

Plant Volatiles Mediate Tritrophic Interactions

Barley, aphids and ladybirds

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Abstract

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The effects of plant-plant interactions via volatiles (aerial allelopathy) on herbivores and their natural enemies were investigated. The model system consisted of four barley varieties, an aphid pest, *Rhopalosiphum padi* (L.), and a common aphid predator, ladybird, *Coccinella septempunctata* (L.).

Aerial allelopathy significantly affected plant leaf temperature and biomass allocation, favouring root growth during the vegetative period, the main period for development of *R. padi* populations in Swedish barley fields. There was no effect of aerial allelopathy on relative growth rate and total biomass. A decrease in biomass allocation to the leaves was compensated for by an increase in specific leaf area. Significant changes in leaf temperature and biomass allocation of responding plants showed that the allelopathic effect was systemic. The effects were strictly dependent on which genotypes were combined, and the capacity of a plant to cause allelopathic induction was not necessarily linked to its capacity to respond.

The four barley cultivars used did not differ in aphid attractivity and acceptance when tested separately. In specific cultivar combinations aerial allelopathy caused significant changes in both laboratory and field experiments. The results from field and laboratory conditions were not immediately congruent. There were differences between those cultivar combinations that caused changes in leaf temperature and those that affected aphid acceptance, indicating that the aphid response was not merely an effect of temperature preference. There were no differences in olfactory attraction of aphids to different cultivars, but significant changes were induced by aerial allelopathy.

Olfactometer experiments with ladybird showed that aphid-attacked plants and previously attacked plants with the aphids removed were more attractive than undisturbed aphids or undamaged plants. Olfactory cues contributed to aggregation of ladybird adults in weed-infested plots in a barley field. Adults of ladybird responded positively to a mixture of barley-weed volatiles but a more complex mechanism possibly involving aerial allelopathy cannot be excluded.

It is concluded that plant-plant interaction in the barley-weed-aphid-ladybird system has a significant effect on each trophic level *i.e.* plant physiology and development, aphid host plant relations and the searching behaviour of a common predator.

Keywords: *Coccinella septempunctata*, *Rhopalosiphum padi*, *Hordeum vulgare*. aerial allelopathy, plant-plant interaction, biomass allocation, aphid acceptance, olfactory response.

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Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Ninkovic V. Effects of plant-plant communication in barley on biomass allocation. (Manuscript).
- II. Pettersson, J., Ninkovic, V. & Ahmed, E. 1999. Volatiles from different barley cultivars affect aphid acceptance of neighbouring plants. *Acta Agriculture Skandinavica Section B, Plant and Soil* 49, 152-157.
- III. Ninkovic, V., Olsson, U. & Pettersson, J. 2002. Mixing barley cultivars affect aphid host plant acceptance in field experiments. *Entomologia Experimentalis et Applicata*, in press.
- IV. Ninkovic, V., Al Abassi, S. & Pettersson, J. 2001. The influence of aphid-induced plant volatiles on ladybird beetle searching behavior. *Biological control* 21, 191-195.
- V. Ninkovic, V. & Pettersson, J. 2002. Searching behaviour of the sevenspotted ladybird, *Coccinella septempunctata* (L.) – effects of plant-plant odour interaction. (Submitted manuscript).

Papers II, III and IV are reproduced by permission of journals concerned.

Introduction

Plants constitute a dynamic food resource for herbivorous insects. Factors such as environmental stress, developmental stage and plant genotype affect host plant quality (Larsson, 1989; McMillin & Wagner, 1995). Coexistence with other plants is the most common type of biotic challenge that a plant individual is exposed to. This may change the physiology of a responding plant with implications for its quality as a food plant, and plant cues used by insects in host plant location and food quality evaluation. Biochemical interactions between plant individuals is called allelopathy and has been defined as 'any direct or indirect harmful or beneficial effect by one plant (including micro-organisms) on another through production of chemical compounds that escape into the environment' (Rice, 1984). The mechanism was first described by Molisch (1937) who named it 'allelopathy' after the Greek *allos* 'of each other', and *pathos*, 'to suffer'. The term allelopathy covers both inhibitory and stimulatory effects of plant interactions. Allelopathy has long been part of agricultural science and has been shown to affect many aspects of plant coexistence and competition (Rice, 1984; Rizvi & Rizvi, 1992). Plinius (first century A.D.) wrote that some plant species such as chickpea *Cicer arietinum* L., barley *Hordeum vulgare* L., and fenugreek *Trigonella foenum-graecum* L., were reported to 'scorch' cornland.

Allelopathic compounds may be released from plants into the environment in different ways, such as volatilisation through aerial parts of the plant, exudation from the roots, leaching from above ground parts of the plant by rain, fog and dew and by leaching from plant residues (Fig.1). The compounds are referred to as allelochemicals, and are usually non-nutritional chemicals that affect the growth and development of neighbouring plants to an extent depending on concentration and environmental condition (Lovett *et al.*, 1989; Rice, 1984). Many allelochemicals and secondary metabolites produced by higher plants with the potential to control pests, diseases and weeds have been identified (see review Misutani, 1999). From an ecological perspective their role is still only partly understood (see Heldt, 1997; Reigosa *et al.*, 1999).

Volatile plant-plant interaction (aerial allelopathy) may affect target plants by changing their phenotypic level of resistance (Karban *et al.*, 2000). Volatiles from herbivore-attacked plant individuals induce a defence response in neighbouring, non-attacked plants making them less attractive for herbivores. The first reports of this phenomenon however (Rhoades, 1983; Baldwin & Schultz, 1983; Bruin *et al.*, 1992) met some criticism, focusing on the experimental design (Fowler & Lawton, 1985; Karban & Baldwin, 1997). However, later investigations have supported the principal findings in plant-plant interaction (Bruin *et al.*, 1995; Pettersson *et al.*, 1996, Bruin & Dicke, 2001; Farmer, 2001). Induction in neighbouring plants is not exclusively dependent on herbivory. Mechanically damaged plants may also produce signals that are transmitted as volatiles to undamaged plants and induce defensive responses to herbivores (Karban *et al.*, 2000). Allelopathic interaction between undamaged plants can also affect the plant/herbivore relation. Farmer & Ryan (1990) found that undamaged *Artemisia tridentata* Nutt., produces methyl jasmonate, which can induce the accumulation of proteinase inhibitors in leaves of

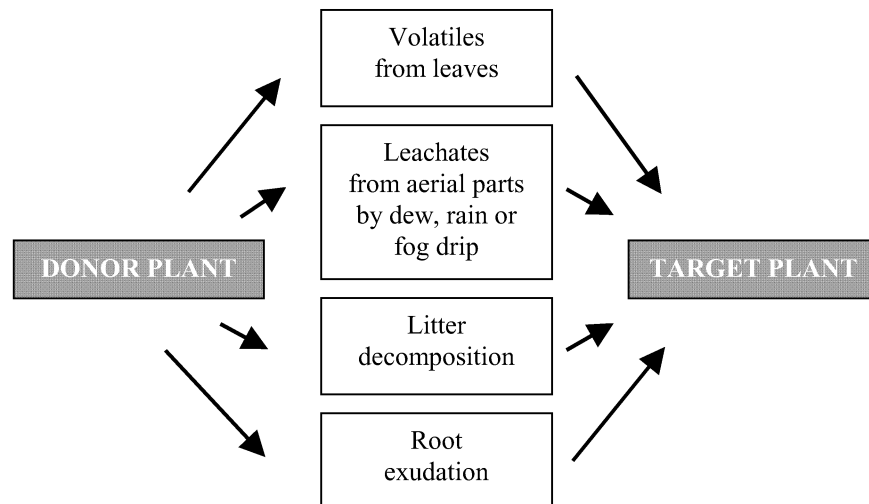


Fig. 1. Conceptual allelopathic interaction between plants mediated by allelo-chemicals.

neighbouring tomato plants. This shows that interspecific aerial allelopathic interactions can activate the expression of genes involved in defence. Based on experiments with aphids, powdery mildew and thrips, Pettersson *et al.* (1996) suggested that induced defence in plants might be comparatively non-specific.

Plant volatiles can also influence the searching behaviour of natural enemies of herbivores. Herbivore-attacked plants release chemical signals that serve as important olfactory cues for parasitoids (Du *et al.*, 1998; Grasswitz & Paine, 1993; Powell *et al.*, 1998; DeMoraes *et al.*, 1998; Guerrieri *et al.*, 1999; Van Loon *et al.*, 2000) and predators (Vet & Dicke, 1992; Drukker *et al.*, 1995; Ninkovic *et al.*, 2001; Dicke, 1999; Sabelis *et al.*, 1999). Also uninfested plants exposed to volatiles from herbivore-attacked plants may release volatiles that attract natural enemies to pest infested areas (Bruin *et al.*, 1992 & 1995). Furthermore, in some cases, natural enemies can use volatiles emitted by undamaged plants to locate the potential habitats of herbivores (Benrey *et al.*, 1997; Elzen *et al.*, 1983; Takabayashi *et al.*, 1998).

Principal aims of this thesis

The present thesis is a study of mechanisms of how plant-plant interactions may affect herbivores and their natural enemies. A model system consisting of four barley cultivars, the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), and a ladybird, *Coccinella septempunctata* (L.), was chosen for the experiments. The conceptual structure of the thesis is shown in Fig. 2.

The following general questions were addressed:

1. Does aerial allelopathy between barley cultivars affect biomass allocation between different plant organs during the vegetative growth period? Can this type of plant interaction affect plant evapotranspiration (leaf temperature)? (*Papers I and II*).

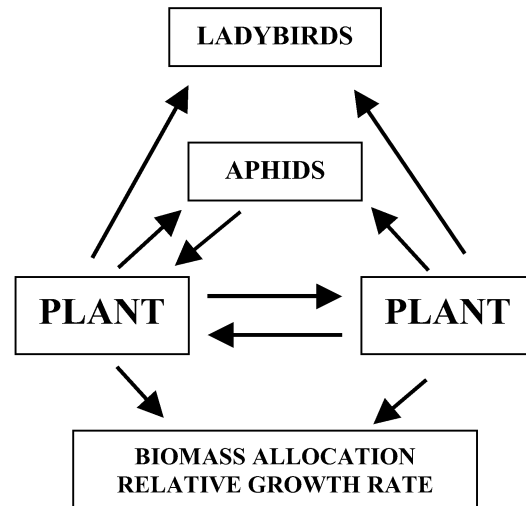


Fig. 2. Conceptual structure of investigated tritrophic interactions.

2. Do volatiles from one undamaged plant affect aphid acceptance of another plant under laboratory and field conditions. Is the effect of barley cultivar interaction on aphid acceptance genotype specific? (*Papers II and III*).
3. How important are volatiles from plants as stimuli for a polyphagous predator, a ladybird? This question was subdivided into:
 - a) Is the behavioural response of the ladybird stimulated by volatiles from infested plants, previously attacked plants, uninfested plants or from aphids alone? (*Paper IV*).
 - b) How do different plant species in mixed stands, and their aerial allelopathic interactions affect the foraging behaviour of the ladybird under field and laboratory conditions? (*Paper V*).

Model system

Plant - Barley

Barley, *Hordeum vulgare* L., is believed to have originated from a wild form, usually designated *H. spontaneum*, in western Asia and northern Africa (Harlan, 1995). Barley is very adaptable and is now grown in all temperate regions from the Arctic Circle to high mountains in the tropics.

Barley is well known as an allelopathically active crop and one of the earliest reports on its allelopathic potential came from Plinius (first century A.D.). In recent literature there are numerous accounts of allelochemicals found in barley. Overland (1966) showed that barley plants delay germination and inhibit growth of *Stellaria media* (L.), *Capsella bursa-pastoris* (L.), and *Nicotiana tabacum* L., but not *Triticum aestivum* L.. Liu & Lovett (1990, 1993) confirmed that root exudates from barley plants have allelopathic effects on white mustard *Sinapis alba* L., when

the two species are sown together. The biological role in plant-plant interactions and defence to pests and diseases of some known compounds has been examined and reviewed by Lovett & Hoults (1995). The germination of *Sinapis arvensis* L., was not affected by barley root exudates, but root and hypocotyl growth was inhibited (Baghestani *et al.*, 1999). The authors suggested that the allelopathic compounds, vanillic acid, o-coumarin and scopoletin, may induce this effect. It is well known that mixing of cultivars can reduce the overall incidence of plant pathogens (see review Wolfe, 1985). Even mixing susceptible barley cultivars can give enhanced levels of resistance to powdery mildew (Ibenthal *et al.*, 1985; Newton & Thomas, 1992).

Barley is sensitive to allelopathic provocation from other plant species. Water extracts of shoots and roots of goosefoot, *Chenopodium murale* L., (10-100% conc.) inhibited germination of seeds, and root and shoot growth of seedlings of wheat and barley. Barley showed more sensitivity to allelopathic effects than wheat (Qasem, 1993). Ray & Hastings (1992) reported that barley tolerance to allelochemicals produced by weeds is genotype specific.

However, the emitted volatiles may also be messengers in interaction with neighbouring plants (*sensu* Molisch, 1937; Rice, 1984). In an interspecific aerial allelopathic interaction, volatiles released from leaves of *Artemisia tridentata* Nutt. var. *vaseyana* (Weaver & Klovich, 1977) and sasa, *Sasa cernua* Makino, (Li *et al.*, 1992) inhibited the growth of barley seedlings and decreased the respiration rate of germinating seeds. These and some other negative effects on barley plants *e.g.* lowered content of water and chlorophyll, were observed in experiments with crude volatile oils and the pure terpenes from leaves of *Eucalyptus globulus* (Labille.) and *E. citriodora* (Kohli *et al.*, 1991). It should be noted that barley is sensitive to volatile compounds from other species even if it is not a significant emitter of them itself. For instance, plants exposed to isoprene gas flowered significantly earlier (Terry *et al.*, 1995) and the leaf temperature of plants exposed to methyl salicylate was significantly changed (Ninkovic *et al.*, unpublished) in comparison with unexposed plants.

Intraspecific aerial allelopathic interactions between plants have rarely been studied. In the case of interaction between barley plants, this phenomenon has been addressed in very few studies and only from the viewpoint of induced resistance. Fujiwara *et al.* (1987) reported that volatile compounds that were released after pruning of barley leaves induced systemic resistance against powdery mildew fungus in intact barley seedlings. This resistance was more prominent in the primary leaf than in the secondary leaf. From the perspective of plant resistance to aphids, Pettersson *et al.* (1996) tested aphid acceptance of plants at the two-leaf stage that were exposed to volatiles from aphid attacked plants or to powdery mildew infested plants. In both cases aphid acceptance of volatile exposed plants was significantly decreased in comparison with plants treated with clean air. The results of these two studies also support that there is a link between induced resistance to herbivores and disease (Walling, 2000).

Four spring barley cultivars were chosen for experiments in this thesis, Alva, Kara, Hulda and Frida. They differ in some genes for resistance to powdery mildew, *Erysiphe graminis* f. sp. *hordei* (see Table 1 in Paper II) and have, as a

quartet, performed well in experiments with mixed cultivars to control this disease (Wiik, 1987).

Herbivore - Aphid

Aphids are important pests mainly in the temperate regions of the world, and the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Homoptera: Aphididae), is a key pest in cereal crops in Sweden (Wikteliuś *et al.*, 1990) as well as in many other European countries (Leather *et al.*, 1989; Hansen, 1995). It damages plants both by direct feeding and by the transmission of plant viruses such as barley yellow dwarf virus (BYDV).

R. padi is a host-alternating species that has bird cherry, *Prunus padus* L. (Rosaceae), as a winter host and a range of grasses, (Poaceae), including cereals as summer hosts (Blackman & Eastop, 1984 ; Leather & Dixon, 1982; Wikteliuś, 1987). Autumn migrants (gynopare) and males are produced on grasses and re-colonise the winter host. According Dixon & Glen (1971), autumn migrants are produced in response to short day length and low temperatures.

In Sweden *R. padi* hibernates as eggs on the winter host. After egg hatching, aphid colonies develop on young leaves and shoots. After two to three generations, alate spring migrants develop and migrate to summer hosts. The development of migrants is initiated by crowding (Wikteliuś *et al.*, 1990) and decreasing food quality (Dixon, 1998). Damage caused by aphid feeding induces the production of methyl salicylate in the winter host which acts as a repellent for alate spring migrants and induces take off (Glinwood & Pettersson, 2000 a, b).

R. padi is polyphagous and may appear on different grasses, including winter and spring cereals. Although some grasses may be preferred, spring sown cereals are the optimal summer hosts, offering high quality food during the early part of the summer (Wikteliuś *et al.*, 1990; Rautapää, 1976; Leather & Dixon, 1982). Aphids have a high capacity for reproduction and intrinsic rate of increase (Dixon, 1998). The response of the host plant to aphid attack is partly expressed as a loss of water. However, aphid saliva also contains a considerable amount of enzymes that affect the attacked plant (Miles, 1999). It has been shown that, over a shorter time perspective *i.e.* during the establishment of the aphid colony, these enzymes cause a change in the attacked plant that improves its food quality (Way & Banks, 1967). At high aphid population densities the damage caused is so serious that plant tissue die. This effect on the plant forces the aphids to leave earlier than if the attack had been less vigorous (MacKay & Lamb, 1996). In general, summer migration by alatae is promoted by crowding and decreasing plant quality (Walters & Dixon, 1982; Wikteliuś *et al.*, 1990). However, a more subtle response to increasing population is shown by apterae (Pettersson *et al.*, 1997; Quiroz *et al.*, 1997) as an increased mobility induced by density related semiochemicals. The search for new host plants and feeding sites by aphid individuals is a stepwise procedure in which a range of different stimuli are important (Fig. 3).

Landing of alatae of *R. padi* is elicited by visual stimuli (Åhman *et al.*, 1985; Nottingham *et al.*, 1991). Studies with different arrangements of coloured traps have shown that aphids usually prefer to land on yellow surfaces (Moericke, 1955,

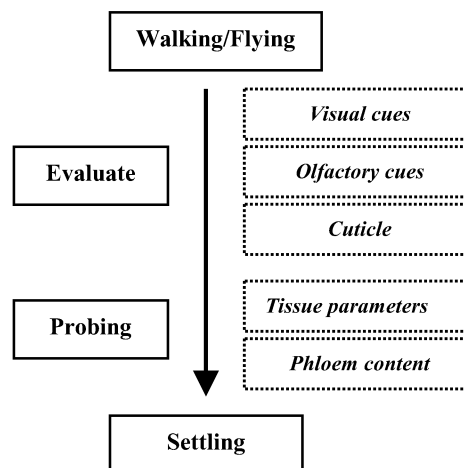


Fig. 3. Conceptual model of aphid settling

1969; Prokopy & Owens, 1983; Åhman *et al.*, 1985; Robert, 1987). However, experiments with monochromatic light showed that *R. padi* and *Aphis fabae* Scopoli, were more sensitive to the green region of the spectrum (Hardie, 1989; Nottingham *et al.*, 1991). Differences between morphs were found in the duration of migratory behaviour and the start of maiden flight (Kennedy & Booth, 1963; David & Hardie, 1988) and the readiness to land increased after starvation (Hardie & Schlumberger, 1996).

Aphids do respond to plant volatiles both in trapping experiments and in olfactometers. Chapman *et al.* (1981) reported odour induced orientation by *Cavariella aegopodii* (Scopoli) towards the host plant volatile carvone in field experiments. Walking apterae also respond to volatiles from host plants in olfactometers (*e.g.* Pettersson, 1970, 1973; Nottingham *et al.*, 1991; Pettersson *et al.*, 1994). Volatiles from oat and wheat plants were attractive to both winged and unwinged morphs of *R. padi*, but their responses differed between different fractions of volatiles (Quiroz & Niemeyer, 1998). It has also been shown that non-host odour can repel walking apterae (Nottingham *et al.*, 1991; Hori, 1999). With electrophysiological methods it has been shown that the aphid antenna carries a series of olfactory organs that contain cells responsive to a range of plant volatiles (Anderson & Bromley, 1987; Pickett *et al.*, 1992; Visser & Piron, 1997; Park & Hardie, 1998). Olfactory organs in the alate antenna are the primary (one on each of the two last antennal segments) and secondary rhinaria, while the antennae of nymph and adult apterae have only primary rhinaria (Pickett *et al.*, 1992). The secondary rhinaria have been proposed to respond to sex pheromone (Marsh, 1975; Eisenbach & Mittler, 1980).

Plant stimuli may also be involved in finding the best feeding site on the host plant. *R. padi* commonly prefer parts of cereal seedlings just beneath the soil surface, but at the beginning of ear emergence they are usually found on the upper leaves (Wiktelius *et al.*, 1990). It has suggested that the apical antennal hairs of

Myzus persicae (Sulz) are contact chemoreceptors used by walking aphids to detect non-volatile cues associated with the cuticle (Bromley *et al.* 1980; Powell *et al.*, 1995). With down waved antennae aphid can touch leaf surface and detect non-volatile chemical cues associated with the cuticle.

One of the better known phagorepellents affecting aphid feeding is DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) in wheat, which delays phloem activity during aphid probing (Givovich & Niemeyer, 1991; Givovich *et al.*, 1994). Some stimuli are associated with the quality of plant sap as aphid food and are related to the content and composition of amino acids (Weibull, 1988; Sandström, 1998) and a type of storage carbohydrate (Weibull, 1990). According to Tjallingii & Hogen Esch (1993), aphid stylets penetrate between cells towards the phloem, but almost every cell is sampled along the way. Most plant allelochemicals are stored inside cells and the aphid thus avoids an important component of the plant's defence. However it is still likely that chemicals from sampled cells are token stimuli for host plant selection (F. Tjallingii, personal communication).

Natural enemy - Ladybird

The seven-spotted ladybird, *Coccinella septempunctata* (L.) utilises an extensive range of prey including aphids and other small insects but it also willingly eats pollen from different plants (Triltsch, 1997). It hibernates as an adult in aggregations in prominent places in the landscape such as water towers, ridges, hills etc. usually on the ground near the bases of grass tussocks, under fallen leaves, and under stones (Hodek & Honek, 1996). Overwintering places are often utilised year after year and the hibernating insects are usually found in groups. It has been suggested that this behaviour is supported by pheromones, and some volatile compounds that may mediate aggregation have been identified (Al Abassi, *et al.*, 1998). In the spring, adults disperse from the hibernating sites searching for food and suitable places for oviposition (Majerus, 1994). Newly emerged larvae eat aphids and, if aphids are in short supply, their first meal may be the egg case. Cannibalism of eggs is common among newly emerged coccinellid larvae. Agrawala & Dixon (1993) showed that young larvae, that have dispersed from their egg clutch, prefer the eggs laid by other females than those laid by their own mother. However, factors regulating food searching are still only partly understood.

Previously, many scientists (*e.g.* Bänsch 1964; Banks, 1957) believed that neither visual nor olfactory cues were important in the prey searching behaviour of ladybirds until physical contact occurred. It is suggested that ladybirds have two main types of prey-habitat location. One of them is long-range location of habitats, which operates over (at least) several meters. This mechanism places the ladybird in the correct habitat with its prey (Hodek, 1973). Visual stimuli are possibly important in the long-range location of habitats for some species (reviewed by Dixon, 2000). However, *C. septempunctata* did not differentiate between short and tall objects, even though this ladybird species prefer herbaceous plants (Khalil *et al.*, 1985).

The second main mechanism of prey-habitat location is area-restricted search. This mechanism provides signals that are used as cues by ladybirds to locate which

individual plants carry prey insects. A combination of visual and olfactory cues from host aphids attracted *Harmonia axyridis* (Pallas), (Obata, 1986). In olfactometry experiments, Ponsonby & Copland (1995) showed that *Chilocorus nyctus* (F.) was attracted to the combination of host plant and host insect volatiles. Thus in addition to being attracted by combination of plant and host odours adults subsequently intensify their searching on patch location (area-restricted search). They move more slowly and turn more frequently in the presence than in absence of the odour of their prey (Sengonca & Liu, 1994).

During close contact with aphids visual cues may play a role. Harmon *et al.* (1998) reported that *C. septempunctata* consumed more of the one of two colour morphs (red and green) of pea aphid that contrasted most with the background colour. Searching can also be enhanced by chemoreception of arrestant host cues such as odour from honeydew (Carter & Dixon, 1984; Heidari & Copland, 1993), wax (Van der Meiracker *et al.*, 1990) and aphid infested host plants (Obata, 1986, 1997; Ninkovic *et al.*, 2001). It has been reported that *C. septempunctata* (Al Abassi *et al.*, 2000) and some other ladybirds species can detect aphid alarm pheromones using them as means of finding its prey (Nakamuta, 1991; Acar *et al.*, 2001). Additionally, ladybirds can detect and orientate to individual prey prior to actual physical contact. In simple arenas, *C. septempunctata* can detect prey up to a distance of 1 cm (Nakamuta, 1984).

Experiments, results and discussions

Plant expression of the effects of plant-plant interaction

(Papers I and II)

Plants living together in communities may interact and compete in different ways to optimise their use of available resources (*e.g.* Tilman, 1988). In these interactions a variety of allelochemical compounds may be active in different ways (Rice, 1984), affecting the growth of plants and their organs. Patterns of biomass allocation between different plant organs have often been used to explain the response of plants to variations in resource availability (Glimskär & Ericsson, 1999).

Effects of plant-plant interaction on biomass allocation of barley plants

The aim of the studies was to investigate whether the aerial allelopathy shown to affect aphid preference (*Paper II, III*) also affects biomass allocation between different plant organs *e.g.* leaves, stem and roots (*Paper I*). How the change in biomass allocation can be reflected in relative growth rate (RGR) and its morphological and physiological components is outlined in Fig. 4. An important physiological component is unit leaf ratio (ULR), the increase in biomass per unit time and leaf area, which is generally strongly correlated with the rate of photosynthesis per unit leaf area (Poorter & Nagel, 2000). A morphological component can be further subdivided into specific leaf area (SLA), the leaf area

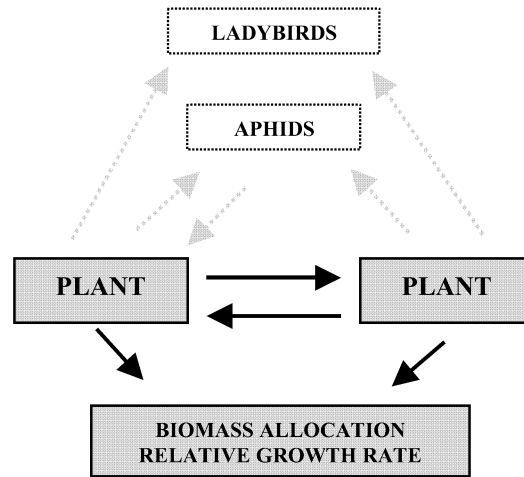


Fig. 4. Allelopathic plant-plant interaction.

per leaf dry weight that reflects aspects of leaf morphology, and the leaf mass fraction (LMF) that reflects biomass allocation to leaves (Poorter & Nagel, 2000). Based on experiments with aphid acceptance (*Paper II, III*), aerial allelopathic interactions between two barley cultivars (Alva and Kara) were selected for studies of biomass effects of allelopathy studies. Exposure of one cultivar to volatiles from the other was carried out in ‘two-chamber cages’ (see figure in *Paper II*) attached to a vacuum tank. The Kara plants were exposed to one of three different treatments: air from Alva, air from Kara or clean air.

The results showed that volatiles from cultivar Alva induced changes in the pattern of biomass allocation in the second cultivar, Kara. Exposed plants allocated more biomass to roots compared with control plants exposed to air from Kara, or to clean air (Fig. 5). However, the total dry weight did not differ between treatments *i.e.* the principal effect is on the allocation of biomass but not on the total biomass, and there were no changes in RGR or ULR. However, when Kara was exposed to volatiles from Alva there was a significant increase in SLA. According to previous studies (Aerts *et al.*, 1991; Boot & Den Duddelden, 1990) a low allocation of biomass to the leaves can be compensated for by high SLA, which is in line with the results of this study.

Thus the results show that aerial plant-plant interaction does not affect total biomass production but does significantly affect biomass allocation in individual plants. There may be differences in the pattern of volatiles of Kara and Alva that induce increased biomass allocation to roots in the exposed Kara plants. The observed influence of one cultivar on another cultivar probably has implication for competition. More roots may be of advantage in a dry situation, increasing stress tolerance. Obviously, such variation would increase the phenotypic stability of mixture of these cultivars, and thus be of competitive advantage.

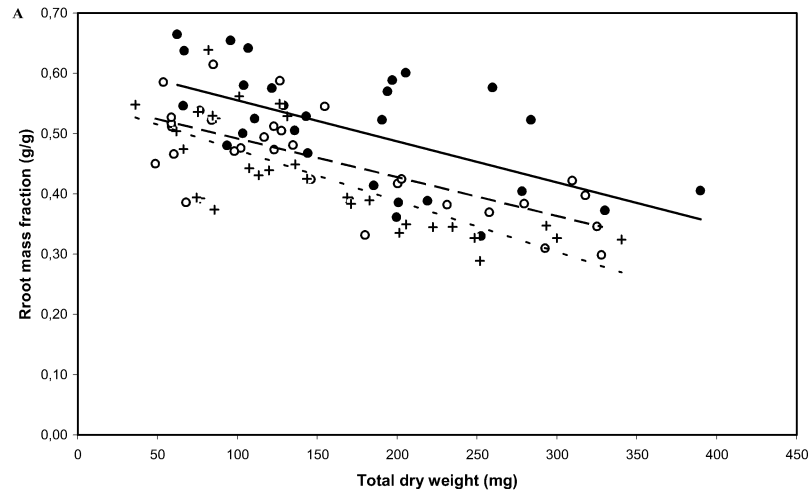


Fig. 5. The tested effects of plants odour on biomass allocation to roots (RMF). Fitted lines of exposed plant of Kara to different volatiles sources: • and — (AK) to volatiles from plants of Alva, ○ and - - - (KK) to volatiles from Kara and + and - . - (OK) to plain air.

Plant-plant interaction and leaf temperature

In laboratory experiments, effects of aerial allelopathic interaction in barley plants exposed to volatiles from undamaged barley plants were measured in terms of changes in leaf temperature. Chaerle *et al.* (1999) used the same parameter in studies on plant pathogens to detect early stages of infestation. Recently this method has been used in studies of plant stomatal role and conductance (Jones, 1999).

After exposure to air from another plant (achieved using ‘two-chamber cages’ (see figure in *Paper II*)), leaf temperature was measured with an infra-red camera. The leaf temperature of plants exposed to volatiles emitted by another cultivar was compared with leaf temperature of two types of control plants. First type of control plants were exposed to air passing no plant at all (non-inducing control), and second control plants were exposed to volatiles from the same cultivar (self-inducing control). To test self-inducing effects (intracultivar interaction) comparisons were done between self-inducing and non-inducing controls.

The majority of the significant changes relate to decreased temperatures in exposed plants (see *Paper II*). The effect was statistically significant only when certain cultivars were combined. Eight of 12 cultivar combinations of cultivars exposed to volatiles emitted from another cultivar showed significantly changed leaf temperature in comparisons to leaf temperature of non-induced controls. When cultivars exposed to volatile from other cultivars were compared with self-induced controls, the number of significant changes was reduced to four. Significant self-inducing effects were found in two of four tested cultivars.

Leaf temperature is regulated by evapotranspiration, which in turn is partly dependent upon plant physiological status and weather conditions. The results

indicate firstly that volatiles from plant individuals can affect the evapotranspiration level of leaves on other plants, and secondly that the response of the exposed plant may be systemic. The changed evapotranspiration can be partly explained by significantly increased biomass allocation to roots in plants exposed to volatiles from different cultivars (*Paper I*). The present results (*Papers I, II*) are also in line with the previous assumption of a strong positive correlation between evapotranspiration and root biomass allocation (Sims & Percy, 1994).

The effects of different cultivar combinations are not congruent with regards to the change in leaf temperature and aphid acceptance (*Paper II*), which is an indication that the aphid response is not merely an effect of temperature preference. This may also suggest that the leaf temperature changes do not fully reflect the physiological response of the recipient plant expressed in changed aphid preferences.

Effects of plant-plant interaction on aphid acceptance

(*Papers II and III*)

So far very few studies have been directed towards the effects of allelopathic interaction between plants on aphid feeding behaviour. It has been shown that aphid-attacked plants produce allelopathic volatiles that promote changes in neighbouring plants making them less acceptable for aphids (Pettersson *et al.*, 1996). In olfactometer experiments, it was shown that volatiles from barley plants treated with a mixture of four allelopathic compounds found in root exudates of couch-grass, *Elytrigia repens* (L.) Nevski., repel apterae of *R. padi* (R. Glinwood, personal communication). Although plants usually grow together with other plants that potentially produce allelochemicals, the role of plant allelochemicals is very poorly studied in the context of aphid plant acceptance. Settling of *R. padi* was significantly reduced when barley plants were exposed to allelochemicals from root exudates of living couch-grass *E. repens* plants (R. Glinwood, personal communication). These substances did not affect or stimulated aphid probing when offered to aphids in artificial diets at the same concentrations as applied to the plants. This indicates that the substances affect the physiology of the treated plant rather than the aphids directly by phagostimulation.

Effects of barley-barley interaction on aphid host plant acceptance

In intraspecific studies of plant-plant interaction, the effects of aphid acceptance of a neighbouring plant was tested in greenhouse and field experiments (Fig. 6) (*Paper II, III*). Four barley cultivars were used. In greenhouse experiments, underground communication by roots was prevented.

After treatment, settling of *R. padi* apterae on exposed plants was compared with that on control plants treated with air from no other plant or air from a plant of the same cultivar (*Paper II*). A preference test was used, in which aphids had access to treated and control plants of the same cultivar. After exposure to air from another plant, significant changes in aphid acceptance were found in seven of 16 possible

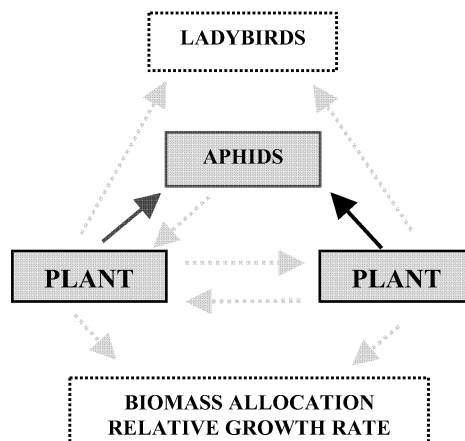


Fig. 6. Allelopathic plant-plant interaction and aphids.

combinations of inducing and responding plants. The change in aphid acceptance was observed only in combinations of certain cultivars, suggesting a genotype-related phenomenon. It was also interesting that changes in aphid acceptance were found in intracultivar interactions. Two of the four cultivars showed this effect (*Paper II*). However, in an untreated state (*Paper II, III*), or in pure stands in the field (*Paper III*), the four barley cultivars did not show differences in aphid acceptance.

In the field experiments, four barley cultivars were sown in pure stands and in pairwise combinations with cultivars side by side in separate rows (*Paper III*). Settling tests were done in situ in the field plots and showed that aphid acceptance changed in some combinations of cultivars. In a laboratory test in which plants of one cultivar were exposed to air from the other cultivars, aphid acceptance was significantly reduced in three of the four cultivars when treated with air from certain other cultivars. Two of these three cultivars showed significant reduction under field conditions but in different combinations. Only Kara showed significantly reduced aphid acceptance both when exposed to volatiles from Alva in the laboratory and when it was mixed with Alva in the field.

All these results support the hypothesis that plant-plant interaction causes responses in neighbouring plants that change aphid host plant acceptance. The results also show that this mechanism is not restricted to optimal growing conditions in the laboratory, although it may be modified under field conditions depending on plant genotype and prevailing growing conditions.

Effects of barley-barley interaction on aphid olfactory response

The odour component of plant-plant interaction, in which aphid settling resistance was induced was tested in two series of olfactometer experiments (Ninkovic *et al.*, unpublished). Plants at the three leaves stage were kept in chambers (see Fig. 1 in *Paper II*) which, after five days of exposure, were directly connected by tubes to

Table 1. *Change in aphid plant attraction after exposure of one barley cultivar to another. AB is a chimney cage where the responding cultivar B was exposed to volatiles from inducing cultivar A. BB is chimney cage with the same cultivars in both chambers, where cultivar B is exposed to volatiles from the same cultivar. 0B is chimney cage without plants in the first chamber, where cultivar B was not exposed to plant volatiles. The number of aphids tested per combination was 20. Data were analysed with Friedman ANOVA. (NS not significant, $P>0.05$).*

Inducing cultivar	Responding cultivar	Sum of number visiting per arm				P value
		AB	0B	BB	Blank	
Alva	Frida	25	20	52	33	NS
	Hulda	40	50	47	41	NS
	Kara	25	20	52	33	0,02
Frida	Alva	32	45	56	34	NS
	Hulda	26	39	34	37	NS
	Kara	15	60	57	40	0,002
Hulda	Alva	26	46	47	43	NS
	Frida	36	38	49	37	NS
	Kara	28	37	31	32	NS
Kara	Alva	37	53	55	38	NS
	Hulda	26	28	19	48	NS
	Frida	37	42	58	36	NS

the arms of a four-way olfactometer (Pettersson, 1970). Air flowing through the system passed over the odour source in the chamber directly connected to the arms of olfactometer, before being drawn out of the centre of the arena from where it was vented through a tube attached to the same vacuum tank used in exposure of the plants. Each of the arm- zones received air from one applied odour source: the odour of plants exposed to volatiles from a different barley cultivar (AB in tables 1, 2), odour from plantsexposed to volatiles from the same cultivar (BB in tables1, 2), odour from unexposed plants (0B in tables1, 2) or clean air (00 in tables1, 2).

Four unexposed barley cultivars were placed in cages connected to the olfactometer to test their inherent attractivity to aphids. No significant differences between the tested cultivars were observed. However, aphid entries into the olfactometer arm were significantly lower in response to volatiles from cultivar Kara exposed to cultivars Alva or Frida, (Table 1). The same combinations were also tested with the inducing cultivars removed from the cages, and only the responding cultivars present. Aphid entries into the olfactometer arm were significantly lower with the inducing cultivar removed only in the combination Kara exposed to Alva (Table 2). This indicates that exposure to volatiles from Alva may induce a systemic change in the volatile profile of Kara, which is in line with results from other experiments (*Paper II, III*). These results also indicate that this

Table 2. Change in aphid plant attraction after exposure of one barley cultivar to another with the provoking cultivars removed after five days exposure. AB* is a chimney cage with different cultivars in the cages where inducing cultivar A was removed. BB* is chimney cage with the same cultivars in both chambers and cultivar B was removed from first chamber. 0B is chimney cage without a cultivar in the first chamber (unexposed cultivar). The number of aphids tested per combination was 20. Data were analysed with Friedman ANOVA. (NS not significant, $P>0.05$).

Inducing cultivar	Responding cultivar	Sum of number visiting per arm				P value
		AB*	0B	0B*	Blank	
Alva	Frida	41	52	30	40	NS
	Hulda	49	48	36	32	NS
	Kara	16	29	38	19	0,03
Frida	Alva	37	39	63	21	0,04
	Hulda	36	33	47	26	NS
	Kara	35	43	55	46	NS
Hulda	Alva	46	38	44	41	NS
	Frida	41	34	61	37	NS
	Kara	32	39	54	25	NS
Kara	Alva	38	54	53	36	NS
	Hulda	28	48	26	22	NS
	Frida	46	48	66	35	NS

phenomenon is genotype specific, not only for the responding cultivar but also for the inducing cultivar.

Effects of plant odours on searching behaviour of ladybirds

(Papers IV and V)

C. septempunctata is an important aphid predator, but its impact as a control agent is variable (Obrycki & Kring, 1998). The searching behaviour of the seven-spotted ladybird has been studied from many perspectives (e.g. Kersten, 1969; Meiracker *et al.*, 1990; Nakamuta, 1991), but so far the effects of herbivore induced volatile semiochemicals and aerial allelopathy have not been considered as factors that affects its behavioural responses.

Odour of aphid infested plants and ladybirds

The literature shows that plant chemical signals emitted from herbivore damaged plants are important cues in the host location process of natural enemies (e.g. Dicke, 2000; see Introduction). Despite the dramatic increase in research in this area in the last 20 years, the role of these types of signals in predator orientation to prey is less well understood (Cortesero *et al.*, 2000). According to Hodek & Honek

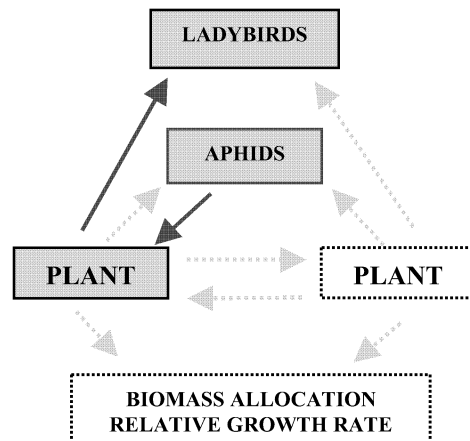


Fig. 7. Aphid induced plant signals and ladybirds.

(1996), the question of whether coccinellids find their prey by visual and/or olfactory cues cannot yet be answered unambiguously.

The olfactory response of adult *C. septempunctata* (Fig. 7) was tested to four sources of volatiles; *R. padi*, *R. padi*-infested barley plants, previously *R. padi*-infested and uninfested plants (*Paper IV*). The aim was to rank these sources according to their influence on food searching behaviour. The volatiles were collected by conventional polymer air entrainment techniques, and used as odour sources in olfactometer bioassays.

Sengonca & Liu (1994) reported that *C. septempunctata* were attracted by volatiles from aphids. However, our results showed that *C. septempunctata* did not respond to volatiles from undisturbed, non-feeding aphids, which is in line with studies by Nakamuta (1984). Adults were significantly more attracted to volatiles emitted by barley plants infested with *R. padi* than to volatiles from uninfested plants. It has been shown that adults of the two-spotted ladybird *Adalia bipunctata* (L.) were more attracted to volatiles from plants of *Vicia faba* L., infested with *A. fabae* than to uninfested plants (Raymond *et al.*, 2000). However, when aphids and aphid products (exuviae and honeydew) were removed from the infested plants, the attraction was lost, so the influence of honeydew and alarm pheromone cannot be excluded in that study. Nevertheless, in the current study previously infested plants were still attractive after the aphids were removed and the plants washed with water. The weak response of ladybird adults to volatiles from uninfested plants indicates that these have a limited impact on prey habitat searching. Hamilton *et al.* (1999) reported that another ladybird species, *Hippodamia convergens* Guerin-Meneville, responded to odours from radish leaves.

The current results indicate that food-searching behaviour of adult seven-spotted ladybird is influenced by volatiles emitted both by barley plants infested with aphids and previously infested plants. It seems that the aphids in this case were undisturbed since there was no response to aphids alone. Disturbed aphids produce alarm pheromone, which attracts *C. septempunctata* (Nakamuta, 1991; Al Abassi *et al.*, 2000) and other ladybirds (Acar *et al.*, 2001).

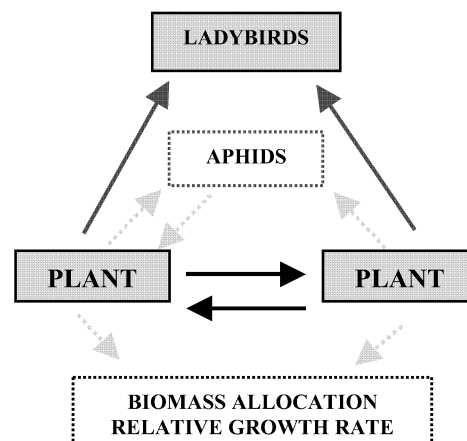


Fig. 8. Allelopathic plant-plant interaction and ladybirds.

Effects of mixed plant odours on ladybirds

It seems to be a general phenomenon that increased botanical diversity reduces pest problems and enhances the impact of natural enemies (Andow, 1991). Although several hypothetical explanations have been suggested the mechanisms behind the positive effects of mixed cropping are still only partly understood, (see Vandermeer, 1992). The effect is usually suggested to be due to increased activity of natural enemies of the herbivores (enemies hypothesis, Root, 1973; Trujillo & Altieri, 1990; Letourneau, 1987) or to difficulty for the pest insect to find its host plants (disruptive crop hypothesis Root, 1973; Feeny, 1976; Vandermeer, 1992). Our main aim was to investigate mechanisms affecting the habitat preferences of *C. septempunctata* (Paper V) (Fig. 8). In a field study, the frequency of adult *C. septempunctata* was higher in barley plots containing high densities of the common weeds *Cirsium arvense* L., and *E. repens* than in control plots with only barley (Paper V).

In view of the ladybird responses to volatiles from aphid-attacked plants, it can be hypothesised that odours may also affect preferences for mixed botanical stands. Thus their importance for the foraging behaviour of *C. septempunctata* was examined in olfactometer experiments using odours from adequate plants from the field observations. Adult *C. septempunctata* showed a significantly stronger attraction to mixed odours of barley and each of the two weeds than to barley alone. Ladybirds responded differently to barley plants that had been exposed to air from the two weeds. The *E. repens*-exposed barley plant lost its attractivity while the *C. arvense*-exposed barley plants maintained attractivity. No differences in ladybird preference were found to odours of the two weeds alone, using barley odour as a control.

As no aphids or pollen were present in the plots during the experiment, the results show that *C. septempunctata* responds to the botanical characteristics of the habitat even if no food resources are available. Tamaki *et al.* (1981) reported that the

occurrence of *Coccinella transversoguttata* Muls., in polycultures is associated with different plants, not with aphid densities. Furthermore, our results strongly suggest that olfactory cues and plant-plant interactions in diversified plant stands can be important mechanisms in predator attraction to sites with a complex botanical diversity even when no aphids are present.

Summary and conclusions

This thesis addressed the question of how aerial allelopathy affects host plants, the aphid, *R. padi*, and its predator ladybird, *C. septempunctata*. The results do not immediately lend themselves to a conclusive discussion linking the different trophic levels together, but each level can be discussed *per se* and hypothetical links can be visualised in the light of existing knowledge.

With reference to the three principal questions raised in the Introduction, the results of the experiments can be summarised and commented on as follows:

1. Does aerial allelopathy between barley cultivars affect biomass allocation between different plant organs during the vegetative growth period? Can this type of plant interaction affect plant evapotranspiration (leaf temperature)? (*Papers I and II*).
 - Aerial allelopathy significantly affected biomass allocation, favouring root growth during the vegetative period, which is the main period for development of *R. padi* populations in Swedish barley fields.
 - There was no effect of aerial allelopathy on the relative growth rate (RGR) and total biomass, but a decrease in biomass allocation to the leaves was compensated for by an increase in specific leaf area (SLA).
 - Effects of aerial allelopathy on biomass allocation and leaf temperature are expressions of a systemic effect in the responding plant.
 - The effects demonstrated were strictly dependent upon which genotypes were combined, and the capacity to provoke effects was not necessarily linked to the capacity to respond to allelopathic induction.
2. Do volatiles from an undamaged plant affect aphid acceptance of another plant under laboratory and field conditions? Is the effect of barley cultivar interaction on aphid acceptance genotype specific? (*Papers II and III*).
 - The four barley cultivars did not differ in aphid attractivity and acceptance when plant individuals were tested separately, but significant effects of intraspecific aerial allelopathy were shown in the laboratory as well as in field experiments.
 - Effects on aphid host plant selection were strictly limited to specific combinations of genotypes and were not immediately congruent under field and laboratory conditions.
 - There was a significant effect of aerial allelopathy (*Paper I*) on leaf temperature (*Paper II*), but results with different cultivar combinations were not congruent with changes in aphid acceptance. This indicates that the aphid response was not merely an effect of temperature preference.

- There was no difference in olfactory attraction of aphids to different cultivars, but significant changes in this response were induced by aerial allelopathy.
- a) How important are volatiles from plants as stimuli for a polyphagous predator, a ladybird? This question was subdivided into:
 - b) Is the behavioural response of the ladybird stimulated by volatiles from infested plants, previously attacked plants, uninfested plants or from aphids alone? (*Paper IV*).
 - c) How do different plant species in mixed stands, and their aerial allelopathic interactions affect the foraging behaviour of the ladybird under field and laboratory conditions? (*Paper V*).
- Olfactometer experiments showed that aphid-attacked plants and previously attacked plants with the aphids removed were more attractive than undisturbed aphids or undamaged plants.
- Olfactory plant cues contributed to aggregation of *C. septempunctata* adults in weed-infested plots in a barley field.
- Adults of *C. septempunctata* responded positively to a mixture of barley/weed volatiles but a more complex mechanism possibly involving aerial allelopathy cannot be excluded.

The experimental results show that aerial allelopathy affects each of the three trophic levels in the model system. This stimulates further work to implement cultural practices based on a better understanding of the active mechanisms in developing sustainable plant production systems.

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