

Chap. 2: Host-plant range and host-plant selection

2.1. Introduction

In most orders of phytophagous insects (except Orthoptera) host range is rather limited and 70% or more of the species are oligophagous or monophagous, that means specialized on a single plant family or plant genus (Bernays & Chapman 1994). The data used for such general calculations, however, come mostly from studies in temperate regions, and it is presently unknown if the majority of herbivorous insects in the tropics is less or is even more specialized. When the herbivore community of 10 tree species of a moist tropical forest (Panama) was investigated, 48% of the herbivore species turned out to be monophagous, 37% oligophagous and only 15% polyphagous (Barone 1998). A proposed explanation for a higher species diversity in the tropics argues that, compared with those in the temperate zone, organisms in the tropics have narrower niches, allowing more species to coexist in a given habitat (MacArthur 1969). Field data of herbivore subfamilies, however, do not show a consistent trend in specificity over the latitudinal gradient, some being to a higher degree polyphagous in the tropics (Fiedler 1998 and literature therein), others have narrower diets than in temperate regions (Barone 1998 and literature therein). Cassidinae are described as one of the most specialized subfamilies within the leaf beetles (Chrysomelidae) (Jolivet 1988). Almost all members are monophagous or narrowly oligophagous (Jolivet 1989). Most tropical species (40%) seem to attack plants of the family Convolvulaceae (Windsor et al. 1992, Jolivet 1988).

Most adaptive explanations of diet breadth in phytophagous insects focus on realized adult fecundity and offspring performance as a function of host plant (Jaenike 1990). A frequent assumption of models of host-plant selection is that adult females can rank hosts according to the fitness they impart on their offspring (optimality models). However the assumption was frequently not supported by empirical tests (see reviews in Jaenike 1990 and Mayhew 1997). Possible reasons for a preference of a low-quality host despite its lower benefits for offspring are deprivation of high-quality hosts, large egg-load, high age or a limited search time (Mayhew 1997). Some species accept low-quality hosts only when there is severe competition for high-quality hosts (density dependence). Others prefer hosts which are less variable in abundance. Furthermore, natural enemies might influence diet breadth (Bernays & Graham 1988, Jaenike 1990, Bernays & Chapman 1994).

In many cases a strong phylogenetic component in host-plant selection is almost certain (Mayhew 1997) and is seen as a non-adaptive constraint. In molecular phylogenies of

different herbivore-genera, species were conservative in their host plant use and fed only on host plants that were closely related to the host plants of their congeners (Mitter et al. 1991, Kelley & Farrell 1998, Köpf et al. 1998)(see chap. 8).

Preference of herbivores can operate at the level of the habitat, the plant species or the within-plant microhabitat (Crawley 1983). When only one food plant species is present specialization on a habitat type may produce an apparently monophagous relationship, yet the insect may actually utilize other species across its geographical range. Restriction of host use as a result of the restriction of habitat use is well known for a number of butterflies that are restricted to open grassland or to forests (Bernays & Chapman 1994).

This chapter investigates the host plant range of nine West African Cassidinae species in the field and examines niche overlap for the niche dimension “food”. I examine whether species show the same host plant preferences in choice tests in the laboratory as in the field. Finally I test the hypothesis that host plant choice in these species is adaptive, in terms of larval development. Thus I focus on the following questions: (1) Which host plant species do the Cassidinae species use? Do the species overlap in their host plant use? (2) Is host plant use in the field identical to host choice in the laboratory? (3) Is host plant choice adaptive; e.g. do beetles prefer those host plant species in the field that are the most beneficial for their larvae (fitness maximization)?

2.2. Material and Methods

2.2.1. Study site and study system

Geography and climate

The Comoé-National Park (CNP) is situated between 9°6′ and 8°5′ of latitude and between 3°1′ and 4°4′ of longitude in the Subsudan- and Sudan-Savanna zone (Poilecot, 1991). With 11500km² the CNP is the largest National Park in West Africa. The largest part lays on a plateau (250-300m above NN) which forms a watershed between the river systems of Comoé and Volta. The study area was restricted to an area of about 300km² where the different sites were spread. The borders of this area were the village Gansé (8° 42,4′N, 3° 50,9′W) in the South, the river Kongo in the North (8° 48,1′N, 3° 46,3′W), the river Comoé in the West and the main road (+1km) in the East. The research camp of the University Würzburg is situated at 8° 45,1′N and 3° 49,0′W (fig. 2.1).

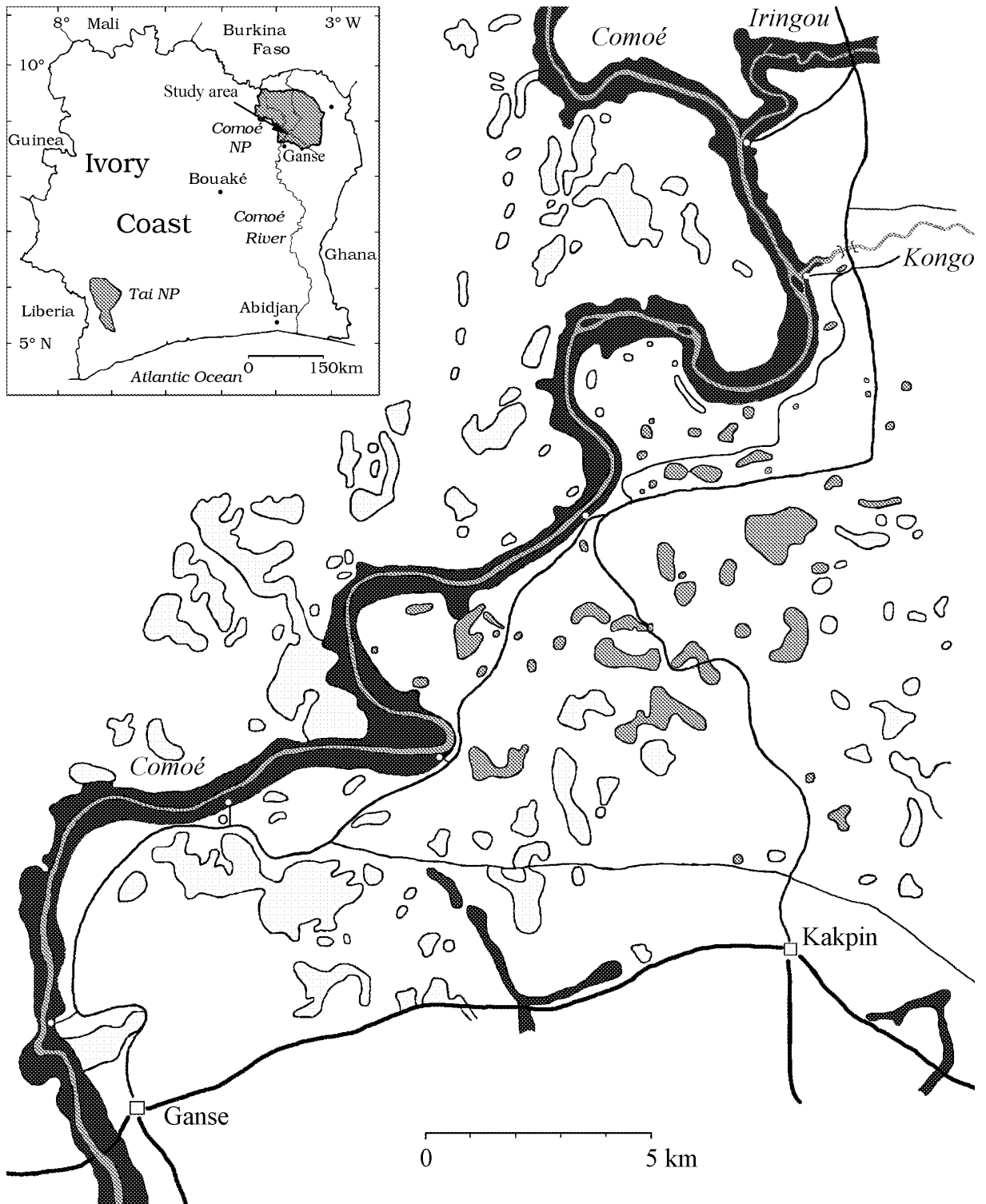


Fig. 2.1.: Map of the situation of the Comoé-National Park in Ivory Coast and map of the study site. The river Comoé is indicated grey in North-South direction and accompanied by a gallery forest (black area). Interspersed forest islands are indicated by grey or white areas (after Hovestadt 1997).

The climate is characterized by a distinct rainy season from March/April to October and a following dry season from November to February/March. The rainy season is divided by a short period in June/July after which the period with the highest precipitation follows (August/September). Total precipitation in average was 900-1100mm per rainy season in 1992-1996 (Rödel 1998). The distribution and quantity of precipitation, however, varies strongly from year to year. The vegetation period lasts a little bit longer than the rainy season, until the ground has dried out, from February/March till December.

Temperature means of the years vary between 25°C and 28°C. The daily variation is larger than during the year; the variations are largest during the dry season (up to 30 °C). In the rainy season the daily means lay between 20°C and 33°C. Relative Humidity varies between around 30% in the dry season and 90% in the rainy season.

The vegetation in the CNP consists of tree-shrub savanna, interspersed by forest islands and gallery forests along the rivers.

A more detailed description of the geography, geology, climate and vegetation of the Comoé-National Park can be found in FGU-Kronberg (1979), Poilecot (1991) and Rödel (1996, 1998).

Beetle species and host plants

The beetle species, species of the genera *Acrocassis*, *Aspidimorpha*, *Chiridopsis* and *Rhytidocassis* (Chrysomelidae: Cassidinae) occurred syntopically on three host plant species of the plant family Convolvulaceae. Eggs, larvae, pupae and adults could all be found on the leaves of the host plants. Eggs and larvae of different species were identified by rearing them to adulthood. Larvae carried fecal shields or exuviae of former stages, like it is generally known in the subfamily Cassidinae. Larval stages of the species were (among other characteristics) characterized by the form of the shield which is often typical for the species. The seven most abundant of these coexisting species, *Acrocassis roseomarginata* B., *Aspidimorpha quinquefasciata* F., *Aspidimorpha confinis* Klug, *Aspidimorpha submutata* Weise, *Chiridopsis opposita* Boh., *Aspidimorpha nigromaculata* Hbst. and *Aspidimorpha indistincta* Boh. were investigated in this study (see color plates). Keys to the genera and species of afrotropical Cassidinae can be found in Borowiec (1994 and following volumes) who kindly also did the identification of the species for this study.

All host plant species were members of the family Convolvulaceae (see color plates). For the whole Comoé-National Park 6 species of *Ipomoea* and 2 species of *Merremia* were reported (Poilecot 1991). A key to the species of the two genera was set up by Lejoly &

Lisowski (1992). Only three species of Convolvulaceae, however, were more abundant in the study area and were therefore used for the investigations. The main growth habitats were the river side (host plant: *Merremia hederacea* (Burm.)Hallier,) and the savanna (host plants: *Ipomoea heterotricha* F. Didr. and *Ipomoea eriocarpa* R.Br). In the gallery forest no Convolvulaceae were found at all, in the forest islands they were quite rare (*I. heterotricha* and *I. eriocarpa*). The density of the host plants in either habitat was highly variable, depending on the time of the year and the site investigated. The Convolvulaceae belong to the geophytes (Strasburger 1983) and, after the end of the dry season in February/March, new plants were observed to either sprout from rhizomes of the previous year, or to recruit from seeds. The plants formed new leaves and stems throughout the vegetation period. Time of flowering was in November/December. In the savanna the vines grew vertically and were interspersed among the grass. At the river side different microhabitats could be discriminated. In full sun vines grew horizontally on large rocks. These flat rocky banks were subject to frequent flooding by the river, later in the rainy season. Further up the bank vines grew vertically up to 10m high on trees and shrubs, partly in deep shade. Microclimate showed large extremes at river bank sites.

2.2.2. Host plant use in the field

To set up a host plant list, as complete as possible, all Convolvulaceae species (vines) found in the south-western part of the Comoé-Park were examined for Cassidinae-species (Fam. Chrysomelidae). However, not all plant species could be investigated with the same intensity, because some were quite rare. In 1994, 1995 and 1996, during the periods of field work, a regular census of the three most abundant Convolvulaceae species, *Merremia hederacea*, *Ipomoea heterotricha* and *Ipomoea eriocarpa* was conducted at several sites (see chap.3, abundance counting). The much rarer *Ipomoea hellebarda* Schweinf. ex Hiern was examined only at three sites. All further *Ipomoea*-species (*I. blepharophylla*, *I. asarifolia* (Desr.) Roem & Schult) were investigated only at one site because they did not occur in the surrounding of the Lola-Camp.

During frequent walks in the study area as often as possible also plants of other plant families were checked for the Cassidinae-species.

2.2.3. Choice tests

In the choice tests two plant species or two leaf age classes were tested in each trial. Per plant species two leaf disks (Ø 0.9cm) were excised of freshly harvested mature leaves and fixed with preparation needles on moist filter paper at opposite sites. The filter paper, with the four leaf disks applied, was placed in a petri-dish (Ø 10cm). Each dish was supplied with one adult beetle. Each beetle individual was used only once for testing of one specific plant species combination or leaf age class. One trial lasted for 5h (*A. quinquefasciata*, *A. indistincta*, *A. nigromaculata*, *A. confinis*) or for 8h (*A. roseomarginata*), depending on the size of the beetle species. The amount of leaf area removed by a beetle was measured [mm²]. Between 9 and 26 replicates were tested for each combination. When the species *A. quinquefasciata* was tested, the petri-dishes were turned upside down because beetles feed only on the lower side of leaves. Attractiveness of different leaf ages was tested in a similar way. Young leaves were tested against mature leaves. Experiments were performed in a climatic chamber in the Biocenter at the University of Würzburg in Germany (27°C, 70% humidity) or under the protecting roof of my hut in Ivory Coast in 1995. Some of the beetle species-plant combinations tested in Africa were repeated in Germany as a control.

2.2.4. Secondary chemistry

Leaf samples of the plant species *M. hederacea*, *I. heterotricha* and *I. eriocarpa* were analyzed in a GC-MS (*M. hederacea*) or a GC (NP-detector, N-selective) for alkaloids in the department of Pharmaceutical Biology in Würzburg. Leaf samples were ground and dissolved in 100µl methanol. Peaks were compared with the internal standard Spartein.

2.2.5. Larval development on different Convolvulaceae-species

Performance of larvae on 2 or on 3 different host plant species (*M. hederacea*, *I. heterotricha*, *I. eriocarpa*) of the plant-family Convolvulaceae was tested for 4 beetle species. In the field the beetles used the host plants differentially; some were not used at all in the field. Beetles were kept and experiments were performed in a climatic chamber at 13h light (27°C) and 11h dark (24°C) and a constant relative humidity of 70%. Vine plants were cultivated in a greenhouse of the Biocenter at 14h light (26°C; 65%rh) and 10h dark (20°C; 80%rh). The experiment was conducted in Nov./Dec. 1996. Twigs of each plant species were supplied with water and placed in plastic boxes (11x11x6cm) (one plant species per box), and larvae, not older than 24h, were placed on the twigs in each box. Six larvae were kept per box and mostly 5 boxes were set up per plant species (3) and beetle species combination. *A. quinquefasciata*

was tested only on *M. hederacea* and *I. heterotricha* because too few larvae were available. Variables of larval development registered, were time of development (day of hatching until day of pupation) and pupal weight (on a Mettler AE160). Only fresh weight of pupae was recorded because pupae were needed alive for further observations.

Boxes were used as sample units and mean values of the individuals per box were used for analysis. Since means are more likely to be normally distributed, I could apply t-test and oneway-ANOVA, in spite of the low sample size.

2.3. Results

2.3.1. Host plant use in the field

All Cassidinae species examined were observed feeding only on plants of the family Convolvulaceae (Tab. 2.1) despite extensive surveys of other plant families. Within the plant family the Cassidinae differed in their host specificity. About half of the beetle species, *A. roseomarginata*, *A. quinquefasciata* and *A. nigromaculata* were found on both host plant genera, *Merremia* and *Ipomoea*, that were available in the study area. Therefore these species are oligophagous. They had, however, mostly a strong preference for one of the host plant genera and were only occasionally found on the other genus (*A. quinquefasciata*, *A. nigromaculata*, *A. confinis*)(Tab. 1: the main host plant is indicated by a shaded bar). Only *A. roseomarginata* showed an equal abundance on both genera in the field. The other half of the species was found exclusively on one host plant genus, either *Merremia* or *Ipomoea*. Those were *A. confinis*, *C. opposita*, *A. submutata* and *A. indistincta*. *R. scutellaris* and *A. silverbergii* were only found once or twice during the whole period of field work and therefore their range of host use cannot be determined.

A. roseomarginata was found several times on the leaves of a shrub, *Combretum nigricans*, in the savanna. However, it never fed on the leaves of the savanna shrub species *Combretum nigricans*, *Pterocarpus erinaceus*, *Securidaca longepedunculata* and *Anogeissus leiocarpus*, tested in feeding trials (Mody, pers. communication).

Tab. 2.1: Host plant range and habitat types of nine Cassidinae species on Convolvulaceae in the south-western part of the Comoé-Park. Main host plant species are indicated by shaded bars.

Beetle species	Plant species	Habitat
<i>Acrocassis roseomarginata</i> B. *	<i>Merremia hederacea</i> Hallier <i>Ipomoea heterotricha</i> F. Didr. <i>I. eriocarpa</i> R.Br.	River side; savanna;
<i>Aspidimorpha quinquefasciata</i> F.	<i>M. hederacea</i> <i>I. eriocarpa</i>	River side; savanna; (forest islands);
<i>Aspidimorpha nigromaculata</i> Hbst.	<i>M. hederacea</i> <i>I. heterotricha</i> <i>I. eriocarpa</i>	River side; savanna;
<i>Aspidimorpha confinis</i> Klug *	<i>M. hederacea</i> <i>I. asarifolia</i> Roem & Schult (Puppen)	River side;
<i>Chiridopsis opposita</i> Boh.	<i>M. hederacea</i>	River side;
<i>Aspidimorpha submutata</i> Weise *	<i>M. hederacea</i>	River side;
<i>Aspidimorpha indistincta</i> Boh.	<i>I. heterotricha</i> <i>I. eriocarpa</i>	Savanna; (forest islands);
<i>Rhytidocassis scutellaris</i> Klug	<i>I. asarifolia</i>	??
<i>Aspidimorpha silverbergii</i> Borowiec	<i>I. hellebarda</i> Schweinf. ex Hiern (syn: <i>I. sepiaria</i>)	Savanna;

These species *, as well as *Aspidimorpha isparetta* Boh., *Aspidimorpha obovata* Klug, *Conchyloctenia signatipennis* Boh., *Conchyloctenia adspersa* F. and *Laccoptera corrugata* Shlb. (Uf. Cassidinae) occur in Thai-Ntl.park (southern part of Ivory Coast) on *Ipomoea batatas* Lam. (sweet potato) (6/1995).

2.3.2. Choice tests between different host plant species

Here I tested whether the beetles show the same host plant preferences in a standardized choice test as they did in the field. Several factors, like habitat, abiotic factors, host plant architecture etc., which may influence the host choice in the field, were excluded in the simplified assay in the laboratory.

Shaded bars in the table indicate the main host plant species in the field (Tab. 2.2). When the plant species *M. hederacea* and *I. eriocarpa* were tested, only one of five beetle species, *A. nigromaculata*, showed a significant preference for one host plant species, *I. eriocarpa*. This was consistent with the host plant preference of *A. nigromaculata* for the genus *Ipomoea* in the field (Tab. 2.1). Although *A. confinis* as well as *A. indistincta* were specialized on only one host plant genus in the field they did not show a significant discrimination in the choice test.

When the plant species *M. hederacea* and *I. heterotricha* were tested, all four beetle species discriminated significantly between them. *A. quinquefasciata* and *A. confinis* significantly preferred their natural (main) host plant *M. hederacea* and *A. nigromaculata* preferred its natural host *I. heterotricha*. Only *A. indistincta* showed differing results. In choice tests in Ivory Coast it preferred *M. hederacea*, which it never used in the field, but when the choice tests were repeated in Würzburg it significantly preferred its natural host plant *Ipomoea heterotricha*. The leaves of *I. heterotricha* are, in contrast to those of *I. eriocarpa*, densely covered with hairs on upper and lower leaf side.

When, *M. hederacea* and *I. hellebarda* were tested in choice tests, none of the two beetle species tested, showed a significant preference, although *I. hellebarda* did not belong to the natural host plant spectrum of the two species (Tab. 2.2).

None of the two beetle species tested showed a significant preference for one of the two different leaf age classes (young and mature) (Tab. 2.3). As “young leaves”, leaves were characterized which were still developing at the tip of the stems, which had a light green color and were soft. As “mature leaves”, leaves were characterized when they were already fully developed, tougher and with a darker green color, showed, however no discoloration or other signs of leaf senescence.

Tab. 2.2: Choice-tests between different host plant species. The amount of leaf area removed by a beetle was measured [mm²]. Shaded areas indicate the main host plant of each beetle species in the field. Tests conducted in Würzburg are indicated by WÜ, those conducted in Ivory Coast are marked with CI. Significance level is based on Wilcoxon matched pairs signed rank test.

	x±SE	x±SE	p	n
	<i>M. hederacea</i>	<i>I. eriocarpa</i>		
<i>A. roseomarginata</i> WÜ	13.3 ± 2.5	8.7 ± 2.1	n.s.	16
<i>A. quinquefasciata</i> CI	13.2 ± 2.8	10.0 ± 3.5	n.s.	21
<i>A. quinquefasciata</i> WÜ	34.7 ± 5.3	48.3 ± 8.4	n.s.	15
<i>A. confinis</i> WÜ	10.4 ± 2.4	7.6 ± 2.1	n.s.	19
<i>A. indistincta</i> CI	6.1 ± 2.1	21.6 ± 6.8	n.s.	9
<i>A. indistincta</i> WÜ	8.9 ± 2.0	14.7 ± 2.3	n.s.	21
<i>A. nigromaculata</i> WÜ	6.6 ± 1.8	14.7 ± 2.2	0.05	26
	<i>M. hederacea</i>	<i>I. heterotricha</i>		
<i>A. quinquefasciata</i> CI	40.2 ± 5.3	0.9 ± 0.7	0.01	19
<i>A. confinis</i> WÜ	14.3 ± 2.6	3.8 ± 1.9	0.001	24
<i>A. indistincta</i> CI	42.6 ± 4.0	13.6 ± 2.7	0.01	23
<i>A. indistincta</i> WÜ	8.9 ± 2.6	18.2 ± 3.2	0.01	23
<i>A. nigromaculata</i> WÜ	0.1 ± 0.1	16.6 ± 2.4	0.001	18
	<i>M. hederacea</i>	<i>I. hellebarda</i>		
<i>A. roseomarginata</i> WÜ	10.1 ± 2.4	13.1 ± 2.4	n.s.	15
<i>A. quinquefasciata</i> WÜ	21.3 ± 5.0	31.6 ± 5.1	n.s.	16

Tab. 2.3: Choice-tests for the preferred leaf age of the beetle species *Aspidimorpha quinquefasciata* and *Acrocassis roseomarginata*. The amount of leaf area removed by a beetle was measured [mm²]; Significance level is based on Wilcoxon matched pairs signed rank test.

	Young	Mature		
	$\bar{x} \pm \text{SE}$	$\bar{x} \pm \text{SE}$	p	n
<i>A. quinquefasciata</i>	30.19 ± 5.38	28.13 ± 7.76	n.s.	16
<i>A. roseomarginata</i>	14.13 ± 1.74	10.67 ± 2.06	n.s.	15

2.3.3. Plant secondary chemistry of three host plant species

M. hederacea was analyzed in a GC-MS-analyzer, with *I. heterotricha* and *I. eriocarpa* only a nitrogen-selective GC-analysis was performed (Department of Pharmaceutical Biology). This analysis did not reveal any alkaloids in the three plant species.

2.3.4. Larval development on different plant species

In this experiment I tested the hypothesis that the duration of larval development is shortest and pupal weight is highest (offspring fitness) on that plant species which is used as main host plant and oviposition site in the field (Tab. 2.4).

In general, significant differences occurred only in developmental time, but not in pupal weight. Only in two of the four beetle species examined, there was a significant difference. *A. quinquefasciata* had a significantly shorter developmental time on its main host plant *M. hederacea* compared with *I. heterotricha*. *A. indistincta* had a significantly shorter developmental time on the non-host plant *M. hederacea* than on one of its natural host plants, *I. heterotricha*. There was, however, no significant difference in developmental time between *M. hederacea* and *I. eriocarpa* in this beetle species. Except for *I. heterotricha*, host and non-host plants (of the same plant family) did not differ in suitability.

Tab. 2.4: Larval development on different host plant species was compared for each of four beetle species. Shaded areas indicate the main host plant of the beetle species in the field. Mean and standard error; Different lower case letters indicate significant difference between food plants. *t-test or oneway-ANOVA/Scheffé.

	<i>M. hederacea</i>	<i>I. heterotricha</i>	<i>I. eriocarpa</i>		
	x ± SE	X ± SE	x ± SE	T/F	p
<i>A. quinquefasciata</i>					
Dev.time [days]	15.4 ± 0.36 a	18.3 ± 0.44 b	-	-5.183*	0,001
Pupal weight [mg]	32.18 ± 0.88	28.97 ± 1.68	-	1.698*	n.s.
N	5	5	-		
<i>A. confinis</i>					
Dev.time [days]	19.1 ± 0.88	20.1 ± 0.61	19.3 ± 0.17	0.793	n.s.
Pupal weight [mg]	19.81 ± 0.68	18.05 ± 0.67	20.18 ± 0.79	2.379	n.s.
N	5	5	6		
<i>A. nigromaculata</i>					
Dev.time [days]	19.0 ± 0.30	18.8 ± 0,40	19.9 ± 0.40	2.357	n.s.
Pupal weight [mg]	11.93 ± 0.38	12.06 ± 0.21	12.01 ± 0.35	0.043	n.s.
N	5	5	5		
<i>A. indistincta</i>					
Dev.time [days]	18.8 ± 0.33 a	21.5 ± 0.68 b	19.6 ± 0.30 a	9.153	<0.01
Pupal weight [mg]	36.22 ± 1.40	34.69 ± 1.13	34.87 ± 0.95	0.505	n.s.
N	5	5	5		

2.4. Discussion

2.4.1. Host plant range and niche overlap in the field

Of the 9 Cassidinae species investigated on Convulvulaceae, 4 species were oligophagous on two host plant genera and 5 species monophagous on one host plant genus (definition after Bernays & Chapman 1994). Two species of the latter group, however, were very rare in the study area and a complete assessment of host range was therefore not possible for them. A polyphagous feeding habit can not totally be excluded because no choice tests were

performed with plants of other families. However, during frequent investigations of plant species of other families in the field, none of the seven beetle species investigated in this study, was ever observed feeding on a plant species other than Convolvulaceae. These results agree quite well with what is already known about the subfamily Cassidinae, which is one of the most specialized among the Chrysomelidae (Jolivet 1988). Convolvulaceae are described as the most important host plant family of Cassidinae in the tropics. This is confirmed for the Neotropics, where Convolvulaceae host 40% of Cassidinae (Windsor et al. 1992). In India, at least one Cassidinae-Convolvulaceae association is described (Singh & Sidhu 1992). In Indonesia, Nakamura et al. (1994) found *Ipomoea* and related genera (Convolvulaceae) to be utilized as host plants by many Cassidinae. The results of this study confirm similar patterns now for the Ivory Coast, West Africa, where all 9 Cassidinae species found in the Comoé National Park in the north-east, as well as 5 additional species in the Thai National Park in the south-west of Ivory Coast, fed on Convolvulaceae host plants.

In the field most beetle species showed a distinct preference for one of the two host plant genera (*Merremia* or *Ipomoea*) or used one exclusively. The two host plant genera, *Merremia* and *Ipomoea*, were adapted to different habitats. *Merremia* grew only at the river side and *Ipomoea* grew almost exclusively in the savanna. The beetle community can be divided into a *Ipomoea*-group (5 species) and a *Merremia*-group (5 species) and thus be separated in their food niche. Only one species (*Acrocassis roseomarginata*) was abundant on both host plant genera (see chap. 3). Species on *Merremia* at the river side completely overlap in their host use, all feeding (more or less specialized) on *M. hederacea*. Species on *Ipomoea* in the savanna feed on different species of *Ipomoea*. Only *A. nigromaculata*, *A. indistincta* and *A. roseomarginata* overlap in the *Ipomoea*-species used.

2.4.2. Host plant preferences in choice tests in the laboratory

Because the two host plant genera occurred in different habitats, it was not possible to distinguish, by simple observations in the field, if the beetle species were selective in terms of their habitat or in terms of their host plant choice (Crawley 1983, Bernays & Chapman 1994).

In choice tests between *Merremia hederacea* and *Ipomoea eriocarpa* (performed in Ivory Coast or in Würzburg) 4 of 5 beetle species showed no significant difference in host choice, no matter if monophagous or oligophagous in the field. Only *A. nigromaculata* significantly preferred *I. eriocarpa* which was also its main host plant genus in the field. When *M. hederacea* was tested against *I. heterotricha* the results were different. All 4 beetle species tested, discriminated significantly between the two species. The two beetle species

whose main host was *M. hederacea* in the field, preferred it also in the choice test. One of the two savanna species preferred its natural host plant *I. heterotricha*. The other savanna species, *A. indistincta*, showed inconsistent results and preferred significantly *M. hederacea* in choice tests in Ivory Coast, however, in Würzburg it preferred its natural host *I. heterotricha*. When *M. hederacea* and *I. hellebarda* were tested there was again no significant difference between the two host plant genera.

Choice tests can show the theoretically possible host plant range of a herbivore and are frequently used in pre-release experiments in Biological Control. In this study, depending on the species of *Ipomoea* tested, in the majority of the tests the beetle species did not discriminate significantly between the two host plant genera *Merremia* and *Ipomoea* (exception: *A. nigromaculata*) and are therefore potentially able to feed on both.

This could mean that habitat selection rather than host plant selection influenced host choice in the field (Bernays & Chapman 1994). However, one has to be aware that there are technical difficulties involved in host specificity tests. Insects in laboratory choice tests often turn out to be less selective than in nature because they can not display their full repertoire of host-finding maneuvers (Zwölfer & Harris 1971).

The second test series (*M. hederacea*-*I. heterotricha*) indicated an exceptional position of *I. heterotricha*. The decline of the two “*Merremia*”-species and the inconsistent choice of *A. indistincta* very probably were due to special physical characteristics of *I. heterotricha*. The lower and upper side of the leaves are densely covered with hairs. Plant hairs are known to influence acceptance of plants by herbivores, preventing them from feeding or oviposition and acting as mechanical defense especially against younger instars (Bernays & Chapman 1994). *A. nigromaculata* seems to be adapted and preferred *Ipomoea* over *Merremia* in both test series.

In conclusion, all beetle species examined feed on both host plant genera either in the laboratory or in the field and are therefore oligophagous (see above). Physical structures, like the plant hairs of *I. heterotricha*, seemed to deter feeding within the Convolvulaceae by beetle species not adapted. These results do not allow to judge whether preferences shown in the field are due to habitat or food preferences.

2.4.3. *Is the host plant choice of the beetle species adaptive?*

A frequent assumption of models of host plant selection is that plants which impart higher fitness to offspring are preferred for oviposition. However, when the literature was reviewed 24% of the studies investigated, did not support this prediction (Jaenike 1990, Mayhew 1997).

In all Cassidinae-species examined, females oviposited directly on the leaves of their host plant and therefore determined the feeding site of their less mobile larvae (Obermaier, pers. observ.). According to the optimality models, my hypothesis was, that larvae of a certain beetle species should develop best on that host plant species, which is the main host plant of the species in the field. Offspring fitness was assessed as duration of larval development and as pupal weight (for a discussion of the method, see chap. 6).

Only in one of four beetle species developmental time of larvae was significantly shorter on the main host of the species, than on the related non-host plant (*A. quinquefasciata*). In two of the beetle species, *A. confinis* and *A. nigromaculata*, no significant difference, neither in developmental time, nor in pupal weight, could be found between the three plant species tested. And one species developed significantly better on a non-host plant than on one of its two host plant species (*A. indistincta*). Therefore, these results do not unequivocally support the adaptive host plant choice hypothesis.

Several constraints are discussed in the literature which can prevent females from ovipositing on the host plant that provide the highest benefit for larval development. There are phylogenetic constraints, as host plant use is known to be a conservative trait (Mitter et al. 1991, Mayhew 1997, Kelley & Farrell 1998, Köpf et al. 1998). (This aspect, as well as other evolutionary hypotheses of host plant specialization in phytophagous insects, are discussed in chap. 8.) Further time-limitation or high egg-load can force females to oviposit on less suitable host plant species. Low abundance of the host plant with the highest quality or high competition on this species (density-dependence) can have the same effect (Mayhew 1997). Finally predators/parasitoids might force females to use the enemy-free space of a less suitable host plant species (Bernays & Chapman 1994, Keese 1997, Mayhew 1997). (Within-plant species variability in enemy free space will be discussed in chap. 7.)

Host plants did not contain any alkaloids which would have been the most probable class of secondary chemicals in leaves of the plant family Convolvulaceae (indol alkaloids (Teuscher & Lindequist 1994) and tropan alkaloids (Frohne & Jensen 1985)). The three host plant species therefore, probably did not differ in alkaloid secondary chemistry. Secondary leaf chemistry is known as an important factor to influence insect host plant range (Ehrlich & Raven 1964, Harborne 1988, Spencer 1988, Roitberg & Isman 1992).

In conclusion, in only one of four beetle species the main host plant species was also the significantly most suitable plant for larval development. In the other species, larval development did not differ between the host and non host plants examined. Therefore, habitat selection or other constraints rather than host plant selection (see above) might trigger host choice. *A. indistincta* might be an example for using a less suitable host (*I. heterotricha*) for oviposition because of its higher abundance in the field compared with the high quality host *I. eriocarpa*. The high quality host *M. hederacea* was not used at all by *A. indistincta* in the field, perhaps because of a restriction of the beetle to the savanna habitat.