# Is there an associational resistance of winter pea–durum wheat intercrops towards Acyrthosiphon pisum Harris?

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Is there an associational resistance of winter pea - durum wheat intercrops towards *Acyrthosiphon pisum* Harris?

**Abstract**

1- *Acyrthosiphon pisum* Harris (Aphididae: Hemiptera), the pea aphid, is an important pest in organic farming systems. In this work, the objective was to gather empirical field data on the associational resistance of durum wheat-winter pea intercrops towards the pea aphid, compared with pure stands of winter pea.

2- Our results showed that intercropping winter pea with durum wheat significantly decreased *A. pisum* abundance in all the situations. Moreover, it was systematically observed that pea grew bigger in pure than in intercropped stands but after considering pea dry mass as a covariate, it appeared that the durum wheat – winter pea intercrop was still significantly less attacked by pea aphids than the sole crop.

3- Intercrop sowing designs had an incidence on infestation levels: substitutive diversification systems of different types are more effective in decreasing the level of aphid infestation than does the additive system. In addition, substitutive row intercrop is significantly less infested than substitutive mixture. These results suggest that a mechanism related to the resource concentration hypothesis may explain the associational resistance of the intercrops of durum wheat - winter pea towards *A. pisum*.

## 1. Introduction

The simplification and intensification of cropping management in Western Europe in the last 60 years was strongly facilitated by better understanding and modelling the relationships between the atmosphere, the soil and populations of cultivated plants. This led to a remarkable increase in food production but not without consequences to the environment (Tilman *et al.* 2002). Several authors have pointed out that changes in landscape use and agricultural practices have pervasive effects on biodiversity, soil erosion, reduction of soil fertility, pollution, and the appearance of new pests, (e.g. Pimentel et *al*., 1995; Flowerdew 1997; Matson *et al*, 1997; Vandermeer *et al.*, 1998; Stoate et *al*., 2001; Tilman et *al*., 2001; Benton et *al*., 2003). Nowadays, it has become widely accepted that ecologically based management strategies must be implemented to increase the sustainability of agriculture (Matson *et al*., 1997). Crop diversification, through the building of a complex network of ecological interactions, is one of those strategies (Malézieux *et al.*; 2008; Lin, 2011).

Intercropping, the simultaneous growing of two or more species in the same field for a significant period but without necessarily being sown and harvested at the same time (Willey, 1979), could be one way to increase the planned biodiversity (Vandermeer *et al.*, 1998; Malézieux *et al.*, 2008). Intercropping is known to often achieve higher grain productivity than pure stands, namely in low N input systems (Hauggaard-Nielsen *et al*., 2008). Niche complementarity and facilitation are common explanations for such overyielding. Interspecific differences in nutriments or environmental requirements allow combinations of certain species to complementarily use resources in space and /or in time (Bedoussac & Justes, 2010a). Eventually they positively interact thus further improving the capture of the resources (Tilman, 2001, 1999; Mommer *et al.*, 2010), e.g. when one of the species forms a symbiotic association with nitrogen-fixing bacteria (Hooper *et al.*, 2005) therefore incorporating N into the system via $N_2$ fixation.

Plant diversity is also known to promote pest regulation (see Risch *et al.,* 1983 and Letourneau *et al.,* 2011 for reviews), and this has been called associational resistance (Tahvanainen & Root, 1972). However, despite an overall positive effect, studies relating plant diversity and population density of herbivores often give variable (Poveda *et al.*, 2008; Shennan, 2008) or even contradictory results (Altieri & Nicholls, 2004). The kind of diversity as well as the spatial or temporal scales at which crops are implemented could influence the success of the biodiversity enhanced measures (Rämert & Ekbom, 1996; Bommarco & Banks, 2003; Altieri & Nicholls, 2004; Hambäck & Englund, 2005; Shennan 2008). Furthermore, associational resistance is considered to occur because of two main ecological mechanisms (Root, 1973; Andow, 1991; but see also Barbosa *et al.* 2009 for revision and discussion on more precise mechanisms behind associational resistance) that are not mutually exclusive (Letourneau, 1987): the *resource concentration hypothesis*, which is a bottom-up or resource-based perspective, predicts that herbivores are more likely to find and remain on host plants that are concentrated, i.e. that occur in dense or nearly pure stands; the *enemies hypothesis,* on a top-down or natural enemy-based perspective, holds that there is a positive correlation between plant species richness and natural enemy abundance, with the consequent reduction of herbivore populations at lower levels in more diverse vegetation stands (Root, 1973). Ever since Hairston *et al*.'s (1960) "the world is green" proposition and Murdoch's (1966) opposite view "the world is prickly and tastes bad", the question of whether the control of herbivores is driven by upper or lower trophic levels has received much attention but not a straightforward answer (Walker & Jones, 2001).

Altogether, the absence of appropriate empirical data prevents the emergence of a synthesis on the response of herbivores to the diversity of vegetation stands. As a consequence, a better understanding of the ecological mechanisms accounting for the differences in pest abundance between unequally diverse systems is lacking. Therefore, field experiments aiming at understanding how schemes of diversification lead to herbivore suppression need to be undertaken.

In Southern France, particular research attention has been paid to cultivation of durum wheat (*Triticum turgidum* L.) in association with winter pea (*Pisum sativum* L.) in low N input systems including organic farming. Beside the fact that the complementary use of N sources between cereals and legumes can be of particular interest in low-N-input cropping systems (Bedoussac & Justes, 2010b), several examples of intercrops with a legume show a reduction in pest and disease attacks when compared to pure stands (e.g. Baliddawa, 1985; Rämert & Ekbom, 1996; Rämert et *al*., 2002; Corre-Hellou *et al.*, 2005). Preliminary observations seem to indicate that the pea aphid, *Acyrthosiphon pisum* (Harris) (Aphididae: Hemiptera), an important pest in organic farming systems, is less abundant in durum wheat (DW)-winter pea (WP) intercrops than in pure stands of WP (Bedoussac, 2009).

Although it has been shown that natural enemies provide an essential ecosystem service by reducing the number of aphids on different plants (Orros & Fellowes, 2012; Diehl *et al.*, 2013), a top-down regulation of aphids' abundance below economic threshold levels is considered unlikely (Dixon, 2000, 2005). For ladybirds but also hoverflies and chrysopids, the developmental time from egg to adult is nearly as long as the lifespan of aphid colonies (Kindlmann & Dixon, 1999). Strategy of prey exploitation that minimizes the risk of starvation before completing development is clearly advantageous in this context. Evolution favours females that lay few eggs early in the development of their prey colonies, and avoid colonies that are already exploited, as the presence of other predators increases the risk of resource collapse (Hemptinne *et al*., 1992). Therefore, the behaviour of predators is shaped by the necessity to avoid prey scarcity at the end of larval development rather than by response to high prey density. Accordingly, predators do not develop strong numerical response to prey density

(Hemptinne *et al*., 1992). The numerical response of aphid parasitoid wasps, is on its side curtailed by adaptive avoidance of hyperparasitism (Hemptinne, 2003; Dixon, 2005). We therefore expect that bottom-up rather than top-down mechanisms play the fundamental role in the reduction of aphid abundance in intercrops relatively to sole crops.

In the present work, our first objective was to gather empirical data to confirm the associational resistance of the DW-WP intercrops towards the pea aphid compared with pure stands of WP, for four years. Additionally, in one year, we analysed the effect of DW-WP additive sowing design (DW plants are added to the original WP plant population, therefore increasing diversity but maintaining the density of the original WP plants) and two types of substitutive sowing designs (WP plants are replaced by DW plants, either by mixing DW and WP or intercalating rows of each; diversity is increased but density of the original WP plants is lowered) in the reduction of aphid numbers.

## 2. Material and Methods

*General field trials*

To assess the associational resistance of the DW-WP intercrops towards the pea aphid compared with pure stands of WP, aphids were counted in the field near Toulouse (France) from 2007 to 2010. We took the opportunity of a large agronomic trial located at the experimental farm of INRA (Institut National de la Recherche Agronomique; Auzeville, 43°31′N, 1°30′E) or implemented by farmers under the control of INRA (Farm A 43°38'N 0°36'E; Farm B 43°16'N 1°42'E; Farm C 43°37'N 0°43'E; Farm D 43°52'N 0°41'E; Farm E 43°51'N 0°54'E). This trial was already on its way to assess the benefit of intercropping winter pea and durum wheat (see for instance Bedoussac & Justes 2010 a and b). Among the plots of this trial we selected those suitable for counting aphids (e.g. 2007, 2008: no insecticide spray and the possibility to get replicates; 2009, 2010: organic farming).

The 2007 and 2008 plots were sown in November in 2006 and 2007 respectively. The 2009 plots were sown in January because weather conditions were inadequate for soil drilling and sowing in autumn. The 2010 plots were sown in November 2009. Plant densities and treatments are described in Table 1. The ratios of the different crop plants in the 2009 and 2010 plots, although similarly standardized across fields at sowing, evolved differently later on mainly due to farmers seeding systems and farms different environmental conditions. The plots in each location were closer to each other than to other possible sources of pea aphids. We can thus consider that they were surrounded by a common environment.

(Please insert table 1 here)

Counting started as soon as aphids were detected in the plots, in March for the first two years and in April for 2009 and 2010. They went on once a week until aphids disappeared, in the beginning of June. There were four 11m² plots in 2007 (2 replicates of sole crops and 2 of intercrops) and 6 in 2008 (3 replicates of sole crops and 3 of intercrops). Ten plants were randomly chosen and each was bent over a 360 cm² plastic box, and shaken to dislodge the aphids that were counted. This sampling method is commonly used (e.g. Hufbauer, 2002) because pea aphids readily drop off plants when disturbed. In 2009 and 2010 aphids were counted in 6 large plots (ranging from 400 to 600 m² depending on the farm), located each year in three different farms - Farms A to E. Farm C was sampled in both years. There were 1 intercrop and 1 sole crop plot side by side per farm. Twenty plants were randomly chosen in each plot and aphids sampled as explained above.

Due to the size of the plots and the tendency for aphids to display an aggregated distribution in the field (Park & Obrycki, 2004), the statistical analyses were performed on the weekly total number of aphids collected in each plot. These numbers were analysed by general linear mixed models (glmm) with a Poisson error (package lme4; R Development Core Team, 2010). The fixed factor was “Crop” (pure stand of peas or intercrop) and the successive periods of time at which the counts were made were considered as continuous random effects. The inclusion of these random effects in the models is a mean to take into account the fact that aphids were counted in the same plots on several successive dates.

*Study of the influence of the winter pea - durum wheat intercropping type on the abundance of aphids*

In 2008, the influence of 3 types of intercrops (additive row, substitutive row and substitutive mixture – Table 2) on the abundance of pea aphids was assessed in a field trial laid down at INRA research station. These 3 types were compared to WP in pure stand. Plot size was 11 $m^2$. There were three replicates of each type of crop. The additive row and the pure stand plots aphid counts had already been used in 2008 for the general field trial (see above).

The aphids were counted as explained above (see *General field trials*). Statistical analyses were performed as described above using a glmm with “Crop” as fixed factor with 4 levels (three types of intercrops and WP pure stand) and the successive periods of time at which the counts were made as a continuous random effect. The means of the fixed factors were compared by *a priori* orthogonal contrasts (Crawley, 2007): 1) the mean of the sole crop treatment compared to the mean of the three intercrop treatments; 2) the mean of the additive intercrop to the mean of the two non-additive intercrops and 3) finally, the means of the two non-additive intercrops.

Contrary to additive intercrops, substitutive mixture and row intercrops were fertilized on May the $7^{th}$ but nevertheless considered in the above mentioned analysis. Indeed, although plant nitrogen content might constrain pea aphid dynamics (Abisgold *et al.*, 1994), Bedoussac & Justes (2010a & b) showed that late nitrogen application has no impact on shoot nitrogen content or plant dry biomass by pea. It is therefore unlikely that this fertilization had an impact on aphid dynamics. However, to assess the possible impact of this fertilization, we also ran the same statistical analysis but considering only the weeks before the $7^{th}$ of May.

(Please insert table 2 here)

*Study of the influence of pea biomass on the abundance of aphids*

To assess the possible confounding influence of plant biomass on the abundance of aphids, three 0.5 $m^2$ areas were randomly selected in the pure pea and intercrop plots laid down at 3 farms on the $15^{th}$ of April and the $15^{th}$ of May 2010 (Table 1). All pea and wheat aerial parts were collected and sorted out. The peas were dried at 80 °C for 48 h and weighed. As we knew the average densities of pea plants in the pure and the intercropped plots (Table 1), the average dry masses/0.5$m^2$ were converted into average dry masses per pea plants. The average dry mass of peas grown in intercrop and pure stands were compared by a glmm with “Crop” (intercrop or sole crop) as a fixed factor and the two weeks at which the observations were made as a continuous random effect. The number of aphids were also analysed by a glmm with a Poisson error. The fixed factors were “Crop” (intercrop or sole crop) and “pea dry mass”.

## 3. Results

*General field trials*

*A. pisum* was present in all the plots and was the only aphid present on pea. Pure stands of WP were always more infested than intercrops (Figure 1). However, as shown in Figure 1, the number of aphids is about the same in early spring on SC and IC and only after the first weeks do aphid numbers differ in the two kinds of stands.

(Please insert figure 1 here)

In the four years of this study, the intercrop plants are always significantly less infested than WP sole crop plants (Table 3, see supplementary material). In the context of the large plots (2009, 2010), the variability between farms is small, with standard deviations of 10.91 and 1.43, respectively. This can also be observed in Figure 1, which shows that the fluctuations of abundance of aphids, in 2010 for example, are similar in amplitude and timing across sites separated by more than 10 km.

*Study of the influence of the winter pea - durum wheat intercropping type on the abundance of aphids*

The comparison of 3 types of intercropping to pure stand of WP in 2008 confirms the previous results: intercropping WP with DW results in pea being significantly less colonized by pea aphids, and the difference is particularly important from the 16$^{th}$ of April to the 23$^{rd}$ of May (Figure 2a). The statistical analysis over the entire growing season indicates that the sole crop of pea is significantly more infested than the three intercrops ($z=17.000$; $P=0.000$). The additive row intercrop is significantly more infested than the two substitutive intercrops ($z=4.05$; $P=0.00005$). Finally, the substitutive mixture is significantly more infested than the substitutive row intercrop ($z=-2.68$; $P=0.007$) (Figure 2b). The glmm fitted to the data before the nitrogen fertilization gives identical results (Sole crop versus intercrops: 16.71: $P=0.000$); additive row versus substitutive intercrops: z=6.79; P=0.000; substitutive mixture versus substitutive row intercrop: z=-5.51; P=0.000).

(Please insert Figure 2 here)

*Study of the influence of pea biomass on the abundance of aphids*

The density of pea / m² and the average dry mass of pea varied substantially between treatments and farms. However, it was systematically observed that pea grew bigger in pure than in intercropped stands (t=7.968; 4 d. f.; P<0.01; Figure 3). The interaction between pea dry mass and cropping system has a significant influence on the number of aphids on peas (z=4.15; P=0.00003). There are less aphids on lighter peas (z=4.49; P=0.000) and on intercropped pea (z=-4.40; P=0.00002). The effect of intercropping on the reduction in the number of aphids compared to the sole crops is stronger than the effect of pea dry mass (estimated reduction of aphid abundance due to intercropping: -2.60; due to dry mass: 0.92).

(Please insert Figure 3 here)

## 4. Discussion and Conclusions

Plant diversity is known to promote pest regulation (Letourneau *et al.,* 2011). Concerning aphids, this was shown for several species (Parajulee & Slosser, 1999; Showler & Greenberg, 2003; Bukovinszky *et al*., 2004; Beizhou *et al*., 2011). Our results establish for the first time that intercropping WP with DW significantly decreases *A. pisum* abundance compared to WP monocultures.

Moreover, our results suggest that the mechanism(s) accounting for the associational resistance of intercrops of DW-WP towards *A. pisum* are probably not affected by changes in the structural attributes or environmental surroundings of the crops. Indeed, our results are consistent over year, spatial scale, geographic location and diversification scheme of intercrop and this despite farmers sowing differences. Furthermore, after taking into account pea biomass, a resource abundance parameter, we still observe significantly less aphids on intercropped than in pure stands of peas. That is, we can state most strongly that intercropping of DW and WP has an important practical application in decreasing pea aphid infestations and therefore on the need for pesticide use.

Although the seminal works of Poveda *et al.* (2008) and Letourneau *et al.* (2011) have shown a general positive impact of plant diversification on pest suppression, the ecological mechanisms accounting for the differences in pest abundance between more or less diverse systems are still under discussion. However, our results bring some new elements of understanding. According to the statistical analyses, there is a difference between high and low density of peas in the intercrop: the additive row intercrop is less effective than the substitutive intercrop system in suppressing aphids. In addition, we also show that among the two less dense intercrops, stand characteristics influence aphid abundance: substitutive row intercrop is significantly less infested than substitutive mixture.

As pea sole crops constitute larger patches of host-plants for pea aphids than intercrops of durum wheat and winter peas, our field results are backed by Hambäch and Englund's model (Hambäch and Englund, 2005) on the relationship between patch area and population density of herbivores. Following their model, this relationship depends on how immigration and emigration rates scale with patch area. The values of these two parameters are in turn influenced by the behaviour of animals. In the case of wind born dispersers like winged aphids, rates are said to be area-dependent. Wingless aphids leave patches by walking; their emigration rate is related to the perimeter-area ratio of patches. Taking into account this behavioural information, the model predicts a positive relationship between patch area and population density. The associational resistance reported in our work is therefore better explained by a mechanism related to the resource concentration hypothesis rather than the natural enemies hypothesis. This is not too surprising because it has been shown that natural enemies of aphids are unable to regulate the abundance of their prey below economic threshold levels (Kindlmann & Dixon, 1999) although they may reinforce demographic differences due to patch size (Diehl *et al.*, 2013).

Our study does not explain how the observed associational resistance of DW-WP towards the pea aphid arose. However, we suggest two lines for future research. Firstly, aphids might have more difficulties in locating and settling on their host plant probably because the information delivered by those plants is masked, i.e., there is an interference of the non-host plants in the herbivore host choice process. It is known that aphids are attracted by the colour (Chittka & Doring, 2007) and odours (Powell *et al.*, 2006; Webster, 2012) of their host plants. Therefore, it is conceivable that a mixed stand of peas and wheat does not reflect light and release odours in the same way as a pure stand of peas.

Secondly, the quality of plants might also change when intercropped (Andow, 1991). Nitrogen content was shown to constrain the survivorship, rate of growth and fecundity of aphids in general (Dinant *et al.,* 2010; Nowak & Komor, 2010) and of the pea aphid in particular (Abisgold *et al.,* 1994). Accordingly, aphids identify and choose hosts of higher nutritional quality (Nowak & Komor, 2010). In intercrops of cereals and legumes, the cereal is a superior competitor for soil inorganic N through a faster developing and deeper growing root system, and greater demand for mineral N (Corre-Hellou *et al*. 2006). As a result, the intercropped legume has to increase symbiotic $N_2$ fixation to satisfy its N requirements (Bedoussac & Justes, 2010b; Naudin *et al.*, 2010). Could this difference in the use of N by peas intercropped with wheat compared to sole crops have an impact on the N available for aphids in peas?

Because the differences in aphid numbers between SC and IC only appear after the first weeks of aphid's infestation, we believe they are not related to differences in the number of winged aphids initially colonizing pea plants but rather to a subsequent distinct proliferation of aphids. Data on the presence of winged aphid colonisers on the plants could clarify this question but, unfortunately, because winged forms are relatively rare and therefore difficult to spot on plants in the initial phase of population development, we are unable to answer this question.

In conclusion, although the intimate mechanisms underlying the associational resistance of DW-WP towards the pea aphid were not the core of this study, our results on associational resistance with different experimental designs provide interesting applied information. Indeed, substitutive designs are known to be more productive than sole crops (Bedoussac & Justes, 2011) and our results also show that they are the most effective in reducing the number of pea aphids. The fact that some of the field research was conducted directly in farmer's fields makes the finding indicative of an actual agro-ecosystem.

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Figure legends

Figure 1- The fluctuation of the number of aphids per plant of winter pea, in sole crops of winter pea and in intercrops of winter pea with durum wheat.

Figure 2- The abundance of pea aphids on winter peas grown in pure stand (SC: sole crop) or in three types of association with durum wheat (AR_IC: additional row intercrop; SM_IC: substitutive mixture intercrop, and SR_IC: substitutive row intercrop). a) variation in aphid abundance throughout the season (mean and standard deviation); b) mean (and standard error) aphid abundance on peas in relation to the four types of crops. Histograms topped by different letters are significantly different.

Figure 3- The average dry mass (g) of pea plants on the 15$^{th}$ of April and the 15$^{th}$ of May 2010 in winter pea and durum wheat intercrop (IC) and pure pea (SC) plots at three farms. SD = Standard deviation.

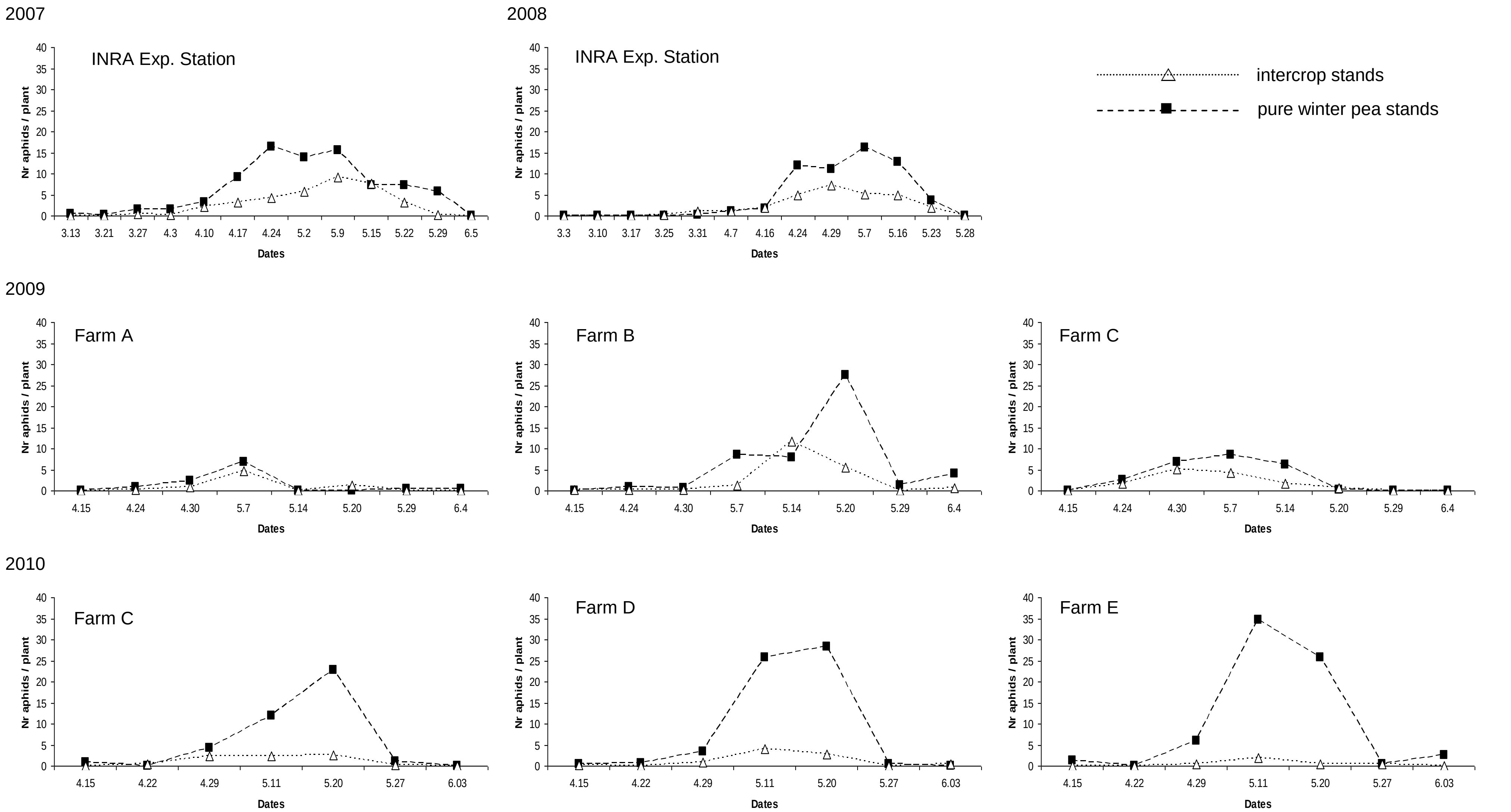


Figure 1- The fluctuation of the number of aphids per plant of winter pea, in sole crops of winter pea and in intercrops of winter pea with durum wheat.

Figure 2

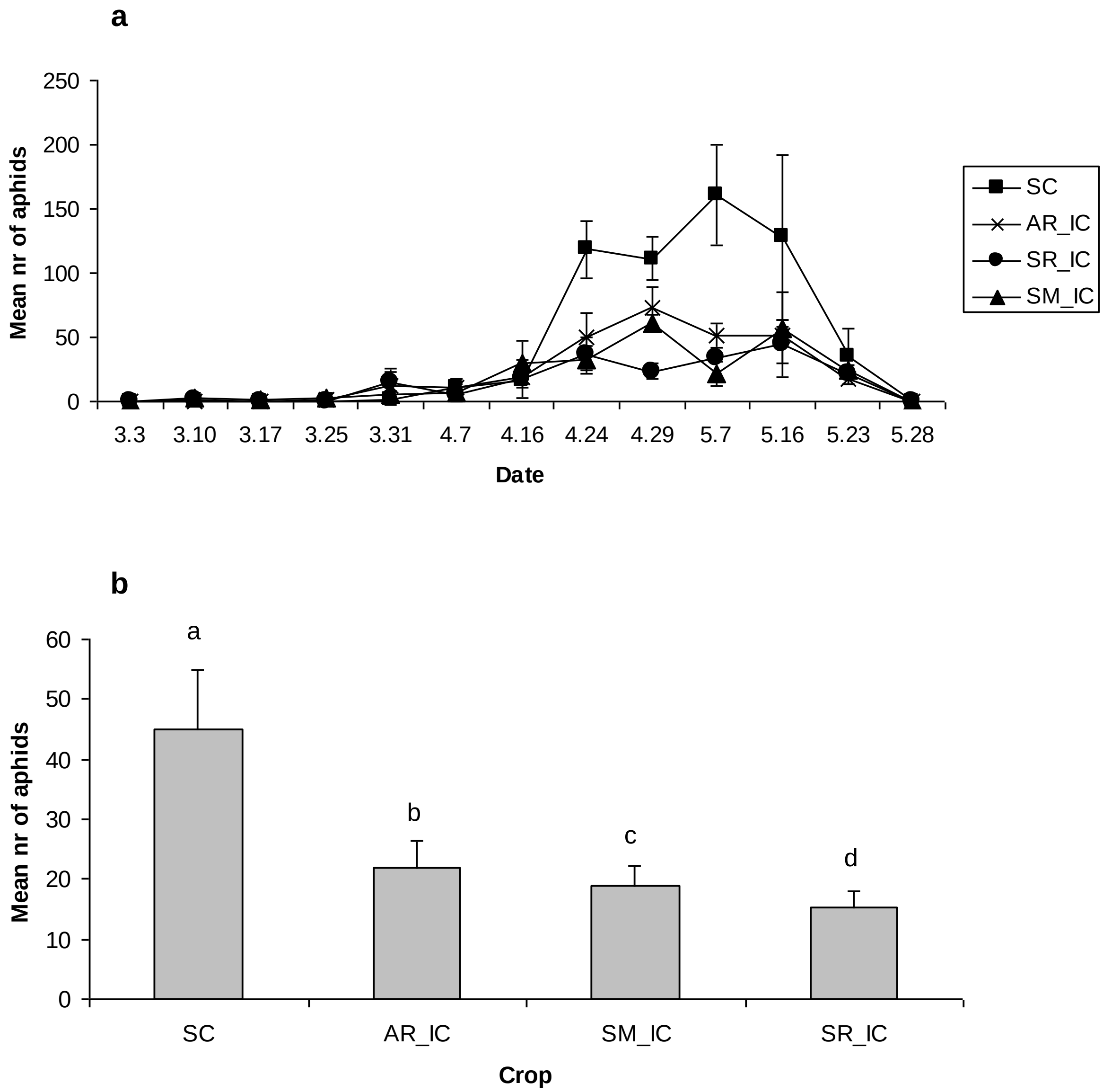


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Figure 3

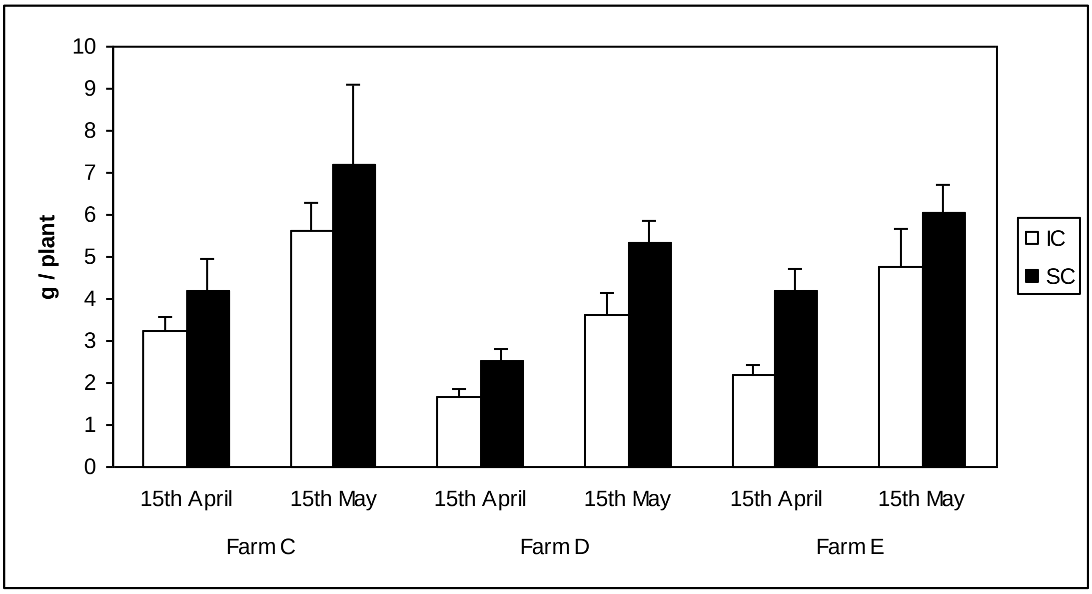



Figure 3- The average dry mass (g) of pea plants on the 15th of April and the 15th of May 2010 in winter pea and durum wheat intercrop (IC) and pure pea (SC) plots at three farms. SD = Standard deviation.

Table 1- Pesticide treatments (F= seed treated with a fungicide; H= herbicide applied 2-4 days after sowing), plant densities of winter pea (WP) and durum wheat (DW) in intercrops (IC) and sole crops (SC), in 2007, 2008 (small plots) and in 2009, 2010 (large plots).

| **Year / Site** | **Pesticide treatment** | **Plant density** (number of plants/$m^2$) | |
|---|---|---|---|
| | | **IC WP / DW** | **SC WP** |
| **Small plots** | | | |
| 2007 | F & H | 28 / 95 | 55 |
| 2008 | H | 62 / 110 | 58 |
| **Large plots** | | | |
| 2009 | | | |
| Farm A | Organic | 51 / 169 | 97 |
| Farm B | Organic | 102 / 82 | 96 |
| Farm C | Organic | 118 / 134 | 117 |
| 2010 | | | |
| Farm C | Organic | 32 / 168 | 70 |
| Farm D | Organic | 85 / 246 | 102 |
| Farm E | Organic | 67 / 175 | 62 |

Note: The ratios of the different crop plants in the large plots, although similarly standardized across fields at seeding, evolved differently later on mainly due to farmers seeding systems and farms different environmental conditions.

Table 2- Sowing design, plant densities (per $m^2$), fertilisation, and pesticide treatments in intercrops (IC) of winter pea (WP) and durum wheat (DW) and sole crops (SC) of winter pea in 2008 (small plots). F= seed treated with fungicide; H= herbicide 2-4 days after sowing. ■ = pea plants; ■ = wheat plants.

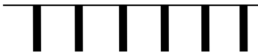
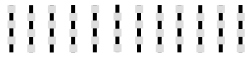
| **Sowing design** | | **Plant densities DW / WP** | **Fertilisation (Kg N $ha^{-1}$)** | **Treatment** |
|---|---|---|---|---|
|  | Pea SC | 0 / 59 | 0 | F & H |
|  | Substitutive mixture IC | 95 / 28 | 35 | F & H |
|  | Substitutive row IC | 109 / 30 | 35 | F & H |
|  | Additive row IC | 109 / 59 | 0 | F & H |

Table 3- The reduction of the mean abundance of aphids in the winter pea – durum wheat intercrop compared to pea sole crop in four experiments realised from 2007 to 2010. (SE: standard error).

| | **Reduction in aphid number due to intercropping** | | | | |
|---|---|---|---|---|---|
| **Years** | **Estimate** | **SE** | **df** | **z value** | **P value** |
| 2007 | -0.707 | 0.080 | 2 | -8.82 | 0.000 |
| 2008 | -0.658 | 0.032 | 4 | -12.155 | 0.000 |
| 2009 | -0.752 | 0.043 | 4 | -17.590 | 0.000 |
| 2010 | -2.175 | 0.054 | 4 | -40.610 | 0.000 |