Effect of Aphid Host Plant on Development and Reproduction of the Third Trophic Level, the Predator *Adalia bipunctata* (Coleoptera: Coccinellidae)

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Abstract

Secondary plant substances, also called allelochemicals, play a major role in pest infestations. Glucosinolates (GLS) and their degradation products are powerful phagostimulants for herbivores feeding on Brassicaceae and deter the noncrucifer feeders but are tolerated by some generalist phytophagous insects such as the peach-potato aphid, *Myzvs persicas* Sultzer. Do the allelochemical substances only effect the herbivores or do they also influence the predators of the pest? Broad bean, *Viciafaba* L (GLS free), oilseed rape, *Brassica tiapus* L (low GLS level), and white mustard, *Sinajris alba* L. (high GLS level), were used in this work as host plant for the prey. Although the two latter Brassicaceae species had positive effects on aphid reproductive rates, host plants displayed mixed influences on the performance of the predaceous twospotted lady beetle, *Adalia bipunctata* L. Both rape and mustard shortened development duration and increased adult weight of the twospotted lady beetle. No significant difference of lady beetle mortality was observed, depending on the prey host plant. Whereas, rape-fed *M. persicae* enhanced larger egg production and larvae emergence, mustard-fed *M.. persicae* induced lower fecundity and egg viability of the beetles. Fitness of M. *persicae* on high GLS plant-fed A. *bipunctata* was lower than the other plants. Biological parameters of aphid predators are closely linked to chemical composition of Brassicaceae species. This work on allelochemical impact gave opportunities to better understand interactions of the ρlant-aphid-lady beetle tritrophic model and demonstrated that successful biological control of pests must integrate the environmental aspects of each trophic level.

Key words: *Myzus persicae* - lady beetle - tritrophic interactions – Brassicaceae

Insect pests have evolved and developed within a multitroρhic environment. Many physiological, ecological, and behavioral aspects are governed by interactions with organisms from other trophic levels (host plant-prey-predator or parasitoid). Lady beetles are polyphagous to a wide range of aphid species (Hodek 1967) and seem unable to detect and avoid toxic aphids (Blackman 1967a). However, previous works indicated that only a limited number of species provide suitable food for coccinellid beetles (Blackman 1967b, Hodek and Honek 1996, Hauge et al. 1998). The influence of the host plant on the foraging efficiency of predators as biological control agents has been sparsely investigated, although the allelochemicals produced by host plants may influence larvae survival and development as well as adult weight of the predators (Hodek 1956, Malcolm 1992, Hauge et al. 1998). Insects are sensitive to the chemical aspects of their environment. The selection of host plant species relies on the detection of secondary plant substances, the allelochemicals, as well as on primary metabolites associated with the physiological conditions of the host plant. As with many higher plants, Brassicaceae contain a large number of secondary substances that may have various physiological properties such as antifungal activity (Mithen et al. 1987), insect feeding deterrence, and toxicity that affect insect pests (Blau et al. 1978, McCloskey and Isman 1993) and vertebrates herbivores (Lamb 1989).

Glucosinolates (GLS), a group of thioglucoside compounds, are present in all parts of the Brassicaceae crop species (Merritt 1996) and were detected in 11 dicotyledone families (Fenwick et al. 1983). The my-rosinase enzyme (thioglucosidasc,E.C.3.2.3.1.) occurs together with GLS although separately and any process which reduces the cellular integrity of the plant tissues results in the enzyme induced breakdown of GLS (Heaney and Fenwick 1995). When tissues are damaged, the toxic hydrolysis products are released. These compounds include thiocyanates, nitriles and isothiocyanates and are thought to constitute part of the plant's defense (Porter et al. 1991).

Whereas GLS or their degradation products (e.g., allylisothiocyanate) may function as feeding deterrents or toxins for some herbivorous insects, most pests of Brassicaceae species, in particular aphids, are attracted and stimulated to feed and oviposit by allyli-sothiocyanate or its GLS precursor, sinigrin (Traynier and Truseott

1991, Huang and Renwick 1994). Although they are attracted to and confined to crucifers as hosts, some phytophagous insects find certain degradation products of glucosinolates toxic (Ahman 1982). Brassicaceae plants probably produce GLS and their derivatives as defensive chemicals. Specialist consumers of crucifers are thought to have evolved ways to minimize the toxic effects of these chemicals and to have then adopted these allelochemical substances as cues for both identification and location of their hosts (Lamb 19S9).

The aim of this work was to determine the effects of CLS from Brassicaceae plants on different trophic levels. Reproductive rates of *Myzus persicae* Sultzer were determined for feeding on three host plant (GLS *free Vicia faba* L., low GLS *Brassica napus* L., and high GLS *Sinapis alba* L.). Aphids reared on the latter were used to feed their natural predator twospottcd lady beetle, *Adalia bipunctata* L. Development and reproduction parameters of the aphidoρhagous beetle were assessed and lead to fitness calculation according to the prey host plant.

MATERIALS AND METHODS

Plant and Insect Culture. Broad beans *(Viciafaba* L., Fabaceae), white mustard *(Sinapis alba* L., Brassicaceae), and oilseed rape *(Brassica ntηnts* L., Alaska, variety, Brassicaceae), which contain no, low, and high GLS levels, respectively, were grown in 10-cm-diameter plastic containers at a $20 \pm 2°C$ temperature and a photoperiod of 16:8 (L:D) h. Although broad beans were cultivated in pots containing a 1:1 mixture of perlite:vermiculite, the two Brassicaceae species were sown in 20 by 30-cm plastic trays containing ordinary compost and transplanted into plastic pots with the same compost when the plants had two hue leaves.

Myzus persicae was reared on broad bean, rape, and mustard in three separated climate chambers. Aphids were kept at least 2 wk on their host plants before being used to feed *A. bipunctata.* Both lady beetle and aphid strains had been reared in the laboratory for several years. Several hundreds of twospotted lady beetle adults continuously constitute the mass-rearing population, which are fed with the pea aphid, *Acijrtho-siphon pisi/m* (Harris), reared on broad beans.

Experiment Observations. *Aphid Reproductive Rate.* Ten host plants of each species were randomly chosen from the plant population and were inoculated with 10 *M. penicae* aρterae adults. Each plant was individually placed in a net cage and was observed every 24 h for 7 d. The aphid numbers were recorded on the 10 replicates of the three plant species and the net reproductive rates were calculated daily.

Evaluation of Laihj Beetle Performance Parameters. For each *M. pcrstcae* host plant, 30 newly hatched larvae of A. *bipunctata* were isolated individually in 5-cm-diameter ρetri dish to avoid cannibalism. The larvae were collected from different egg clusters of lady beetle stock culture fed with *A. pisum.* Each experiment was repeated twice resulting in 60 replicates, which we used to assess the effect of the prey host plant on the beetle development parameters, Aphids removed from their host plants, which were cultivated in three separated climate rooms, were offered to the larvae ad libitum. Hatching lady beetle larvae were kept at $20 \pm 2°C$ and a photoperiod of 16:8 (L;D) h and observed every day to determine the survival rate and to note changes in developmental stage. Duration of each nymphal and pupal stages was recorded. After emergence, lady beetles fed with aρhids from the same host plant were pooled in aerated plastic boxes to allow mating and egg production {three aphid host plant and two replicates, resulting in six containers each including the survivals of the 30 lady beetles from the beginning of each test). Clusters of eggs were set individually in 5-cm-diameter petri dishes to allow hatching. Numbers of eggs laid per box were recorded daily and egg viability determined at the same tirne. Lady beetle survival rate, adult weights, larval and total developmental durations were assessed for each aphid host plant experiment. To compare the suitability of the prey from the various host plants for the lady beetle, fitness (r) was calculated as a performance measure by integrating development time *(D)* and potential fecundity (V) via the equation: $r = (Ln\ V)/D,$ where Ln = natural logarithms (McGruw and Caswell 1996).

Statistical Analysis. Net reproductive rates of aphids were calculated for each day on 10 replicates and were analyzed using two-way analysis of variance (ANOVA) (host plant and day as main and second factors) followed by the Tukey test. Mortality (total percentage per experiment) and egg viability (expressed as daily percentages) were first transformed using the angular transformation (arcsineVx, Dagne-lie 1973) before ANOVA and mean comparison using Tukey tests. Other lady beetle parameters were analyzed directly using ANOVA, followed by Tukey mean comparison test. Lady beetle larvae were set individually for the first part of this study, whereas the adults were pooled by experiment on individual boxes. Under these conditions, observations related to reproduction were calculated per day and per box resulting in two replicates of 21 observations each (n = 42) for each of the three aphid host plant.

Two-way ANOVA were calculated for the reproductive parameters (fecundity, egg cluster production and egg

viability) considering host plant and day as factors. MINITAB (version 11.2) software was used for the statistical analysis (Minitab 1998).

RESULTS

Aphid Net Reproductive Rate. After analysis with two-way ANOVA the daily net reproductive rates of M. *persicae* reared on the three host plant, significant interaction was observed between plant and day (F = 7.24: df = 12,189; *P* < 0.001). One-way ANOVA was performed separately and revealed significant differences according to host plants (F = 53.73; df = 2, 207; *P* < 0.001). Mean comparison test demonstrated that each host plant was significantly different the ones from the others *(t* = 2.23, df = 209, *P* ≈ 0.068 and (= 10.22, df = 209, *P* < 0.001 and *t* = 7.98, df = 209, *P* < 0.001 for GLS free *V.faba/high* GLS S. *alba,* GLS free *V. faba/low* GLS B. *napus* and high GLS S. *alba/low* GLS *B. napus* comparisons respectively). The Brassi-caceae species, namely *B. napus* and *S. alba,* had a positive effect on the *M. persicae* aphid development (Fig. 1).
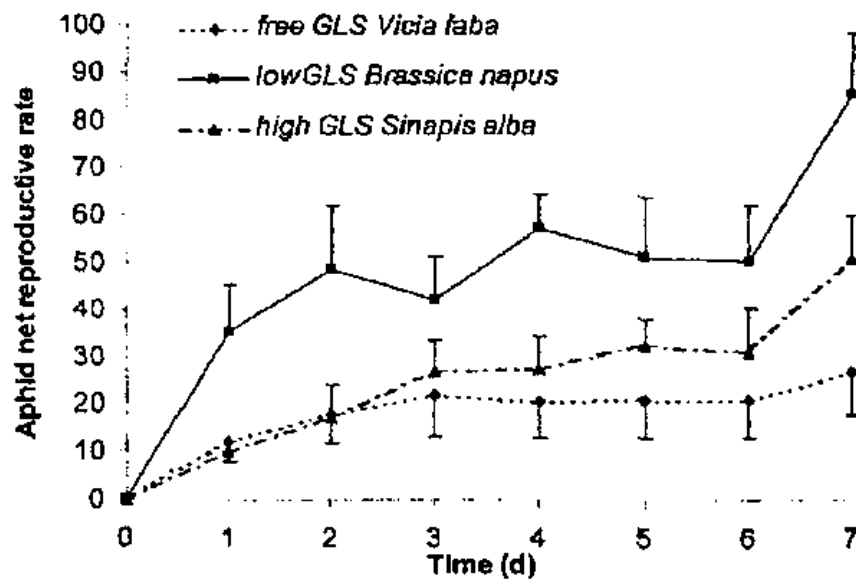

Fig. 1. Effect of the host plant on the Myzus persicae *net reproductive rate. Daily means were calculated on 10 replicates. Error bars represented standard deviation of the means.*

Performance Parameters of *Adalia bipunctata*. Mortality and Development Duration.
Lady beetle mortality differences were not significant (F = 0.45; df = 2,6; P = 0.656), depending on the aphid host plant (Table 1). Development durations of *A. bipunctata* larvae were significantly different depending on the prey host plant *(F* = 108.13; df = 2,179; P < 0.001). Lady beetles fed with aphids reared on Brassicaceae plants, namely *S. alba* and *B. naptts,* reached the pupa] stage significantly faster than with *M.. persicae* aphid reared on GLS free V. *faba (t —* 11.66, df= 179, P< 0.001 and t = 12.82, df = 179, F< 0.001). There was no significant variation of predator larval duration when the aphid preys were reared on S. *alba* or *B. napus,* the two Brassicaceae species (t = 0.98, df = 179, P = 0.245). Pupal duration of lady beetles fed with *M. persicae* aphid differed significantly following the prey host plant (F = 6.05; df = 2, 179; P = 0.003). Duration related to low GLS *B. napus* was significantly higher than for the two other combinations (*t* = 2.88, df = 179, P = 0.007 and *t* = 3.21, df = 179, P = 0.003.). Total developmental duration of lady beetles fed with *M. persicae* aphid reared on GLS free V. *faba* was significantly higher than the two Brassicaceae species, namely *B. napus* and S. *alba (t* = 10.23, df = 179, P < 0.001 and *t* = 8.82 df = 179, P < 0.001 for *M. persicae* aphid reared on GLS free V. *faba/m. persicae* reared on high GLS S. *alba* and *M. persicae* reared on GLS free V. *faba/M. persicae* reared on low GLS *B. napus* comparisons respectively). No significant difference of development duration was observed between lady beetle larvae fed with aphids reared on high GLS S. *alba* and on low GLS *B. napus* (t= 1.33, df = 179, *P* = 0.164).

Significant differences of predatory beetle adult weight were observed, depending on the host plant that prey were fed (F = 13.03; df = 2,179; P < 0.001). At emergence, adults of A. *bipunctata* lady beetle fed with aphids from either high GLS S. *alba* or low GLS *B. napus* were significantly larger than those fed with *M. persicae* reared on GLS free *V. faba* (t = 4.69, df = 179, P < 0.001 and t = 3.68, df = 179, P < 0.001). There was no significant difference of predator adult weight fed with aphids reared on S. *alba* or *B. napus,* the two

Brassicaceae host plant (t = 0.94, df = 179, P = 0.255).

Lady Beetle Reproduction. Aphid host plant has an effect on A. *bipunctata* fecundity and egg viability (Table 2). Fecundity (number of eggs per female and per day, Fig. 2) was analyzed by two-way ANOVA and revealed a significant interaction between plant and day (F = 2.20; df = 40, 63; P = 0.003). Therefore, a one-way ANOVA had to be performed separately and revealed significant differences according to host plants (F = 10.60; df = 2, 123; P < 0.001). Mean comparison test demonstrated that high GLS *S'. alba* induced lower lady beetle fecundity than GLS free V. *faba* and low GLS *B. napus (t* = 3.63, df = 125, *P* = 0.001 and *t* = 4.27, df = 125, P < 0.001, respectively) when used as prey host plants. The observation day also induced significant differences of predatory beetle fecundity (F = 7.22; df = 20,105; P < 0.001) even if the egg number per female did not significantly change from a day to an other for the first nine days *(t* = 0.24-3.05; df = 125; *P* = 0,985-0.240 depending on the days considered). Significant differences of lady beetle fecundity were observed from the 10th day until the end of the experiment *(t* = 3.81-5.56, df = 125, *P* = 0.03 to < 0.001, depending on the considered days).

Egg viability of the twospotted lady beetle showed highly significant differences (F = 8.96; df = 2,51; P < 0.001), depending on the host plant that was used to feed the prey (Fig. 3). *M. persicae* aphid reared on high GLS *S. alba* induced lower egg hatching than aphid preys reared on low and GLS free plants *(t* = 4.20; df = 101; *P* < 0.001 and (= 2.54; df = 101; P = 0.037 when fed with *M. persicae* reared on GLS free V. *faba* and low GLS *B. napus* respectively).

Table 1.   Developmental performance of the predatory ladybird, Adalin bipunctata, according to the aphid host plant (GLS free Vina fabai*, low GLS* Brassica napus *and high* GLS Sinapis alba*)*

Aphid host plant	Larval development, d	Pupal development, d	Egg to adult development, d	Adult wt, mg	Mortality, %	No. of adults
Vitro *faba*	13.5 ± 0.7a	5.9 ± 0.7a	23.4 ± 1.0a	12.5 ± 1.7a	12.2 ± 4.1a	79
Brassica napus	11.7 ± 0.8b	6.3 ± 0.8b	22.0 ± 0.7b	13.S ± 2.2b	13.3 ± 0.0a	51
Sinapis alba	11.9 ± 0.7b	5.9± 0.4a	21.8 ± 0.8b	14.0 ± 1.6b	15.0 ± 1.7a	52

Numbers are means ± SD. Letters indicate significant differences at P = 0.05.

Clusters of eggs laid by lady beetles were counted daily for 3 wk and were significantly different depending on the prey host plant (F = 17.25; df = 2, 63; P < 0.001) and on the observation day *(F* = 5.84; df = 20, 63; *P* < 0.001). No significant interaction was observed between the host plant and the day (F = 1.20; df = 40, 63; *P* = 0.257). Each host plant was significantly different from the others *(t* = 5.87, df = 125, *P* < 0.001 and *t* = 2,90, df = 125, *P* = 0.013 and *t* = 2.97, df = 125, *P* = 0.01) when fed with *M. persicae* aphid reared on GLS free V. *faba/high* GLS *S. alba,* on GLS free V. *faba/low* GLS *B. napus* and on high GLS *S. alba/\ow* GLS *B. napus* comparisons respectively). Significant differences of predator egg clusters were observed from the fifth day *(t* = 3.86-5.34, df = 125, *P* = 0.04 to < 0.001, depending on the day considered).

Lady beetle fitness was calculated for each prey host plant and were presented in Table 2.

Table 2.   Part of the predatory ladybird, Adalia bipunctata *reproductive performances according to the, aphid host plant (GLS free* Vicia faba*, low GLS* Brassica napus *and high GLS* Sinapis alba*)*

Aphid host plant	Laying/♀/day	Preoviposition duration, d"	Fecundity, egg/♀/day	Total egg viability, %	Fitness (r)[a]
Vicia faba	0.67 ± 0.26a	4.6 ± 1.5a	6.82± 2.78a	64.9 ± 3.9a	0.139 ± 0.016a
Brassica napus	0.53 ± 0.21a	5.0 ± 0.0a	10.35 ± 4.27b	57.6 ± 0.5b	0.160 ± 0.014a
Sinapis alba	0.33 ± 0.12b	3.5 ± 0.7b	4.42 ± 2.65c	48.8 ± 0.5c	0.075± 0.006b

Numbers are means ± SD of daily observations (2l d and 2 replicates, n = 42). Letters within a column indicate significant differences at P = 0.05. " Means and standard deviations were calculated on average number per replicate for each aphid host plant *(n = 2).*

DISCUSSION

Brassicaceae plants such as oilseed rape, *B. napus,* represent a useful model for exploring the impact of allelochemical substances on insects (Pickett et al. 1995). Whether the crucifer secondary substances, such as GLS, displayed deterrent property for many phytophagous insects, several herbivore and ento-mophagous insects were attracted and stimulated to oviposit by these compounds (Lamb 1989, Matsumo 1970). In regard to insect-plant interactions, it is useful to determine the effect of the allelochemicals not only on the herbivores but also on the performance of the natural predator to obtain optimal biological control. Although toxicity of GLS

metabolites from Brassicaceae plant is well known (Erickson and Feeny 1974, Blau et al. 1978), the influence of these substances on predators through aphid prey still has to be determined.

Aphid reproductive rate was positively linked to the Brassicaceae species used as host plant, both low GLS *B. napus* and high GLS *S. alba*. Although white mustard already provided higher reproductive rates of aphids after 1 wk, oilseed rape induced aphid reproduction and corresponded to a 2.57 increasing factor when compared with the GLS free control, *V. faba*. These results are in accordance with previous works which demonstrated that *M. persicae* on oilseed rape produced offspring with higher survival, heavier weight and faster development than aphids transferred to beet (Gladders and Peters 1986). Nault and Slyer (1972) showed feeding behavior increase of *M. per-sicae* when sinigrin, a well known GLS, was present in the aphid diet. In addition to biological observations, chemical analyses of aphids reared on each host plant were performed by liquid chromatography and revealed trhe presence of significant amounts of GLS in *M. persicae* fed on white mustard and rape (Francis et a]. 2001).
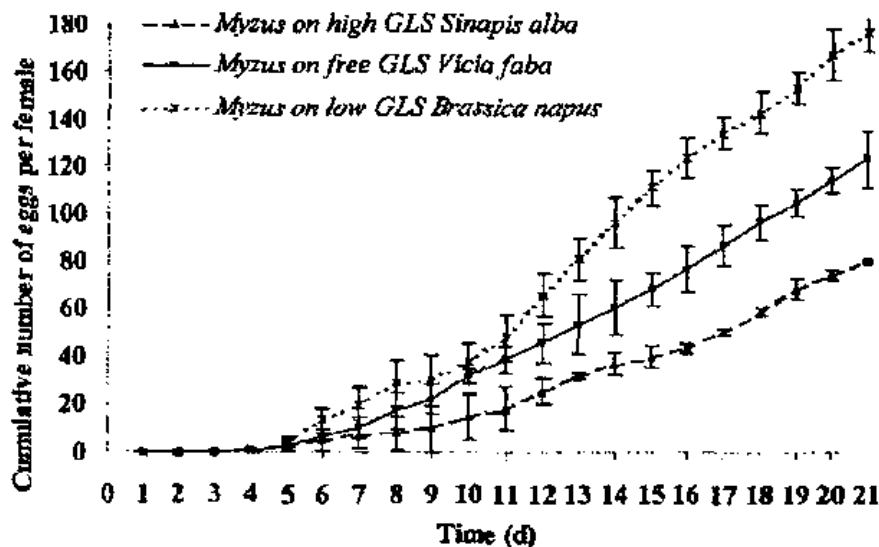

Fig. 2. Effect of the aphid host plant (GLS free *Vicia faba,* low GLS *Brassica* napus and high GLS *Sinapis alba)* on the predatory twospotted lady beetle, *Adalia bipunctata,* fecundity expressed in cumulative number of eggs per female a*nd* per day. Means of daily egg number were calculated on two replicates for each host plant, Error bars represented standard deviation of the means. Time (in days) corresponding to the abscise axis represents duration after adult emergence.
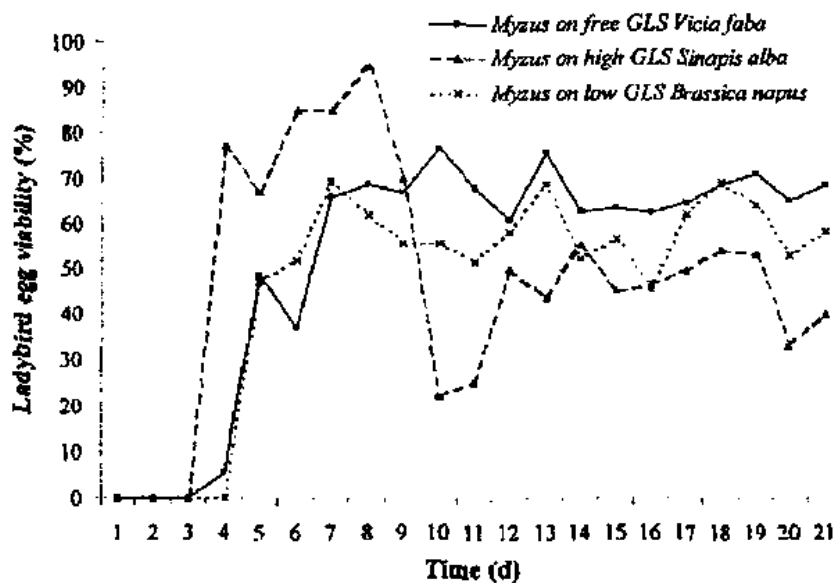

Fig. 3. Effect of the aphid host plant (GLS free *Vicia faba,* low GLS *Brassica napus* and high GLS *Sinapis alba)* on the predatory twospotted lady beetle, *Adalia biumctata,* egg viability expressed as percentage. Daily means were calculated on two replicates for each host plant. Error bars represented standard deviation of the means. Time (in days) corresponding to the abscise axis represents duration after adult emergence.

Current studies suggest that glucosinolates are important feeding stimulants for the Brassicaceae specialist feeder (such as the cabbage aphid, *Brevicoryne brassicae* L.), whereas nutrients, represented by amino acids concentrations, stimulate the generalist *M. persicae* (van Emden 1990). Dixon (1985) suggested a close relationship between nutrition and development. Jansson and Smilowitz (1986) showed that the population growth rate of *M. persicae* was positively correlated with the free amino acid concentrations in potato leaves. Cole (1997a, 1997b) indicated that it was not always the case. Although she concluded that the glucosinolate profiles of Brassicaceae plants had a significant impact on the development and performance of both *B. brassicae* and *M. persicae* aphid species, the regression analysis only showed a significant correlation between phloem amino acid concentrations and the intrinsic rate of increase of *B. brassicae* hut not of *M. persicae.* Moreover, phloem saps of several Brassicaceae species, differing in host suitability to the mustard aphid, *Lipaphis erysimi,* were analyzed for their amino acid composition. The slow population growth of aphids was not found to he related to the total concentration and the individual composition of amino acids. The difference of aphid reproductive rate was estimated to be due to other than nutritional factors of phloem sap (Weibull and Melin 1990).

If plant composition, such as GLS content, induce changes in aphid biological parameters, what is the effect of these substances on pest predators? A closed relation can be assumed between the presence of allelochemical substances in aphid preys and the biological variations of the predatory lady beetle parameters such as development durations and adult weight at emergence. In regard to *A. bipunctata* fecundity, *V. faba,* taken as free GLS host plant, corresponded to an intermediate situation between *S. alba* and *B. napus,* the two other Brassicaceae species. Although the former plant species showed a negative effect on two-spotted lady beetle egg production (35% decrease compared with GLS free *V.faba),* low GLS *B. napus* induced a higher egg production of the twospotted lady beetle (43% increase compared with GLS *V.faba).* Our observations are not in complete agreement with some of the general conclusions of previous works. Glucosinolates, such as sinigrin, are known to increase egg production in Brassicaceae related insects, such as *Delia brassicae* L., but resulted in oviposition inhibition to noncrucifer specialists (Lerin 1980). Here, we also reported lower fecundity when the twospotted lady beetles were fed aphids reared on high GLS *S. alba,* but an increase of egg production was observed in die twospotted lady beetle, a generalist predator, in the presence of low GLS content in *B. napus* as aphid host plant. The continuous decrease of lady beetle egg viability seemed to be linked to the increase of GLS levels in plants. After the ninth day, there was an inversion of the aphid host plant effect on the predator egg viability. Indeed, this phenomenon could he linked to a GLS accumulation from ingested prey, which induced a delayed sublethal toxicity. Even if no direct effect of allelochemicals from the plant through the aphid prey on the predator (no toxicity during insect development) was observed at the beginning of the experiment, GLS in *M. persicae* aphid could influence the lady beetle reproduction rates. It has been postulated that aphids containing toxic substances obtained them from the host plant. By example, the adverse effect of *Aphis sambuci* L. was due to the presence of the glu-coside sambugrinin (precursor of hydrocyanic acid) in *Sambuscus nigra* L. (Hodek 1967). Other aphid species have been shown to be poisonous and rejected by coccinellid predators because of the allelochemical presence from plants. As examples, *Macrosiphum ac-onitum* vander Goot feeding on *Aconitum* sp. (including aconitin), *Aphis nerii* Boyer de Fonscolombe infested oleanders (including oleadrin and neriin), *Macrosiphum albifrons* Essig and *Aphis jacobaeae* Schr. feeding on *Lupimts mutabilis* L. (including quinoliz-idine alkaloids) and *Senecio* sp. (including pyrolizidine alkaloids), respectively, were reported by Hodek and Honek (1996). Even if no toxicity was induced, the prey host plant had an important impact on both development and reproduction of aphidophagous predators such as *A. bipunctata.* When lady beetle fitness were calculated using high GLS *S. alba* as aphid host plant, the latter significantly reduced beetle fitness (half value compared with GLS free *V.faba* plant). The fitness consequences of feeding aphidophagous hoverflies *(Epi-syrphus balteatus* Degeer and *Syrphus ribesii* L.) on different prey species were studied by Sadeghi and Gilbert (2000). The authors demonstrated that fitness was broadly constant with some exceptions. Differences in quality among aphid are not consistent among studies even using the same predator species, suggesting that variable host plant chemistry might be the source of tritrophic interactions. The role of aphid toxins as a defense against the predators was one of the potential explanations. Here we confirmed that prey hosl plant such as *B. napus* and *S. alba* containing GLS compounds can strongly influence the fitness of aphi-dophagous insects.
Taking into account the relationship between herbivore pests and host plants on one hand, and given the increasing knowledge of the plant allelochemicals, however, the chemical ecology aspect of the plant-insect relationships will undoubtedly be a starting point to develop alternative control measures in integrated pest management programs. The current work illustrates the biological effects of allelochemicals from aphid host plant on the development and reproduction of one of ils predators. The knowledge improvement of the impact of the secondary plant compounds such as glucosinolates is critical to understanding the tritrophic interactions between plants and insects. Sequestration of allelochemicals by aphids might provide protective compounds against their predators. The differences in secondary plant substance composition and utilization by specialist and generalist pests may constitute useful information in further studies designed to develop biological control of

aphid pests by beneficial insects.

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