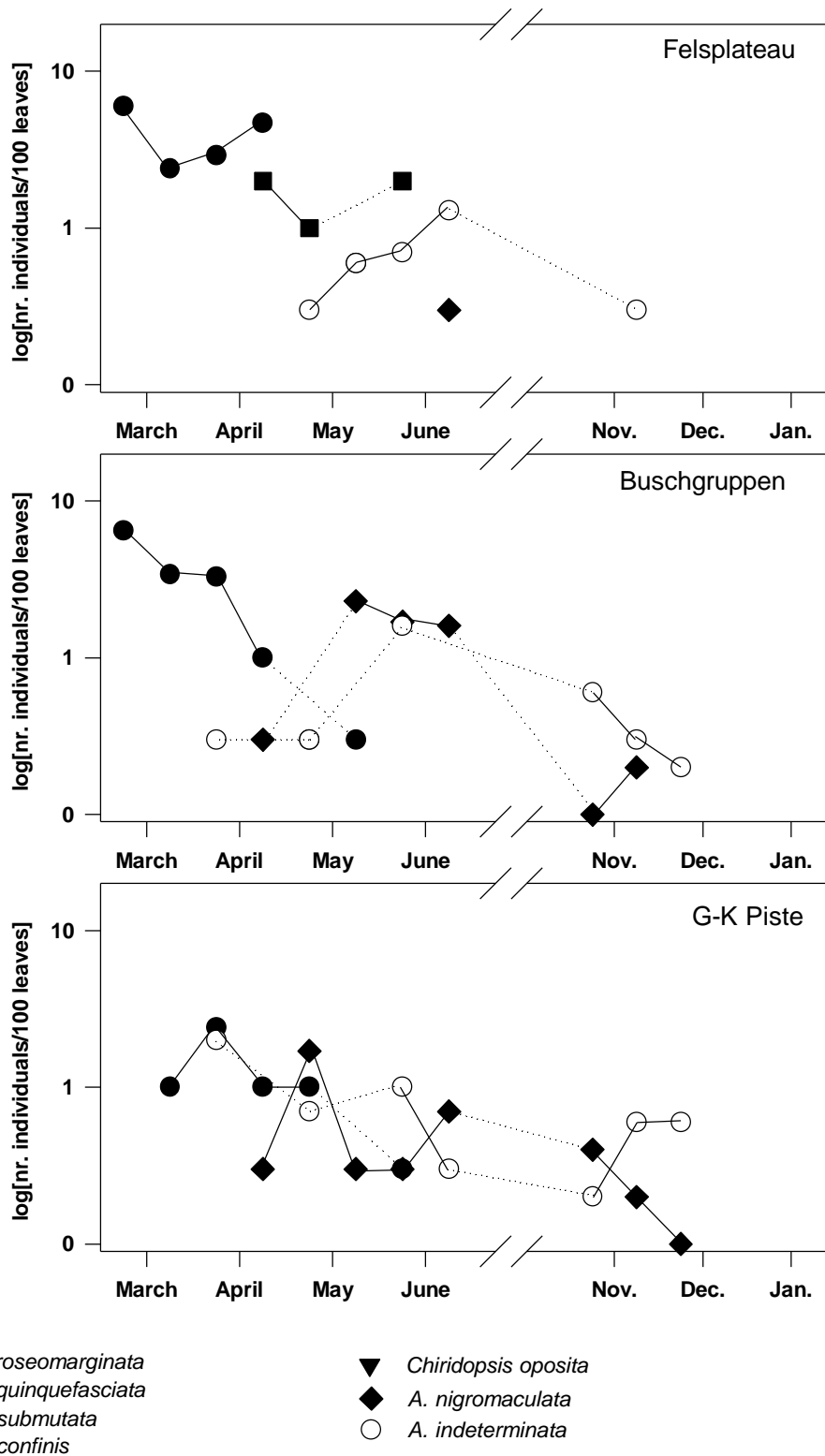


Fig. 3.2.b: Total population curves of all species on savanna sites. Y-axis is on a log-scale. Abundance censuses every 14 days March-June and Nov.-Dec. 1995. Dotted lines are exploitations.

Fig. 3.3 shows the species abundance (with zero-values) on a river side-site (Vofapl.1) from March '95 till March '96. There were no beetles visible during the dry season, in January and February. At that time of the year there were also no host plants available. In March in 1996 there was already one species present, probably because of the early first rains in that year. The first species is not, as in the year before, *A. roseomarginata*, but *C. opposita*. The latter species was found only at the end of the rainy period in 1995.

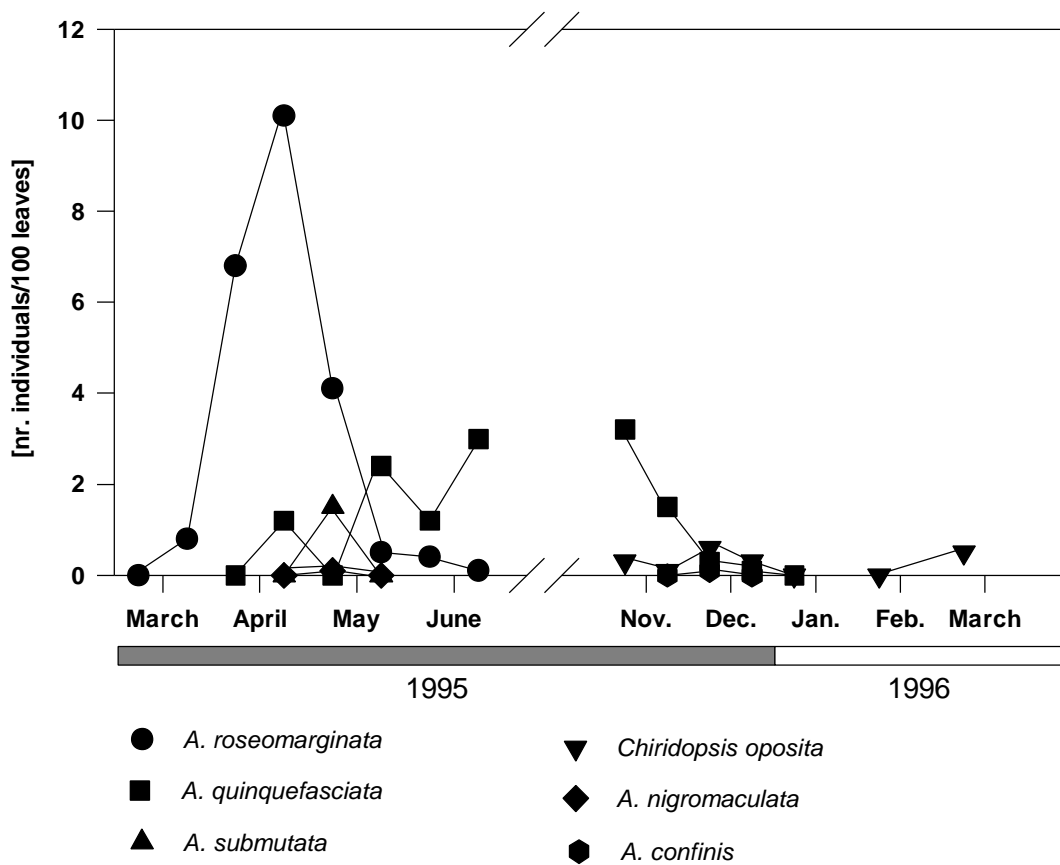


Fig. 3.3: Total population curves (linear scale) on a river side site. Also the zero-values (no presence) are shown. March-June, Nov./Dec. '95; Jan-March '96.

3.3.4. Resource use and limiting resources: leaf damage analysis

To evaluate to what extent food resources (host plants) were used by the beetles over the season and whether food became a limited resource at a certain time in the year, leaf damage was analyzed at each of 6 research sites in March till June and November till December 1995 (Fig.3.4). Leaf damage was assessed in 4 classes and was averaged over one plant and afterwards over the 10 plants of the site examined at one time. Leaf damage during most times of the season fluctuated between classes 1 and 2 (5-30% leaf damage) at the river side sites and between classes 0 and 2 (0-30% leaf damage) at the savanna sites. Only at one time in May leaf damage exceeded class 2 (>30% leaf damage) at the “Lola”-site. Local infestations and total defoliation by caterpillars did only slightly increase the mean leaf damage on the two sites (“Bapl” and “Vofapl.”) at the 5/31/1995. At river side sites, leaf damage showed little increase after May whereas at savanna sites damage increased continuously over the season. A complete removal of mean leaf mass at a site did never occur.

Only twice, during the observation period, a larger, but locally restricted, outbreak by herbivores was observed on the vine-plants. This was once caused by unidentified Lepidoptera-larvae and the other time by larvae of Pterophoridae (see also the discussion of this chapter: stochastic events). I found additionally very few individuals of Lepidoptera-larvae, Orthoptera and Coleoptera (Chrysomelidae and Curculionidae), and few individuals of Homoptera and Heteroptera in samples, taken once with the beating tray at 8 sites on host plants at the beginning of December in 1995 (Obermaier, unpubl. data).

3.3.5. Resource availability over the season

Quantitative resource availability

Host plant abundance differed strongly between sites (Fig. 3.5). Whereas at the site “Bapl.” only 0-20% of the sampling units included vines, at the site “Lola” the percentage decreased from 70% in March till 20% in December. At the 5/3/1995 there was a large flooding of some sites due to a heavy rain. The water inundated some of the area with host plants and led to a strong decline in host plant availability at the sites “Bapl.” and “Lola”.

At almost all sites (except “Lola”) the proportion of sampling units with host plants and thus the quantity of resources, more or less increased over the season.

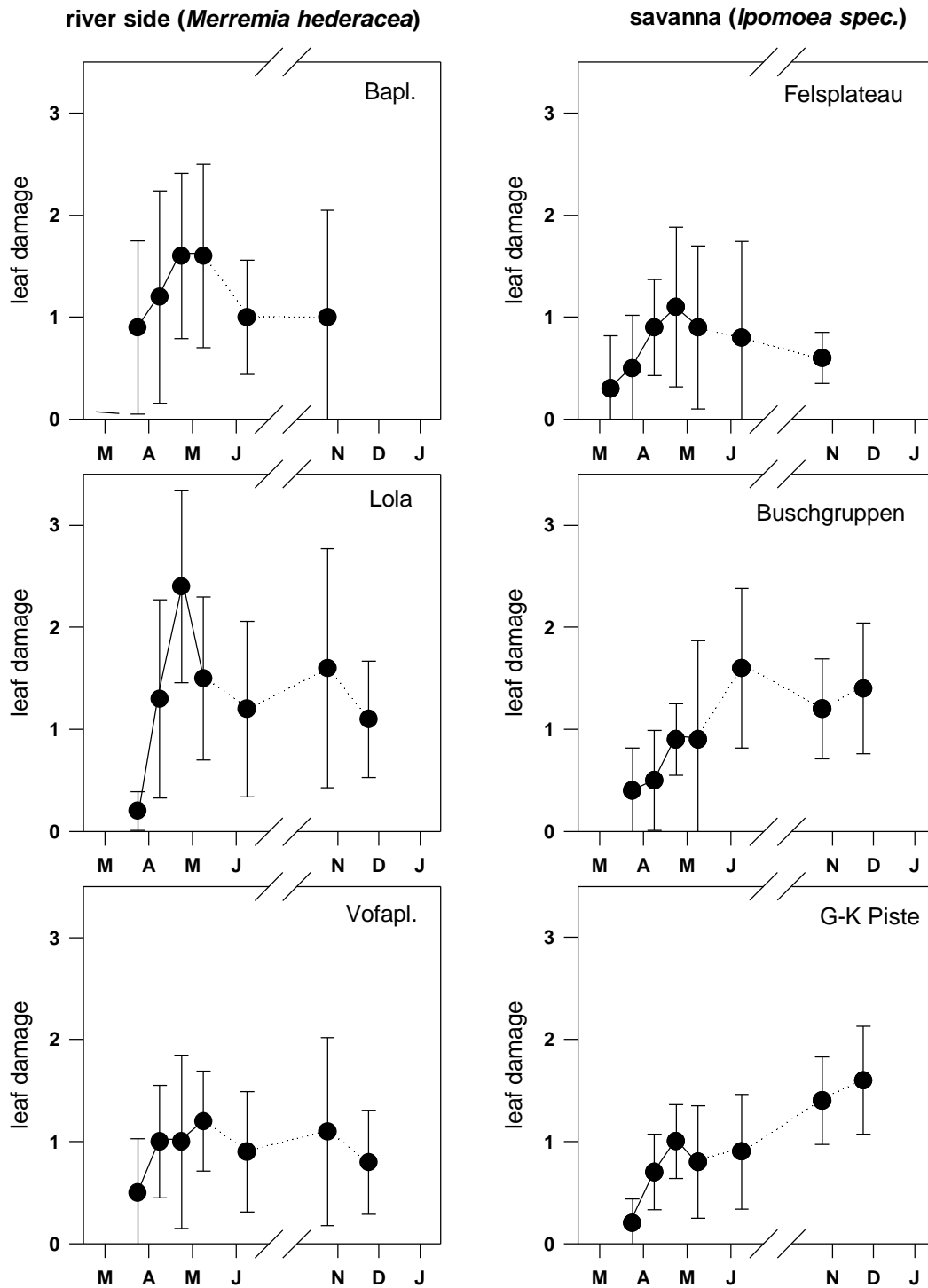


Fig. 3.4: Leaf damage over the season on 3 river side sites (left) and 3 savanna sites (right) in 1995. Leaf damage classes: 0=0% leaf damage; 1=0-4%; 2=5-29%; 3=30-99%; 4=100%.

Given are means and standard errors.

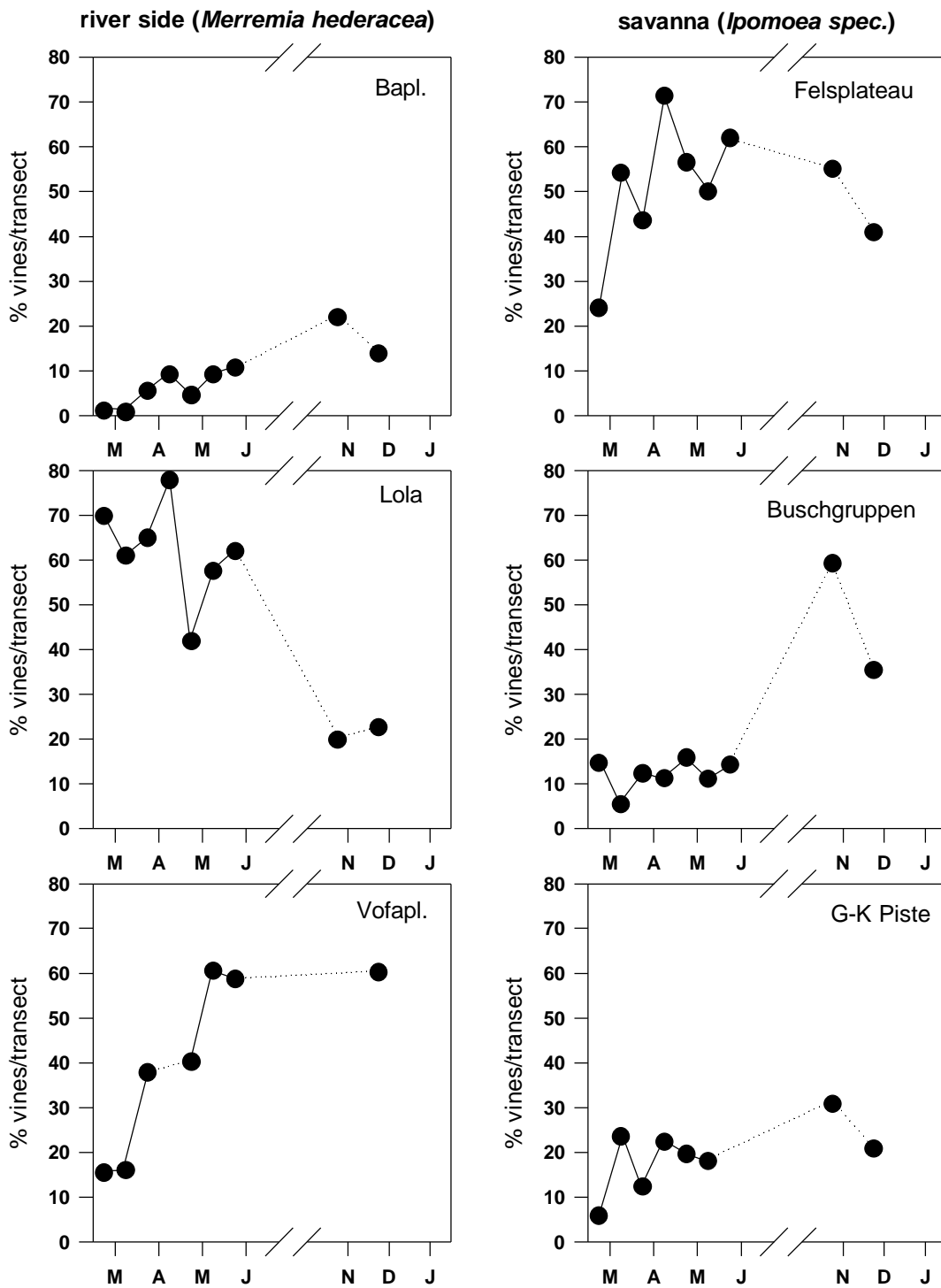


Fig. 3.5: Percentage of sampling units with vines on 6 sites during the season in 1995.

Qualitative resource availability

Leaf age classes

I distinguished between three leaf age classes, young, mature, and senescent. The proportion of leaf age classes changed over the season (Fig. 3.6). The proportion of young leaves declined after mid-June, the proportion of senescent leaves tended to increase after mid-May. The proportion of mature leaves stayed more or less the same at about 50-60%. (The high value in mid-April might have been a sampling artifact).

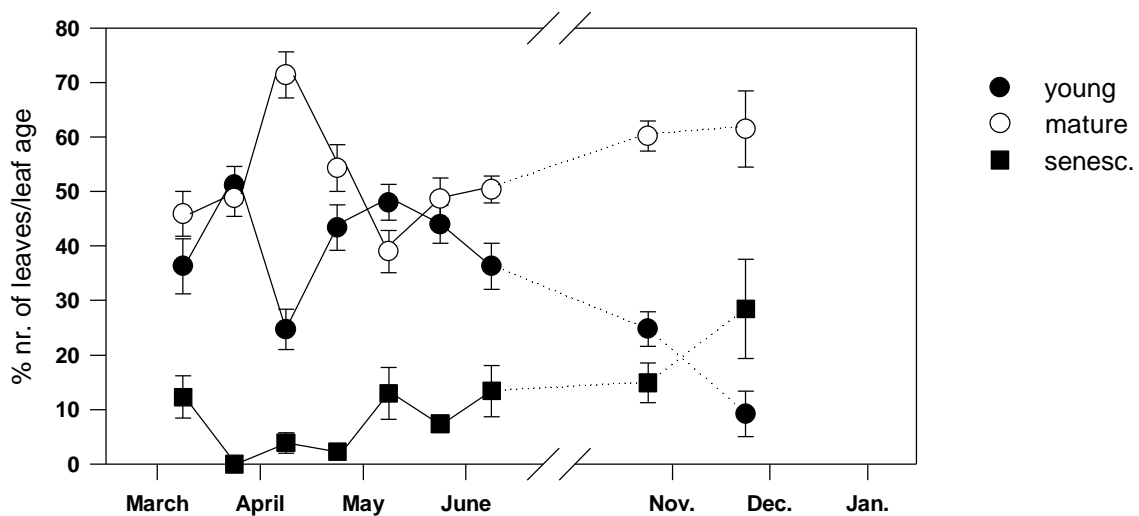


Fig. 3.6: Proportional number of leaves in different age classes (young, mature, senescent) per plant (*Merremia hederacea*) during the season in 1995; n=10 plants. Means and standard error.

Host plant quality

Quality of the host plant *Merremia hederacea* was measured as leaf-nitrogen content, leaf-carbon content and leaf-water content (Fig. 3.7). Leaf-nitrogen and leaf-carbon content were analyzed from a leaf mixture of 10 plants per sampling date, leaf water was analyzed separately for each plant (n=10) and averaged. Leaf-nitrogen stayed more or less the same over the season. Carbon was more or less constant all over the season. Leaf-water content decreased over the season. For nitrogen- and carbon-analysis leaf samples of different plants (10) were mixed per sampling date (only one mixed sample was analyzed per date), for leaf-water analysis individual plants were analyzed separately (n=10 samples per date).

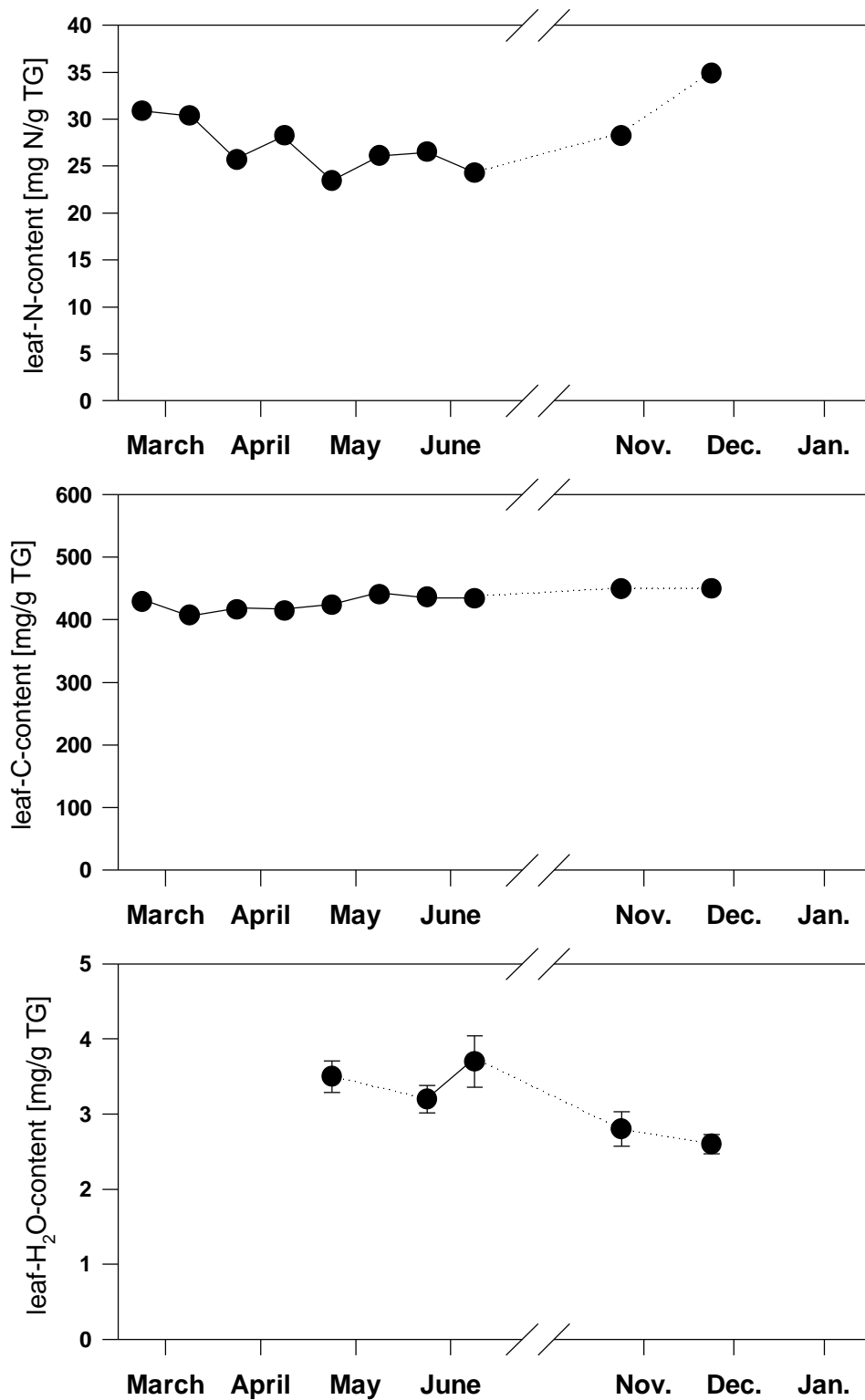


Fig. 3.7: Leaf-nitrogen content, leaf-carbon content (samples mixed), leaf-water content (n=10) of *Merremia hederacea* during the season in 1995.

3.4. Discussion

3.4.1. Seasonality

Throughout the whole rainy season and part of the dry season (April till December) most of the shield beetle species examined could be found active on their host plants without obvious peaks in abundance. An exception was *A. roseomarginata* which appeared directly after the onset of the first rains already in March, had its abundance maximum in April, its numbers declining continuously afterwards. *C. opposita* was found only at the end of the rainy season in 1995, in 1996, however, it could also be observed throughout the whole vegetation period.

The seasonal patterns of the West African species of this study were not entirely consistent with observations on Cassidinae species in Panama, which experienced their maximum abundance in general in the first two months of the rainy season (Windsor et al. 1992). However, *Acromis sparsa*, another Cassidinae species from Panama, reappeared with the onset of the rains after dry season and continued to be active until the beginning of the next dry season and thus was more similar to the species of this study (Windsor 1987). *Aspidimorpha miliaris*, occurring on *Ipomoea* in a tropical savanna in Sumatra, was present during the whole rainy season, its active period was only intercepted by a winter (dry season) and a summer diapause (Nakamura & Abbas 1989). Continual seasonal occurrence without abundance peaks in the West African Cassidinae species agreed quite well with predictions by Janzen (1988), that aseasonal tropical systems may have no fixed yearly population peak of herbivores. An example for this was also *Mecistomela marginata* (Chrysomelidae), Brasil, which did not show sizeable variations in adult numbers throughout the year (Valverde de Macedo et al. 1994). In contrast to the West African Cassidinae the Panamanian species oviposited in synchronized reproductive bouts which followed at approximately two month intervals indicating separate generations (Windsor 1987). In the European Cassidinae species *Cassida rubiginosa* also two distinct generations per year could be distinguished (Ward & Pienkowski 1978, Obermaier & Zwölfer 1999). In the West African species, in contrast, distinct generations within one rainy season could not be separated and no oviposition bouts could be observed (Obermaier unpubl. data). In summary the West African species were active throughout the rainy season and showed no abundance peaks and no distinct generations within one rainy season.

The West African beetle species examined in this study seemed to survive the dry season, when no food was available (January, February), as adults under tree bark or hidden elsewhere. When kept in a cage with different material, adult beetles did not bury in the ground but stayed on the wall or hid under dry leaves. Two beetle individuals were found

under tree bark in January in 1996 (Salewski, pers. comm.). There are no quantitative data available on this subject. In Panama, as well, the 3-4 month dry season was accompanied by a great reduction in numbers of Cassidinae adults (Windsor et al. 1992). Accordingly Flowers (1991) reports that adults of six panamenian Cassidinae species aggregated and survived dry season as adults apparently in dormancy. Beetles sat in aggregations on the lower side of leaves on non-host plant trees growing in humid spots. In temperate regions, Cassidinae also overwintered as adults and suffered great losses during that time (mean overwinter survival=21%, Kosior & Klein 1970, Spring & Kok 1997).

There was no clear temporal niche differentiation between the seven West African Cassidinae species investigated. Most beetle species could be observed during the whole vegetation period (March-December) in 1995, and partly also in 1994 and in 1996 when observations were not as complete as in 1995. One species (*A. roseomarginata*) occurred only in the first part of the rainy season in all three years, but still showed considerable overlap with the other species from April till August. *C. opposita* could be found only in Nov./Dec. in 1995, and nearly during the whole growing season in 1996, but had a complete overlap with other Cassidinae species in both seasons.

3.4.2. Availability and quality of the host plants and seasonal phenology of the beetles

Host plant availability increased after mid-March (savanna sites; host plant genus *Ipomoea*) or mid-April (river side sites except “Lola”; host plant genus *Merremia*) at almost all sites over the season and decreased again from November onwards in 1995. Host plant quality was measured by the proportion of different leaf age classes over the season and by a chemical analysis of the host plant leaves. Both, nitrogen- and water-content of the food are important factors for insect nutrition and can limit growth and development (Mattson 1980, Tabashnik & Slansky 1987, Simpson & Simpson 1990). A decrease in plant quality was suspected by the relative increase of senescent leaves and the relative decrease of young leaves after mid-June till the end of the growing season. Young leaves of *M. hederacea* were shown to have a significantly higher nitrogen concentration than senescent leaves (chap. 5). However, although the proportion of senescent leaves increased over the season, nitrogen content showed no consistent trend in 1995 and varied between 24mg N/g DW and 35mg N/g DW. In the Palaearctics, in contrast, leaf-nitrogen decreased in a non-flowering plant from 28-19mg N/g DW (*Achillea millefolium*), in flowering plants from 59-22mg N/g DW (*Cirsium arvense*) and 46-26mg N/g DW (*Centaurea scabiosa*) during the season (Obermaier & Zwölfer 1999). An explanation for the differences in *Merremia hederacea* could be the low nutrient

availability in tropical soils and the special growth form as a vine, which showed a continuous production of new leaves during a large part of the season. Water content, in contrast, decreased, as expected, over the season.

Thus, although the percentage of young leaves per plant as well as the leaf-water content declined over the season, temporal variation in food quality of *M. hederacea* in general seems to be rather small, compared to plant species in temperate climates. This was especially true for the leaf-nitrogen content. The food quality should therefore not have represented a strong selection factor for the phenology of its herbivores.

Except for *A. roseomarginata*, all other species feeding on *M. hederacea* were not specialized phenologically. In March in 1995, *A. roseomarginata* was the first species to occur after the onset of rains and was often observed to oviposit directly on the seedlings (Obermaier, pers. observ.). Here, developing larvae could use the higher nitrogen concentrations of very young leaves (chap. 5). Larvae of *Galerucella nymphaeae* (Coleoptera: Chrysomelidae), for example, were observed to gain a higher pupal weight when feeding on young leaves (Kouki 1993). A further advantage of this early season feeding strategy could have been a lower risk of flooding of the river bank early in the rainy season (see further below). Disadvantages were the unpredictability of consecutive rainfalls and an accordingly high risk of desiccation of the seedlings where oviposition had already taken place (Obermaier, pers. observ.).

3.4.3. Stochastic events during the season and possible consequences for beetle populations

Apart from the seasonal change between dry and wet season which triggered availability of the host plants and was quite predictable, there were a number of events which could have reduced population densities profoundly and which occurred relatively unpredictably during the season in 1995 (Obermaier, unpubl. data): (1) In March, after the dry season, first rains fell only at irregular intervals and with several weeks delay to the next. Host plant seedlings where beetles with an early occurrence (*A. roseomarginata*) had already oviposited on, were regularly found dried up. Eggs and larvae were lost. (2) After heavy rains flooding of the river banks occurred. In the first part of the rainy season there was only one large flooding on the 3rd of May in 1995. From September till the beginning of November all river side sites were permanently flooded and only host plants which had grown up high in the trees stayed alive. (3) In May 1995 there was a heavy infestation of caterpillars on *M. hederacea*-plants which caused a total defoliation over several square meters (sites Bapl. and Vofapl) and in November 1995 there was a similar heavy infestation by larvae of Pterophoridae (site

Vofapl2). Both infestation events, however, were locally very restricted and had no overall strong impact on mean leaf damage per site at that time. (4) Finally, on the 28th of November in 1995 I found a large colony of driver ants (probably *Dorylus (Anomma) nigricans*; Fam. Dorylidae) at one site (Vofapl2). *Anomma* takes caterpillars and other insect larvae as prey (Linsenmair, pers. comm.). Driver ants in general could be capable to eliminate large quantities of insects. However, too little is known yet on prey composition and effect on prey populations.

These catastrophic events were partly locally very restricted, but might have been a significant element in population dynamics in some of the species. Especially for r selected species which exploit unstable habitats, such as the river side habitat, local events could have had an important impact on survival. A study of *Gastrophysa viridula* (Chrysomelidae) on a river bank and a shingle island, which was subject to flooding, showed that each flood caused a 100% larval mortality and an up to 50% egg mortality (Whittaker et al. 1979). The probability of flooding of the island and therefore the risk of mortality increased over the season. Under these circumstances the patterns of natality and mortality of conventional population models were not appropriate for the survival of the population (Whittaker et al. 1979). A similar stochastic event like the irregular first rains in early wet season, might be the bud burst of oak trees in temperate regions in spring. In two (competing) Lepidopteran species stochastic mortality factors drove population change independently of competition. They favored the specialist species, and overrode the otherwise competitive superiority of the generalist species (Hunter 1990). The unpredictably changing yearly rainfall quantities in Sumatra, Indonesia caused high fluctuations in the population dynamics of a herbivorous beetle species, *Epilachna vigintioctopunctata* (Inoue et al. 1993).

In my study system long term population investigations would be useful to reveal if such locally restricted events do influence overall population dynamics.

3.4.4. Food as a limiting resource?

One possibility, how coexistence in the shield beetle community could be realized, is by a reduction of interspecific competition (see hypotheses-section in chap.1). Competition, in that case, would trigger a specialization of competing species and a separation of their niches (Putman 1994). This process is one of the main characteristics of deterministic equilibrium models (Putman 1994, Linsenmair 1990, 1995).

One of the conditions, the competitive exclusion principle demands for interspecific competition to take place, are limited resources (Begon et al. 1986). Therefore leaf damage

per plant was investigated in the field over the season to test the hypothesis that food represented a limiting resource in the study system. Leaf damage fluctuated between 0-30% damage and a complete removal of leaf mass did never occur on the six sites investigated, in 1995. Although local defoliation of some square meters did occur in rare cases (see above) this result clearly speaks against interspecific competition as a major force structuring this beetle community. A study on two *Aspidimorpha* species in a tropical savanna in Indonesia revealed similar patterns as observed at Ivory Coast. The Indonesian *A. miliaris* and *A. sanctaecrucis* remained at low levels of population density for most of the study period although a shortage of food never occurred (Nakamura & Abbas 1989).

One might argue that even a small leaf damage would have been sufficient to cause competition if leaves of single plants differed in leaf quality, if there was induced defense or host plants within a site were not equally suitable to the beetles (plant quality, predators, microclimate). The last point was thoroughly investigated (see chap. 5, 6 and 7) and could not be totally excluded. The first two assumptions, however, were tested in choice tests and can thereafter be rejected. Choice tests between different leaf age classes showed no significant difference (Obermaier, unpubl. data) and an investigation on 10 sites showed no preference of a certain leaf age class (chap. 4, logistic regression analysis). Neither seemed induced defense to occur, because abundance of beetles was positively correlated with leaf damage (chap. 4, logistic regression) and choice tests showed no significant difference in preference between formerly damaged and undamaged leaves (Obermaier, unpubl. data).

Although so far, all my results speak against interspecific competition in the beetle community investigated, more intense investigations would be needed to make a final statement. Investigations should be done over several years, direct field experiments on competition should be performed and the importance of local heterogeneity in the context of competition should be examined.