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Oecologia

The food plant preferences of *Phratora vitellinae* (Coleoptera: Chrysomelidae)

A. Field observations

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Abstract. In the Upper Rhine (Petite Camargue, Saint Louis, France) study site, *Ph. vitellinae* are found mainly on *Salix nigricans* on which they are bivoltine. Some beetles are occasionally observed on *S. purpurea*, especially in Spring, but never on *S. alba, S. caprea* and *S. cinerea.* In other European localities, *S. nigricans* or *S. hegetschweileri* at higher elevations are frequently recorded as host-plants. However, some populations are also found on *S. purpurea*, *P. tremula* and *P. trichocarpa* × *deltoïdes*, usually when neither *S. nigricans* nor *S. hegetschweileri* are present.

All the Salicaceae on which *Ph. vitellinae* was observed in the field have leaves rich in phenylglycosides and with glabrous lower surfaces, at least in Spring. *Ph. vitellinae* was never recorded on those *Salix* species with leaf undersurfaces densely covered with trichomes.

At the time of emergence of the beetles from hibernation, *S. nigricans* leaves are more developed than those of *S. purpurea* and *S. cinerea.* Moreover, those *S. nigricans* trees with the longer shoots in Spring support the largest number of beetles at their emergence. The preference of *Ph. vitellinae* for *S. nigricans* might be reinforced by these phenological differences.

In the Petite Camargue, the same *S. nigricans* trees support the largest populations of beetles from one generation to the next and from year to year. This suggests that *S. nigricans* does not respond to defoliation with induced resistance to the beetles.

All shoots on the branch seem to be equally suitable and attractive for oviposition. The older leaves at the base of the shoot and the younger ones at the top are less favored by ovipositing females. Survival of the egg batches and the groups of freshly emerged larvae is lower on the distal shoots of the branch and on the younger leaves. This might be due to a higher degree of exposure to predators.

Phratora vitellinae is a common leaf beetle often reported from willow and poplar plantations (Hutchinson and Kearn 1930; Munster 1935; Wain 1943). Clonal resistance of poplar to this beetle has recently been analysed in detail (Finet and Gregoire 1981; 1982; Finet et al. 1983) on the basis of field observations and of greenhouse and laboratory experiments. These studies, however, have all been carried out in plantations where human influence is strong and into which many non-native varieties of plants have been introduced. There is actually very little information available on the precise species of Salicaceae eaten by *Ph. vitellinae* in undisturbed habitats. A better understanding of the food plant preference of this beetle in natural conditions might be useful for the selection of resistant clones in plantations.

Ph. vitellinae adults aggregate in the Autumn. They overwinter in groups in cracks in bark or other sheltered places, not necessarily on the host tree. When these adults colonise young leaves of salicaceous trees in the spring, in order to feed, mate and reproduce, finding an adequate host tree is critical. The eggs are laid in batches on the lower side of the leaves, where the larvae also feed. Pupation occurs in the soil directly beneath the tree, and the young emerging adults of the summer generation have merely to climb back onto the tree to feed on the young leaves at the tip of the branches. There may be a second generation later in the Summer if climatic conditions are favorable.

The Chrysomelini, larvae and adults, are known to be chemically defended (Pasteels et al. 1984, in press). Like many of the species feeding on Salicaceae, the larvae of *Ph. vitellinae* incorporate salicin, a phenylglycoside contained in the leaves of some willows and poplars and use it as a precursor for their secretion, salicylaldehyde (Rowell-Rahier and Pasteels 1982). This is thought to correspond evolutionarily to a host plant switch from herbs to trees. Other Chrysomelini feed mainly on herbaceous plants and their larvae secrete autogenously synthesised methylcyclopentanoid monoterpenes (Pasteels 1984, in press).

The various central European *Salix* species can be divided into at least two categories according to the secondary chemistry of their leaves. Some species, such as *Salix fragilis, S. nigricans, S. purpurea* and *S. repens*, have leaves rich in phenylglycosides, salicin being one of the more common compounds, but lacking proanthocyanidins, a form of condensed tannin. Other species, such as *S. alba, S. aurita, S. caprea, S. cinerea* and *S. viminalis*, have no phenylglycosides in their leaves but are rich in proanthocyanidins (Hegnauer 1973). It is therefore to be expected that among the different species of *Salix* present in the marshes and riversides where *Ph. vitellinae* commonly lives in central Europe, this beetle should select the *Salix* species rich in salicin, which is necessary to the beetle for its own defense.

The main aim of this paper is to establish the food plant preferences on *Ph. vitellinae* in relatively undisturbed vegetation in central Europe. A population of beetles in a swamp in the Upper Rhine valley was studied in detail for three consecutive summers. More restricted observations were also made in a number of other European locations.

The data presented in this paper will serve as a base for comparison with results of detailed laboratory studies of the food plant preference of different populations of *Ph. vitellinae* and of some of the factors influencing these preferences (Rowell-Rahier 1984).

Material and methods

In the field site (Petite Camargue, Haut-Rhin, Saint Louis, France) three willow species (*S. cinerea, S. nigricans, S. purpurea*) are present in an isolated island patch where *Ph. vitellinae* is abundant. I estimated the number of *Ph. vitellinae* adults on these trees at regular time intervals. The proportion of observed adults in copula was also recorded on each host tree species. The phenology and growth of *S. nigricans, S. purpurea* and *S. cinerea* was observed. For the major host plant, *S. nigricans*, individual differences between trees were investigated. Oviposition sites and differences in survival of the eggs on *S. nigricans* were studied.

Salix species studied in the field site

A total of 29 *Salix* trees belonging to three species, 14 *S. nigricans*, 3 *S. purpurea* and 12 *S. cinerea* were individually marked. These 29 trees were of roughly similar age (8 to 10 years) and size (2–3 m high).

Observations were also made on nearby (within 500 m) *S. alba, S. caprea, S. fragilis, Populus tremula* and *P. nigra italica.*

S. nigricans, S. purpurea and *S. fragilis* have leaves rich in phenylglycosides but devoid of proanthocyanidins. The undersurfaces of the young leaves of these species are glabrous in Spring. *S. cinerea, S. alba* nad *S. caprea* have leaves without phenylglycosides but rich in proanthocyanidins. The undersurfaces of the leaves of these species are densely covered with trichomes.

Population estimates of Ph. vitellinae adults

On 18 separate occasions (3 in 1981, 10 in 1982 and 5 in 1983), 2 observers counted the number of beetles seen on each tree during 2 min. The counts were added and the mean number of beetles counted per tree of each species was calculated. These data were treated by Friedman's analysis of variance (Siegel 1956). The number of beetles seen in copula was also recorded.

The phenology of S. cinerea S. purpurea and S. nigricans

In 1982 and 1983, the length of the most developed leaves was measured during the growing season. Additionally, the number of leaves per shoot and the number of shoots per 30 cm of branch were counted in the spring of 1982. I consider as shoot the new growth of the year. In the early spring special attention was given to the timing of bud opening and to the length of the shoots of the three species.

Individual differences between S. nigricans trees

In 1982 and 1983, the 14 *S. nigricans* trees were ranked according to the abundance of the beetles on them (these data were analysed by Friedman analysis of variance). The Spearman coefficient of rank correlation between the different censuses were then calculated.

The Spearman coefficient of rank correlation between the length of the new shoot of each *S. nigricans* tree and the number of beetle observed on them at the date of emergence of the beetles (15 May 1982) was calculated.

Oviposition site and egg survival

Four branches of each of 6 highly infested *S. nigricans* were thoroughly examined for freshly laid batches of eggs on the third warm day after a prolonged cool period in June 1983, during which no eggs had been laid. The age of the leaves on which egg batches were found (as indicated by the position of the leaves on the shoot of the year) was noted, as was the position of the shoot on the branch. Four days later, a sample of freshly hatched larvae was similarly measured. These data were submitted to χ^2 analysis and tested for goodness of fit to the distribution of the eggs (Siegel 1956).

Results

Geographic variation in the food plants of Ph. vitellinae

Table 1 gives the food plants of *Ph. vitellinae* and the habitat in which the observation was made, for a number of European localities. *S. nigricans* and the closely related *S. hegetschweileri* are the most frequently recorded host plant species. It should be noted that they do not occur in Belgium.

Estimates of beetle population on S. nigricans, S. purpurea and S. cinerea

The mean numbers of adult *Ph. vitellinae* found on these three *Salix* species at different times of the year are given in Fig. 1. A Friedman two way analysis of variance of the data collected in 1981 and 1982 shows that there is a highly significant difference ($P<0.001$, χ^2 obs. $=26$, $N=13$, $df=2$) between the number of beetles present on the three *Salix* species studied, *S. nigricans* being strongly favored. In the Spring, some beetles are also found on *S. purpurea* and a very few on *S. cinerea.* These numbers decline with time and by mid-June no adult *Ph. vitellinae* are found on these two *Salix* species. In 1982, there were two generations of adults on *S. nigricans.* In 1981 and 1983, no systematic censuses were made during the end of the Summer but sporadic observations also showed two generations.

No *Ph. vitellinae* were observed on the nearby *S. alba, S. caprea, S. fragilis, P. tremulae* or *P. nigra.*

Proportion of the population of Ph. vitellinae in copula

The proportion of *Ph. vitellinae* adults which were in copula during the censuses on these three *Salix* species is given in Table 2.

The peaks of mating activity correspond to the peaks of abundance of the adult beetles on the trees.

Phenology and leaf growth of S. nigricans, S. purpurea and S. cinerea

Figure 2 summarizes the phenology of leaf production and the increase in leaf length in *S. nigricans, S. purpurea* and

Table 1. Observed food-plant of *Ph. vitellinae* in the field. Records on unspecified *Salix* and *Populus* are not cited

Site	Habitat	Host-plant	Reference
Belgium:			
Oignie	swamp	*P. tremula*	pers. obs.
Grammont	plantation	*P. trichocarpa* × *deltoïdes*	Finet (1982) pers. obs.
France:			
St. Louis	swamp	*S. nigricans* *S. purpurea*	pers. obs. pers. obs.
Switzerland:			
Herrliberg	garden	*S. purpurea*	pers. obs.
Beckenried	meadow	*S. nigricans*	pers. obs.
Tarasp	riverside	*S. nigricans*	pers. obs.
Zinal	riverside	*S. hegetschweileri* *S. glauca*	pers. obs. pers. obs.
Lötschental	riverside	*S. purpurea*	pers. obs.
Germany:			
Frankfurt	swamp	*S. nigricans*	pers. obs.
Seewiesen	swamp	*P. tremula*	pers. obs.
Austria:			
Innsbruck	riverside	*S. hegetschweileri*	pers. obs.
Great Britain:			
Bristol	plantation	*S. alba vitellinae* *S. purpurea* *S. repens* *S. fragilis* *S. nigricans*	Hutchinson and Kearns (1943) Wain (1930)
Norway:			
		P. balsamifera	Munster (1935)
Finland:			
Joensu	meadow	*S. nigricans*	Tahvanainen, pers. com.

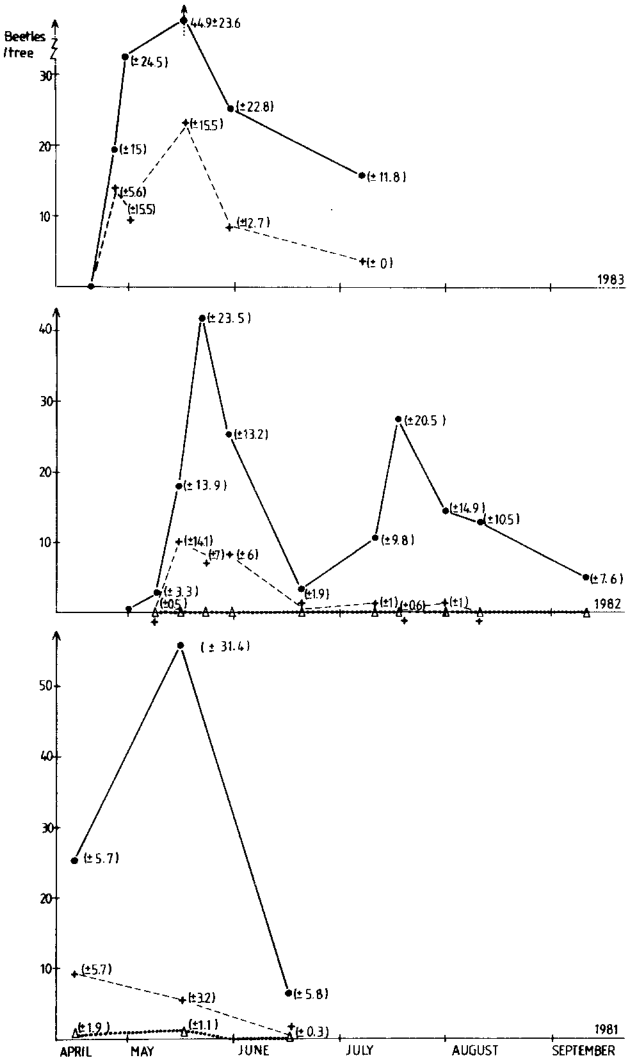

Fig. 1. Mean number of beetles counted per tree on three *Salix* species at different time of the year. The standard deviation is given in parentheses. ·—·—· *S. nigricans*; +-+-+-+ *S. purpurea*; ▵··▵··▵ *S. cinerea*

Table 2. Proportion (in %) of *Ph. vitellinae* in copula on the different *Salix* species studied in the Petite Camargue at different times of the year. n is the total number of beetles censused at this date

Date	*S. nigricans*	*S. purpurea*	*S. cinerea*
8.5.82	4% n = 49	0% n = 1	0% n = 1
15.5.82	26% n = 310	50% n = 28	0% n = 5
22.5.82	77% n = 740	25% n = 24	0% n = 0
29.5.82	52% n = 450	25% n = 24	0% n = 0
19.6.82	0% n = 39	0% n = 0	0% n = 2
10.7.82	3% n = 175	0% n = 3	0% n = 7
17.7.82	10% n = 458	0% n = 1	0% n = 5
1.8.82	53% n = 251	0% n = 3	0% n = 3
11.8.82	38% n = 217	0% n = 0	0% n = 0
10.9.82	0% n = 86	0% n = 0	0% n = 0
27.4.83	13% n = 300	2% n = 28	
30.4.83	24% n = 478	17% n = 24	
17.5.83	58% n = 673	48% n = 46	
31.5.83	65% n = 380	44% n = 18	
7.7.83	5% n = 236	0% n = 8	

S. cinerea in 1982 and 1983. It can be seen that in both years the buds of *S. nigricans* began to open two weeks before those of *S. cinerea*. For a similar shape, the *S. cinerea* leaves were only 82.6% as long as those of the favored *S. nigricans* at the time of emergence of the first adults in 1982 and only 72.7% as long in 1983. The same average number of leaves were present on the shoots of both trees (S. nigricans: 10.8 +/−2.6, n = 59; *S. cinerea:* 10.9 +/ −3.2, n = 40). However, the number of shoots per 30 cm length of branches was smaller for *S. cinerea* (15.4 shoots +/− 2.6, n = 7) than for *S. nigricans* (23.1 shoots +/−3.4, n = 19). The buds of *S. purpurea* opened after those of *S. nigricans* but before those of *S. cinerea, S. purpurea* leaves are longer but much narrower than those of *S. nigricans* and *S. cinerea.*

The length of *S. nigricans* leaves on the date of emergence of *Ph. vitellineae* was not significantly different in 1982 and 1983.

Preference for individual Salix trees in 1982 and 1983

14 *S. nigricans* trees were studied. Their ranking according to the number of beetles observed on them during the cen-

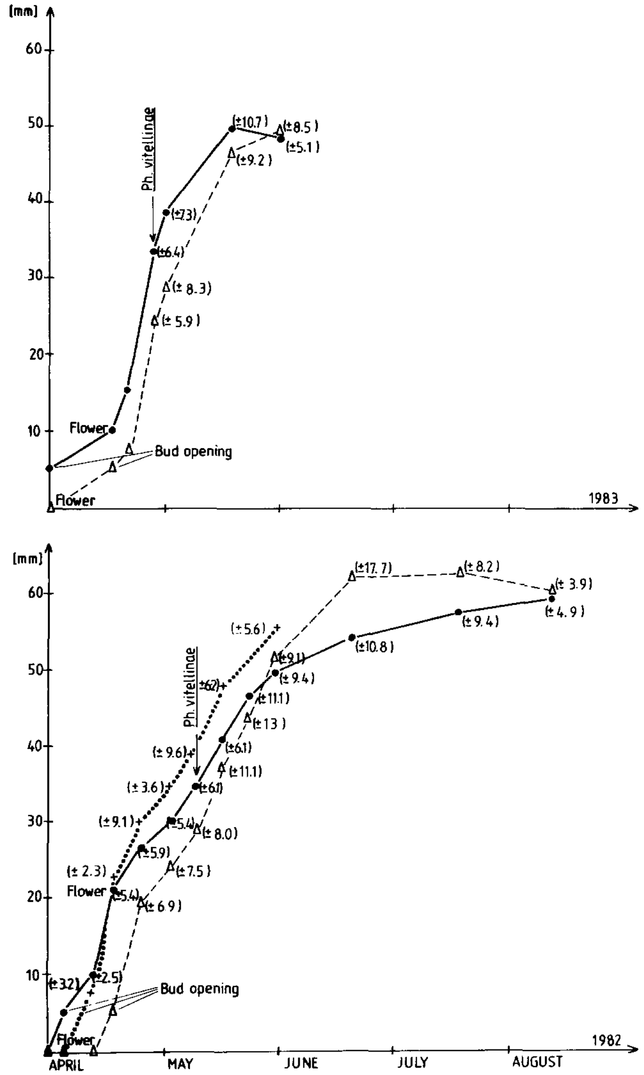

Fig. 2. Mean length of the most developped leaves of three *Salix* species at different times of the year. The standard deviation is given in parentheses. —·—·— *S. nigricans*; +··+··+··+ *S. purpurea*; △--△--△--△ *S. cinerea*

Table 3. Ranking of the 14 studied *S. nigricans* trees according to the number of *Ph. vitellinae* counted upon them

Tree	Date					
	15.5. 1982	22.5.	10.7.	17.7.	27.4. 1983	17.5.
a	1.5	2	4	4	6	2
b	7	7.5	5	3	3.5	9
c	9	3	11.5	1	11	10.5
d	5	6	6	9	1	5
e	1.5	5	9.5	11.5	3.5	7
f	9	4	11.5	2	9	3
g	11	9	3	8	13	12
h	3	10	7.5	5	2	8
i	14	14	13.5	13	14	13
j	12	12	2	6	5	10.5
k	4	1	1	7	10	6
l	9	7.5	7.5	10	7.5	1
m	13	13	13.5	14	12	14
n	6	11	9.5	11.5	7.5	4

Table 4. Distribution of egg batches and groups of newly hatched larvae according to the position of the shoot on which they were observed on the branch

Number of	Position of the shoot on the branch				X^2	p
	A	B	C	D		
Egg batches	30	30	33	30	0.22	NS
Groups of larvae	41	35	30	19	8.34	0.001
Goodness of fit:					8.98	0.001

A = Shoot on the first (proximal) quarter of the branch; B = shoot on the second quarter of the branch; C = shoot on the third quarter of the branch; D = shoot on the fourth (distal) quarter of the branch

These quarters are defined relative to the total number of shoots present on the branch, and not relative to the length of the branch

suses is given in Table 3. The 14 trees varied significantly in this respect ($P < 0.001$). First, within one year, their value of rank order is positively and significantly correlated between the emergence of the adults (15 May 1982) and the peak of their first generation (22 May 1982) ($r_s = 0.64$, $P < 0.01$), and the latter and the peak of the second generation (17 July 1982) ($r_s = 0.58$, $P < 0.05$). Secondly, in two consecutive years, there is also a positive and significant correlation between the rank order of the trees both at the beginning of the infestations (15 May 1982 and 27 April 1983, $r_s = 0.65$, $P < 0.01$) and the peaks of the first generations (22 May 1982 and 17 May 1983, $r_s = 0.55$, $P < 0.05$). This shows that the same trees are favored by the beetles throughout the summer and from year to year.

There is a weak, but not significant, positive correlation ($r_s = 0.36$) between the length of the new shoots of each *S. nigricans* tree and the number of beetles counted on them at the time of emergence of the adults from hibernation (15 May 1983).

Oviposition site and egg survival

The distribution of batches of eggs and of groups of freshly emerged larvae is given in Table 4, according to the position on the branch of the shoot on which they were found. The egg batches are uniformly distributed over both the lower and higher shoots of the branches, but the newly hatched larvae are less abundant on the shoots situated distally on the branch than on the proximal shoots. The distribution of the larvae is significantly different from that of the egg batches. Since all the young larvae observed were still on the leaves on which they had hatched, these data suggest that survival of the eggs and of the very young larvae is higher on shoots situated on the proximal part of the branches.

The distribution of egg batches and of groups of newly hatched larvae according to the age of the leaves (as indicated by the position of the leaves on the shoot) is given in Table 5. Egg batches are not uniformly distributed; most

Table 5. Distribution of egg batches and groups of newly hatched larvae according to the position of the leaves on which they were observed on the shoot of the year

Number of	Position of the leaves on the shoot				X^2	p
	a	b	c	d		
Egg batches	8	47	47	21	37.1	0.001
Groups of larvae	15	55	43	12	42.8	0.001
Goodness of fit:					11.5	0.001

a = Leave on the first (proximal) quarter of the shoot; b = leave on the second quarter of the shoot; c = leave on the third quarter of the shoot; d = leave on the fourth (distal) quarter of the shoot.

These quarters are defined relative to the total number of leaves present on the shoot and not relative to the length of the shoot

are found on leaves situated on the middle the shoot. Here again the distribution of the young larvae is significantly different from that of the egg batches. These data suggest that the survival of the eggs and of the very young larvae is higher on the older (i.e. lower) part of the shoot.

Discussion and conclusions

In the 13 geographically distinct *Ph. vitellinae* populations I have personally observed, a total of 6 species of Salicaceae were confirmed as food plants. Half of the populations were found on either *S. nigricans* or *S. hetgeschweileri*, which are very closely related (Chmelar and Meusel 1979). Additionally, Tahvanainen (personal communication) found *S. nigricans* to be the favorite host species of *Ph. vitellinae* in Finland (Joensu). The observation on *S. glauca* was made early in the spring in Zinal when neighbouring *S. hegetschweileri* were heavily infested (see below). The record on *P. trichocarpa* × *deltoides* stems from a habitat heavily influenced by humans where many non-indigenous poplar clones had been introduced. That in natural conditions, the preferred host of *Ph. vitellinae* at low elevation is *S. nigricans* is suggested by the fact that at the main study site of the Petite Camargue the beetles show a strong preference for *S. nigricans*, although *S. purpurea* is also present. At higher elevation, *S. hegetschweileri* seems to replace *S. nigricans* as preferred host. Large populations of *Ph. vitellinae* were however observed either on *P. tremula* or on *S. purpurea* in localities where *S. nigricans* and *S. hegetschweileri* are not present. Thus the evolution of "local specialist" sensu Fox and Morrow (1981) or "functional monophage" sensu Crawley (1983) on alternative host plants (e.g. *S. purpurea* or *P. tremula*) is very likely. Laboratory investigations which clarify the food plant preferences of *Ph. vitellinae* originating from different populations will be reported upon in a subsequent paper of this series (Rowell-Rahier, 1984).

The field study in the Petite Camargue shows that *S. purpurea* is attacked by *Ph. vitellinae*, but not as heavily as is *S. nigricans* and mainly in the Spring. The reasons for the absence of a marked summer generation on *S. purpurea* are unclear. Possibly a seasonal change in leaf quality makes *S. purpurea* a suitable host for the beetles in the Spring but not in the Summer. It is also possible that the adult beetles found on *S. purpurea* in the spring were there only accidentally while searching for their favored host (*S. nigricans*) and that *S. purpurea* is not suitable for oviposition and larval development. The same phenomenon could also explain the observation of *Ph. vitellinae* on *S. glauca* in early Spring in Zinal, where *S. hegetschweileri* supports large numbers of beetles. This hypothesis must be tested by further laboratory studies.

In Spring, *S. nigricans* is the most precocious *Salix* species in the Petite Camargue. Its greener appearance (greater leaf length and higher numbers of leaves per shoot) than *S. cinerea* and *S. purpurea* at the time of emergence of the beetles in the Spring might contribute to render the orientation of *Ph. vitellinae* towards *S. nigricans* easier. Alternatively the beetles could have adjusted their time of emergence to the phenology of the most suitable host.

Although *Ph. vitellinae* cause substantial defoliation of *S. nigricans* trees in the study site, the same *S. nigricans* trees support the largest populations of adult beetles from one generation to the next and from one year to the next. The basis of these preferences could be environmental (e.g. microclimate) or chemical (e.g. leaf nutritional quality or phenylglycosides content). There is however, no clear relationship between the size of the trees of their locations and the abundance of the beetles on them. Whatever the causes, these results suggest that *S. nigricans* does not respond to defoliation with long term induced resistance, at least not to the beetles.

Hutchinson and Kearns (1930) and Finet & Gregoire (1982) reported that eggs were laid on the lower part of the branches of *Populus* and *Salix* species in plantations. These trees however have a simplified linear structure, their trunk is unbranched. On *S. nigricans*, on the other hand, numerous shoots ramify from the branches every year. New leaves develop all summer long at the tip of these shoots, so that the leaves at the base of the shoot are the older ones. In this situation, all the shoots on the branch seem to be equally suitable and attractive for oviposition. The older leaves at the base of the shoot and the younger ones at the top are however less favored by the ovipositing female. These observations are similar to those made by Raupp (1983) on the oviposition preferences of *Plagiodera versicolora* on *S. babylonica*. The older leaves might indeed be less suitable for subsequent larval development because of their reduced total nitrogen and water content (Rowell-Rahier 1984). The avoidance of the younger leaves by the ovipositing females might be selected for by the possibility of competition between the larvae and the adults, which prefer the younger leaves (Rowell-Rahier, unpublished observations).

Eggs on the younger leaves are probably also subjected to a higher predation pressure, as indicated by the reduced survival of eggs laid there. These leaves, as well as the distal shoots on the branches might indeed be more exposed, accessible and visible to predators. Predation by sawflies (*Tenthredo olivacea*), anthocorid bugs (unidentified), neuropteran larvae (*Anisochrysa prasina*) and spiders (*Xysticus* species) was observed in the study site. No parasites were obtained from the larvae and the adults collected in the Petite Camargue in the course of the work. Survival of the eggs is also lower on the distal shoots of the branch, even though these are not avoided by the ovipositing females. These shoots might confer compensatory advantages upon the larvae which survive predation, such as greater insolation leading to increased speed of development.

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