

# Effects of plant competition and herbivore density on the development of the turnip root fly (*Delia floralis*) in an intercropping system

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**Abstract** In this study, interactive effects of plant competition and herbivory on plant quality and herbivore development were examined in a greenhouse experiment where cabbage plants [*Brassica oleracea* L. var. *capitata* (Brassicaceae)] were intercropped with red clover [*Trifolium pratense* L. (Fabaceae)]. Cabbages were grown with two red clover densities and attack rates by the root feeding herbivore the turnip root fly, *Delia floralis* Fall. (Diptera: Anthomyiidae). Above ground and below ground cabbage biomass was reduced through intercropping and larval damage. Intercropping also resulted in lower nitrogen and higher carbon root levels compared with levels in the roots of monocultured cabbage. Furthermore, both root nitrogen and carbon levels increased with herbivory. Root neutral detergent fibre (NDF) and lignin content increased in response to both increased plant competition and higher egg densities. For lignin, an interaction effect was observed in the form of elevated levels in intercropped plants

subjected to larval damage, while levels in roots of monocultured cabbage remained unchanged. The quality changes brought about by clover competition affected *D. floralis* development negatively, which resulted in reduced pupal weight. In addition, increased egg density also decreased larval growth. The effects on the development of *D. floralis* in relation to host plant quality are discussed.

**Keywords** Host-plant quality · Cabbage · *Brassica* · Root herbivory · Induced response · NDF · Lignin

## Introduction

In natural environments, where competition from other plants and attack by herbivores and pathogens are major challenges, plants are often regarded as facing a dilemma in the allocation of resources between growth and defence (Herms and Mattson 1992). Much of the theory surrounding such trade-offs is based on the aerial parts of plants. However, root herbivory interferes with the basic functions of plant roots, including resource uptake (van der Putten 2003), and this may seriously reduce the capacity of the plant to grow or defend itself and thus to compete in natural systems. At the same time, the constraints placed upon the plant by competition from neighbouring plants may change the quality of the plant as a resource for herbivores and influence the manner in which the plant responds to insect attack. There are two major hypotheses concerning the impact of bottom-up effects on insect herbivory. White (1984) proposes in the ‘plant stress hypothesis’ that stressed plants are likely to become more susceptible to herbivores due to the physiological changes that take place in protein synthesis. In contrast, the ‘plant vigour hypothesis’ (Price 1991) predicts that herbivores will preferentially feed on plants or plant

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tissues that are growing vigorously. Empirical evidence exists in support of both hypotheses (Sarfranz et al. 2007).

Intercropping systems often suffer less herbivore damage than monoculture systems (Vandermeer 1989) and have therefore been studied frequently for their effects on herbivore behaviour and abundance of natural enemies (Tukahirwa and Coaker 1982; Booij et al. 1997; Finch and Collier 2000). The impact of intercropping on the host plant and its subsequent effect on herbivore development is less well studied. This is unfortunate, as the population growth rate of the pest population may depend on both the survival rate and size of the offspring, which are ultimately influenced by the quality of the host plant (Awmack and Leather 2002; De Bruyn et al. 2002).

In terms of the nutrient utilisation by plants, intercropping may enhance the efficiency of nutrient use (Willey 1979; Zhang and Li 2003), and thus increase total yield (Skovgård and Pääts 1997; Yildirim and Guvenc 2005). However, when cabbages are intercropped with clover, cabbage yield losses have been reported as a consequence of competition with the companion plant (Langer 1996). In systems such as cabbage-clover, the main agronomic aim is to reduce yield losses due to insect damage, and decreased crop growth due to competition may be accepted as long as pest insects are controlled (Theunissen et al. 1995). However, plants in direct competition with an intercrop are likely to be altered physiologically by that competition. Thus they present a different food source for herbivorous insects when compared with a plant of the same genotype grown in monoculture. Differences in plant composition caused by environmental influences can be expressed in terms of changes in plant nutrient and fibre content (Widdicombe and Thelen 2002) and possible induced responses (Stamp et al. 2004). Any changes in the composition of plant tissues may consequently alter their suitability as a food source (Simpson and Raubenheimer 1995). These effects may thereafter influence the rate of development and survival of an individual herbivorous insect in complex systems according to the degree of plant competition, as well as the degree of herbivore attack.

In this study we examined the interactions between the turnip root fly (*Delia floralis* Fall., Diptera: Anthomyiidae) and cabbage in an intercropping system. The aim was to study how the development of *D. floralis* is affected when the host plant is grown in a cabbage-clover intercropping system compared with a cabbage monoculture. An additional aim was to examine the effect of larval density on both larval development and plant growth. Therefore, cabbage was grown alone or with one out of two red clover densities. We examined *D. floralis* pupal weight and survival on cabbage plants at four different egg application rates. To examine the underlying processes, we measured the effects of plant competition and root herbivory on plant

growth in terms of the weight of cabbage roots and above ground parts at the end of the experiment. We also analysed aspects of plant quality, in the form of the nitrogen and carbon content of roots and shoots, as well as root neutral detergent fibre (NDF) and lignin.

## Materials and methods

### Plant material

Cabbage, *Brassica oleracea* var. *capitata* L. (cv. Castello), and red clover plants, *Trifolium pratense* L. (cv. Betty), were grown in modules (50 mm × 50 mm × 50 mm) containing potting soil (Hasselfors Garden AB, Hasselfors, Sweden). Seven-week-old clover plants and 5-week-old cabbage plants were transplanted into plastic boxes (360 mm × 255 mm × 215 mm) filled with 15 l of a mixture of 1/3 washed sand (grain size 0.5–5 mm) and 2/3 potting soil (Hasselfors Garden AB, Hasselfors, Sweden).

### Insect material

Fly eggs were obtained from a *D. floralis* culture kept at the Department of Ecology (Swedish University of Agricultural Sciences) at 20°C, 70% r.h. and in a L16:D8 regime. The culture was based on pupae collected from a field experiment site growing cabbage at Röbbäcksdalen, Umeå, in the north of Sweden (63°45' N; 20°15' E) in 2002 and 2003 (Björkman et al. 2007). Flies were fed with a standardised diet of honey, milk and yeast-powder (based on Finch and Coaker 1969). A petri dish with a fresh piece of swede placed on moist sand functioned as an oviposition site. Eggs were floated from the sand and sieved through a black cloth before they were inoculated onto the plants.

### Experimental procedure

Cabbage plants were transplanted alone into the boxes (M) or among clover plants growing at one of two densities. Red clover plants were transplanted into the boxes in either one row of four clover plants on each side of the cabbage plant (IC1) or two rows of four plants on each side (IC2). The plant distance within clover rows was 5 cm, and clover rows were planted at a distance of 10 cm from the cabbage in the IC1 treatment. In IC2, the two clover rows on each side were planted at a distance of 10 and 15 cm from the cabbage plants. Cabbage and clover were then left for 2 weeks to establish properly in the boxes before egg inoculation. For the duration of the experiment the boxes were placed in a greenhouse, which was maintained at 17°C during the day and 12°C during the night. Light

conditions were supplemented between 6 am and 9 pm with 400 W sodium lamps when natural light was below 100 W/m<sup>2</sup>.

The total number of boxes in the experiment was 120, and for practical reasons, one complete set of all treatments, hereafter block, was set up per day for ten successive days (i.e.,  $N = 10$ ). Each block contained 4 boxes per plant density treatment, and each box within a plant density treatment was allocated to one of four egg density treatments (0, 10, 20 or 40 *D. floralis* eggs), leading to a total of 12 treatments within each block. The eggs (<24 h old) were inoculated after 2 weeks of plant establishment on to the stem base of the cabbage plants using a fine brush. At the time of egg inoculation, cabbage plants were at the 6–7 true leaf stage.

Throughout the experiment, only water was added to the boxes as the aim was to create a competitive environment in the intercropped treatments for space, light and nutrients. The plants were watered based on their need, as the boxes with clover needed more water and we did not want drought to influence survival of the flies. This resulted in water being added in moderate doses twice a day. The first week after egg inoculation, a spray bottle was used to keep the soil near the stem base moist and to avoid the unhatched eggs being washed away from the stem base by the usual watering system.

Six weeks after egg inoculation, the experiment was terminated one block per day in the same order as they were set up. The timing was chosen to match the developmental time of *D. floralis* under similar conditions. The green parts of cabbage and clover were cut to ground level and weighed. The cabbage roots were freed from soil and weighed. Samples from the green parts and roots were dried at 70°C. Dry weights were taken and the plant samples were thereafter ground in a cutting mill prior to analysis for nitrogen and carbon content using an elemental analyser. The root samples were analysed for neutral detergent fibre (NDF) through the method described by Chai and Udén (1998). The NDF includes cellulose, hemicellulose and lignin as the major components (Van Soest et al. 1991). Root lignin content was analysed specifically through the permanganate-method (Van Soest et al. 1991). At the termination of the experiment only a small amount of root material was recovered from plants inoculated with 40 eggs and these treatments were excluded from fibre analyses. For the other treatments, material from two temporally adjacent replicates were pooled together, leading to five replicates in the fibre analyses. After removing all plant material for analysis from each block, the soil in the growing boxes was mixed with water and poured through a sieve to separate the fly pupae. The resulting pupae were counted and weighed individually.

## Statistical analyses

All plant and pupal parameters were analysed with an ANCOVA, with blocks, using egg density and clover density as factors. Before analysis, cabbage root and shoot dry weights, above ground clover dry weights and *D. floralis* pupal weights were natural log transformed, as appropriate for growth data (Rees and Brown 1992). Models were simplified by removing variables that did not improve the explanatory power. This was done by comparing the simplified model with the original model using an *F*-test (Crawley 2002).

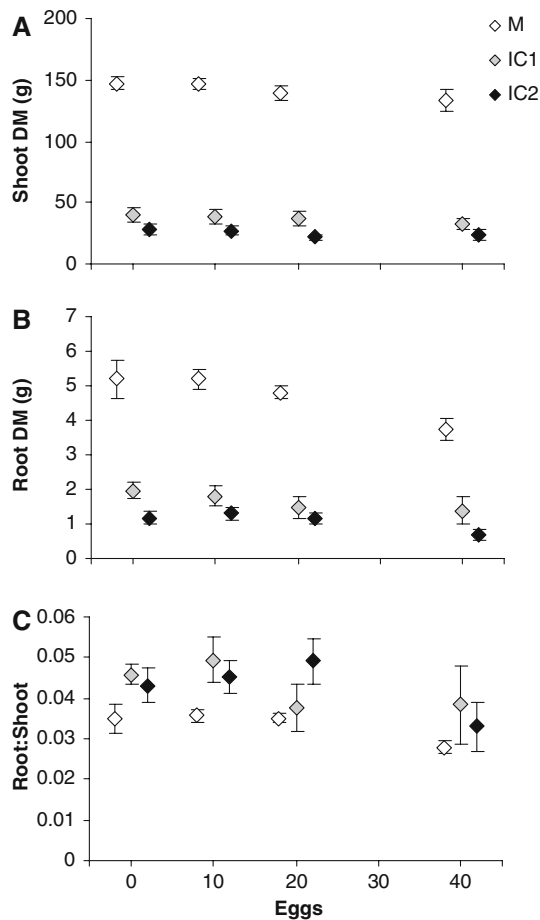
To identify possible correlations between variables associated with insect development and plant characteristics, correlation analyses were made between pupal weight, cabbage root dry weight, nitrogen, carbon and fibre contents. Pupal and root weight were natural log transformed before correlation analysis. All analyses were made using S-PLUS statistical software (Insightful Corp. Seattle, USA. S-PLUS® 6.2).

## Results

### Plants

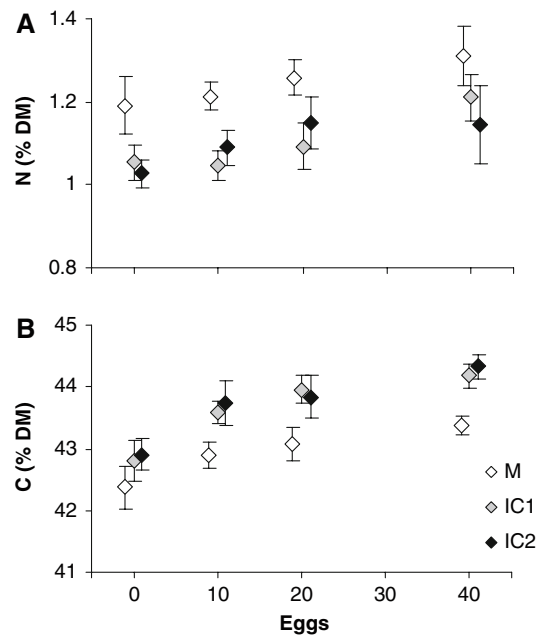
Intercropping and *D. floralis* damage both affected cabbage growth, but there were no interaction effects. Dry weight of cabbage foliage was strongly reduced both by plant competition ( $F_{2,107} = 414.0$ ,  $P < 0.001$ ) and by increasing density of *D. floralis* eggs ( $F_{1,107} = 7.4$ ,  $P = 0.007$ , Fig. 1a). Cabbage root dry weight was similarly reduced by both plant competition ( $F_{2,95} = 155.8$ ,  $P < 0.001$ ) and egg density ( $F_{1,95} = 12.8$ ,  $P < 0.001$ , Fig. 1b). Differences were small between IC1 and IC2 for both cabbage shoot and root dry weights (Fig. 1). The root:shoot ratio was consistently higher in intercropped cabbage ( $F_{2,96} = 15.4$ ,  $P < 0.001$ ), while there was no effect of egg density ( $P > 0.05$ ) (Fig. 1c). Percent dry matter in cabbage foliage increased in response to intercropping ( $F_{2,105} = 5.3$ ,  $P = 0.006$ ), but only in the IC2 treatment at high egg densities due to an interaction between clover and egg density ( $F_{2,105} = 3.6$ ,  $P = 0.03$ ). Percent root dry matter increased in response to increasing egg density ( $F_{1,96} = 11.8$ ,  $P < 0.001$ ). Despite the initial difference in clover density between IC1 (two rows) and IC2 (four rows) at the start of the experiment, final clover dry weights did not differ between treatments ( $P < 0.5$ ).

The content of nitrogen and carbon in cabbage leaves was unaffected by treatment, and did not show any consistent response to treatment. On average, shoots contained 1.7% nitrogen and 38.4% carbon on a dry matter (DM) basis. In the roots, however, nitrogen content was lower in

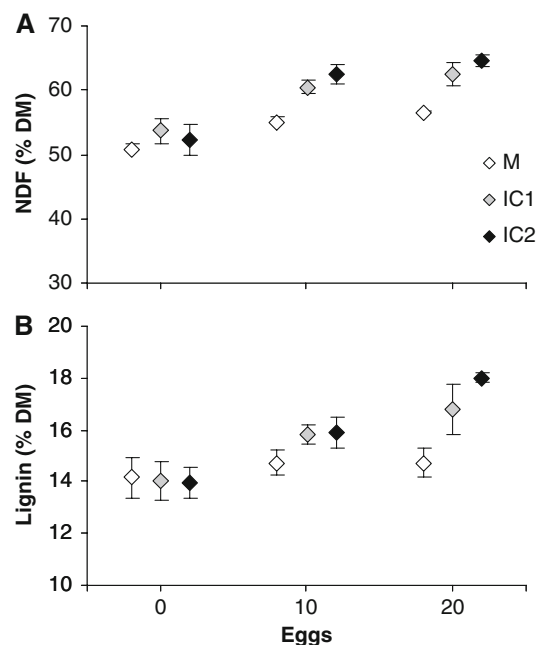


**Fig. 1** Effects of intercropping density (M, IC1 and IC2) and *D. floralis* egg density (0, 10, 20 and 40 eggs) on (a) cabbage shoot dry weight; (b) root dry weight (DM); and (c) root:shoot ratio (M = monoculture, IC1 = low clover density, IC2 = high clover density)

intercropped plants compared with monocultured plants ( $F_{2,105} = 11.3$ ,  $P < 0.001$ ). The percentage root nitrogen increased with egg density in both monoculture and intercropping treatments ( $F_{1,105} = 12.5$ ,  $P < 0.001$ , Fig. 2a). Root carbon was higher in intercropped roots ( $F_{2,114} = 5.6$ ,  $P = 0.005$ ) and increased with egg density ( $F_{1,114} = 28.1$ ,  $P < 0.001$ , Fig. 2b). The effects on root carbon and nitrogen resulted in a higher C/N ratio in intercropped roots ( $F_{2,105} = 11.5$ ,  $P < 0.001$ ). The analysis of root fibre content showed that root NDF was increased by both intercropping density ( $F_{2,41} = 11.4$ ,  $P < 0.001$ ) and egg density ( $F_{1,41} = 48.1$ ,  $P < 0.001$ , Fig. 3a). The content of lignin also increased in response to plant competition ( $F_{2,35} = 6.5$ ,  $P = 0.004$ ) and egg density ( $F_{1,35} = 37.4$ ,  $P < 0.001$ ). However, a significant interaction between clover density and egg density was evident ( $F_{2,35} = 6.4$ ,  $P = 0.004$ ), because the content of lignin increased with egg density in roots of intercropped cabbage but not in roots of monocultured cabbage (Fig. 3b).



**Fig. 2** Effects of intercropping density (M, IC1 and IC2) and *D. floralis* egg density on the content of (a) nitrogen and (b) carbon in cabbage roots (M = monoculture, IC1 = low clover density, IC2 = high clover density)



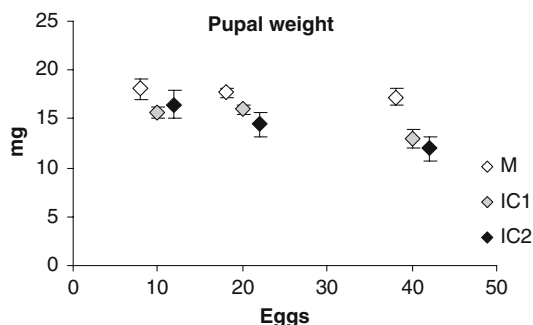
**Fig. 3** Effects of intercropping density (M, IC1 and IC2) and *D. floralis* egg density on the content of (a) NDF and (b) lignin in cabbage roots (M = monoculture, IC1 = low clover density, IC2 = high clover density)

## Flies

Pupal weight was lower when the larvae fed on intercropped cabbage ( $F_{2,81} = 8.6$ ,  $P < 0.001$ ) and when they

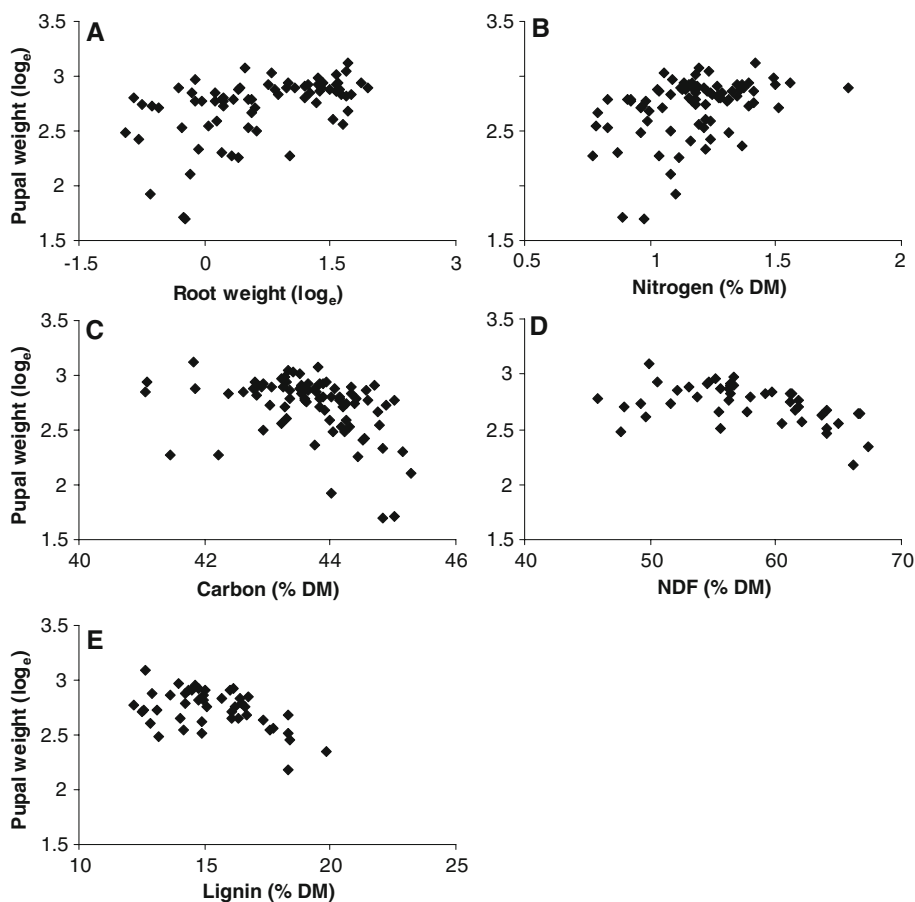
shared their host plant with higher densities of conspecific larvae ( $F_{1,81} = 9.6$ ,  $P = 0.003$ , Fig. 4). The survival of *D. floralis*, in terms of the number of pupae resulting from initial egg densities, did not differ significantly between treatments ( $P > 0.05$ ). However, survival tended to be higher in the monoculture treatments and ranged from 47 to 61% with an increasing egg density. Survival in intercropped treatments ranged from 36 to 54%.

The correlation analysis showed that pupal weight was positively correlated with root dry weight ( $r = 0.48$ ,



**Fig. 4** Effects of intercropping density and *D. floralis* egg density on the final pupal weights of *D. floralis* (M = monoculture, IC1 = low clover density, IC2 = high clover density)

**Fig. 5** Correlations between final *D. floralis* pupal weight and (a) cabbage root weight; (b) root nitrogen; (c) root carbon; (d) root NDF; and (e) lignin content



d.f. = 73,  $P < 0.001$ , Fig. 5a) and root nitrogen content ( $r = 0.39$ , d.f. = 81,  $P < 0.001$ , Fig. 5b). Pupal weight was negatively correlated with root carbon content ( $r = -0.38$ , d.f. = 81,  $P < 0.001$ , Fig. 5c), root NDF ( $r = 0.48$ , d.f. = 43,  $P < 0.001$ ; Fig. 5d) and root lignin ( $r = -0.50$ , d.f. = 43,  $P < 0.001$ , Fig. 5e) content.

## Discussion

This study found that both plant competition and *D. floralis* egg density not only affected the growth of cabbage but also its composition in terms of cabbage root nitrogen and fibre content (Figs. 1, 2, 3). This change in plant quality ultimately affected developmental rates of *D. floralis* larvae. Pupal weight was reduced by host plant effects due to competitive interactions between cabbage and clover, and by intraspecific competition at higher *D. floralis* densities.

The negative effects of intercropping on the growth of cabbage and on root:shoot ratio are expected consequences of interspecific plant competition (Theunissen et al. 1995; Agele et al. 1999; Bonifas et al. 2005). The presence of competing clover plants evidently reduced both light and nutrient availability for the cabbage crop. The effect on

nutrient availability was presumably more important, considering the higher root:shoot ratio in intercropped cabbage plants (Bonifas et al. 2005). Nevertheless, cabbage plants that had been grown in competition with clover clearly represented a poorer feeding resource for *D. floralis*, as the pupae recovered from these plants were smaller at all *D. floralis* densities. The negative effect on pupal weight due to increasing herbivore density has previously been reported for *D. floralis* feeding on the roots of swedes (*Brassica napus* ssp. *rapifera* L.) (Hopkins et al. 1993). In both cases, the poor performance of *D. floralis* is likely to be brought about by poorer food quality, by limited food availability or by a combination of both. The effects of intercropping and increasing herbivore density may actually both be associated with reduced food resource availability, as both more eggs and the smaller intercropped cabbage plants led to an increase in the relative herbivore density. The positive correlation between pupal weight and root dry weight (Fig. 5a) indicates that food source constraints are a possible cause of the impaired development in the intercropped treatments.

In addition to the reduction in overall growth, the presence of the competing clover plants and the root herbivore *D. floralis* were both associated with changes in the composition of the cabbage plants. The positive impact of high nitrogen level on herbivore development has been established in several studies (Bethke et al. 1987; Hunt et al. 1992) and could have contributed to the positive effect on pupal size in the monoculture, where nitrogen levels were higher (Fig. 2a). However, the correlation between pupal weight and nitrogen content (Fig. 5b) was positive, despite the fact that within the monoculture and intercropped treatments, pupal weight decreased with increasing egg density while the nitrogen content increased (Figs. 2a, 3). The reason behind this pattern remains unclear but it indicates that there are other factors more important than nitrogen for explaining the reduced pupal weight at the higher egg densities in this study.

The plants responded to the root feeding of *D. floralis* with an increased content of NDF and lignin, confirming the results in earlier studies on kale (*Brassica oleracea* var. *acephala* L.), rape (*B. napus* var. *napus* L.) and swede (Hopkins et al. 1995). The increase in NDF and lignin content of the roots in relation to the insect damage may be the result of two different processes. Firstly, if *D. floralis* larvae preferentially feed on parts of the root with a low fibre and lignin content, feeding indirectly lead to a net increase in the mean fibre content of a root sample. Secondly, damage caused by insects and pathogens has been shown to induce an array of responses in plants, including lignification. Lignification has been associated with wound repair in plants (Rittinger et al. 1987) and has

been observed in many plant species following challenge by pathogenic organisms (Moerschbacher et al. 1990; Li et al. 2007). There is also evidence that lignification is an important mechanism for disease resistance (Nicholson and Hammerschmidt 1992; Mert-Türk 2002). There are clear increases in the lignin content of *Brassica* roots around damage sites and around the xylem and phloem of damaged roots (Hopkins, unpublished data). This may be associated with protection against secondary infection at wound sites. The rise in lignin content in this study is therefore likely to be the result of both preferential feeding and herbivore-induced lignification, and this interpretation is supported by the greater difference in lignin content between monocultured and intercropped roots with higher *D. floralis* larval density (Fig. 3b). Lignin content was apparently unaffected by intercropping in the absence of herbivory, which indicates that plants responded with an increase of other parts of the NDF fraction when subjected to competition only.

The degree to which chewing phytophagous insects can digest fibre is poorly understood (Slansky 1990), and no studies of the digestibility of NDF for *D. floralis* have been reported. The indications from studies of other systems are that a minor proportion of the NDF can be utilised by phytophagous insects (Hochuli et al. 1993; Hochuli and Roberts 1996). An increase in NDF is generally associated with a decrease in food quality for herbivorous insects (Hochuli et al. 1993), and consequently the increase in NDF in the roots of intercropped cabbage plants may well be a contributing factor to the reduced *D. floralis* pupal weight in intercropped treatments (Figs. 3a, 4). This result is supported to some extent by earlier studies of *D. floralis* performance on swede, kale and rape, where a modest negative correlation between *D. floralis* pupal weight and the NDF content of roots was found (Hopkins et al. 1995).

Whilst we found that lignin content was negatively correlated with the weight of the *D. floralis* pupae, the impact of lignin on herbivore development is debatable. Wainhouse et al. (1990) found a dose-dependent negative effect of lignin on spruce bark beetle development (*Dendroctonus micans* Kug.). Studying different sorghum lines for resistance to the fall armyworm (*Spodoptera frugiperda* Smith), Diawara et al. (1991) observed significantly higher average lignin content in the panicles of sorghum lines identified as resistant, compared with lines identified as susceptible. However, lignin concentration was negatively correlated with the duration of larval stage within the resistant group. The contradictions apparent in these results lead to the conclusion that a clear general relationship between reduced lignin content and susceptibility to insect attack cannot be clearly demonstrated (Pedersen et al. 2005). Further information on the impact

of lignin on the feeding and development of different insect herbivores is required.

The relationship between the chemical and structural composition of roots and the performance of *D. floralis* remains unclear, although the suitability of *Brassica* roots as food for the turnip root fly is known to vary considerably between different cultivars (Hopkins et al. 1995). There are certainly several other aspects of food source quality than those investigated here which are important for root fly development. The importance of sugars for the growth of *D. floralis* was demonstrated by Hopkins et al. (1993), who found a positive correlation between pupal size and the sugar levels of swede roots. Furthermore, Marazzi and Städler (2005) found that sulphur stimulated oviposition of the closely related *Delia radicum* L., and that larval survival, adult emergence and adult weight were influenced by the host plant sulphur level, possibly through effects of the sulphur application on the glucosinolate concentration of the host plants (Marazzi et al. 2004). There is no doubt that defining host plant quality requires information on factors other than those addressed in our study. The other factors mentioned above could also compromise the nutritional quality of roots as food for *D. floralis* larvae and may have been affected by plant competition through intercropping, with subsequent impact on *D. floralis* development.

Studies of the effects of intercropping on herbivore behaviour (Finch and Collier 2000) and natural enemy population dynamics (Tukahirwa and Coaker 1982; Booiij et al. 1997) are undoubtedly of great importance for increasing the knowledge on pest regulation in intercropping systems. Yet this study proves that there is a clear need for a better understanding of the indirect effects of intercropping mediated by quality changes in host plants as a food resource for phytophagous insects.

The results from this study show that intercropped plant systems may affect the quality of crop plants through inter-specific competition with companion plants and that this change in food source quality can have a negative impact on the development of root feeding herbivores. Plant quality may be affected by interactions between plant competition and herbivory, as was shown with the lignin content of *Brassica* roots. Although the competitive conditions in this experiment exceeded an acceptable field situation, the results provide further insight into plant responses in complex systems. Knowledge of plant responses to herbivory in controlled complex systems, as in this study, may be useful in identifying mechanisms that affect herbivores negatively.

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