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ORIGINAL PAPERS

Drought and soil fertility modify fertilization effects on aphid performance in wheat

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Abstract

Agricultural intensification and climate change are expected to affect pest performance through excessive inputs of chemical fertilizers and increased probability of extreme drought events. Potential interactive effects of fertilization and water availability on aboveground pest performance may depend on soil fertility because of its effect on nutrient availability. In a greenhouse experiment, we examined the effects of inorganic fertilization on the performance of the grain aphid (*Sitobion avenae*, F.), an important pest of wheat, under different conditions of soil fertility and water availability. We found soil fertility and water availability to influence the positive effects of inorganic fertilizers on aphid growth, i.e. fertilization promoted faster aphid development time and higher fecundity and biomass under low fertility and under well-watered conditions. Moreover, although increased soil fertility favored aphid growth under well-watered conditions, it simultaneously sustained plant development. The current practices promoting soil fertility do not have direct negative consequence on crop protection under conventional cropping systems.

Keywords: Agricultural intensification; Cereals; Climate change; Grain aphid; Nitrogen; Soil organic matter; Water availability

Introduction

Insect pests represent a severe threat to crop production, being responsible for an estimated yield loss of 15% worldwide (Maxmen 2013). Agricultural intensification has been shown to alter pest dynamics through excessive input of chemical fertilizers and promotion of monoculture cropping systems, potentially increasing herbivore pressure (Matson, Parton, Power, & Swift 1997). Moreover, extreme weather events, such as prolonged summer droughts, are known to affect plant–herbivore interactions (Johnson, Staley, McLeod, & Hartley 2011) and to potentially exacerbate pest problems in several cropping systems (Fuhrer 2003).

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However, the mechanisms driving pest dynamics are far from being well understood (Welch & Harwood 2014) and large knowledge gaps remain to understand the consequences of adopting different soil management strategies under extreme climatic conditions (Vermeulen, Campbell, & Ingram 2012).

Inorganic fertilization is a widely adopted practice known to affect pest performance (Mattson 1980). Fertilizer supply rapidly modifies nutrient balance in plants, enhancing plant tissue quality and improving the performance of pests, particularly of sap feeding insects (Awmack & Leather 2002). For example, high concentration of nitrogen in phloem sap has been shown to increase growth rate, development speed and fecundity of this herbivore guild, boosting population growth (Nevo & Coll 2001; Douglas 2003; Rousselin et al. 2016). Nevertheless, plant nutrient status also depends on other concomitant factors such as water availability and soil quality, which are also expected to influence herbivore dynamics (Meyer 2000; Huberty & Denno 2004). Understanding the potential interactions between inorganic fertilizer application and other agronomic factors and their effects on herbivore performance is therefore important to predict pest dynamics in agroecosystems.

Farming practices aiming at supporting the health and fertility of agricultural soils in the long term, such as manure application and crop residue incorporation, increase the content of plant nutrients and enhance soil structure (Mäder et al. 2002; Birkhofer et al. 2008). Fertile soils generally present higher soil organic matter content, improving ecosystem functioning, moisture holding capacity and plant nutrient availability (Kononova 2013). Increased levels of soil organic matter content support a more gradual release of nutrients to plants, avoiding disproportionate enhancement of nutrients in plant tissues caused by inorganic fertilizers and, presumably, undesired pest population boost (Altieri & Nicholls 2003; Wurst, Langel, Reineking, Bonkowski, & Scheu 2003; Pimentel, Hepperly, Hanson, Douds, & Seidel 2005; Ke & Scheu 2008). Soil management strategies aiming at enhancing soil fertility in the long term have been greatly encouraged (Matson et al. 1997), although some studies showed contrasting effects on pests (Garratt, Wright, & Leather 2010; Garratt, Wright, & Leather 2011; Williams, Birkhofer, & Hedlund 2014). Nevertheless, the outcomes of increased soil fertility on aboveground pest performance have rarely been tested and the potential interactions with inorganic fertilizer inputs remain largely unknown (Garratt et al. 2011; Bommarco, Kleijn, & Potts 2013).

Prolonged water stress in plants can limit sap-feeding insect performance (Huberty & Denno 2004) because of altered phloem properties (e.g. sap viscosity) and decreased turgor, which compromise feeding activity (Hale, Bale, Pritchard, Masters, & Brown 2003; Pescod, Quick, & Douglas 2007; Tariq, Wright, Rossiter, & Staley 2012). Nevertheless, the magnitude of drought effects on plants and pests is also expected to depend on soil properties: soil organic matter for example, improves soil physical properties, generally increasing water holding capacity (Bot & Benites 2005). Fertile soils, that typically present higher levels of soil organic matter, might therefore mitigate water stress to plants and to the insects feeding on them (Kononova 2013). The understanding of how farming practices influence plant-pest interactions in response to water stress is particularly important, considering that summer droughts are predicted to increase in frequency, duration and/or severity in response to climate change (Schröter et al. 2005; Gustafson 2011; Solomon 2007; Dai 2011).

Among sap-feeding insects, aphids are considered severe pests of crops world-wide, potentially causing enormous economic losses in several cropping systems (Dedryver, Le Ralec, & Fabre 2010). Aphids are in fact characterized by high reproductive potential, dispersal capacities and adaptability to local environmental conditions, potentially building up remarkably large populations in a short time (Van Emden & Harrington 2007). The grain aphid (*Sitobion avenae* F.) is an important pest of wheat and other cereals in Europe, Asia and the Americas (Tatchell 1989; Van Emden & Harrington 2007). This aphid negatively affects cereal yield by removing plant nutrients through sap feeding, by reducing photosynthetic ability of plants as the result of honeydew secretions onto leafs and by transmitting plant viruses (Fiebig, Poehling, & Borgemeister 2004). *Sitobion avenae* outbreaks are common and driven by both climatic and biotic conditions (Kindlmann, Jarosík, & Dixon 2007). High nutrient and water availability in plant tissues generally boost grain aphid growth (Pons & Tatchell 1995; Aqueel & Leather 2011).

Our study aims to examine the effects of inorganic fertilization on the performance of the grain aphid under different levels of soil fertility and water availability. In a greenhouse experiment we exposed wheat plants infested with *S. avenae* to contrasting levels of inorganic fertilizer, soil fertility and water availability. The selected high levels of soil fertility and fertilizer input represent realistic values for intensive cropping systems. We hypothesized that: (i) high levels of inorganic fertilization and soil fertility would increase aphid performance and that the fertilizer effect would be greater than the effect of soil fertility; (ii) drought would limit aphid population growth. We also expected (iii) that the three experimental factors (inorganic fertilization, soil fertility and water availability) would interactively shape aphid performance.

Materials and methods

Study set-up

Soil fertility and plant material

The soil was collected in May 2013 at an experimental field of Wageningen University & Research located in Vredepeel (Limburg, The Netherlands) where a long-term experiment on soil health has been underway since 2006 (Korthals, Thoden, Van den Berg, & Visser 2014). To investigate the effect of soil fertility on aphid performance keeping all the other physical and biological properties comparable, the soil was collected from the same area at two depths: 0–20 cm (topsoil layer rich in nutrients and organic matter) and from C horizon (~100 cm, parent material) and then stored in plastic bags under similar environmental conditions. The high soil fertility treatment was obtained by mixing the C horizon with the top layer in a 1:9 mixture, whereas the low fertility treatment was obtained using a mixture of 1:1. We used a concrete mixer for mixing the soils. Samples were taken for the analyses of the main soil parameters (Sequi 2000). High fertility soil presented higher soil organic matter content, available P, exchangeable K, Mg and Ca compared to low fertility soil (Table 1). Higher levels of soil fertility did not increase water holding capacity even though enhanced soil organic matter content was expected to improve it (Kononova 2013). The mixing process probably altered the physical structure of the soil organic matter (i.e. porosity), which is considered an important factor supporting soil ability to retain water (Bot & Benites 2005). We therefore did not expect soil fertility to influence the effects of water availability on aphid growth.

Table 1. Physical–chemical characteristics of the soils (high vs. low fertility treatment) used in the experiment.

	Soil fertility	
Soil parameters	High	Low
Soil organic matter (%)	3.1	1.7
Sand (%)	94.2	96.8
Lime (%)	1.8	1.0
Clay (%)	4.1	2.3
Total N (%)	0.3	0.2
Available Olsen P (mg kg^{-1})	95.6	55.1
Exchangeable K (mg kg^{-1})	112.5	94.5
Exchangeable Na (mg kg^{-1})	13.8	13.0
Exchangeable Mg (mg kg^{-1})	119.8	75.0
Exchangeable Ca (mg kg^{-1})	993.4	631.0
pH	6.2	6.0
Water holding capacity (%)	25.4	24.5

After sieving (1.0 cm mesh) soil was filled into 112 pots (5 L, 56 pots per soil fertility treatment). Six pairs of spring wheat seeds (*Triticum aestivum* var. Tybalt) were sown into the prepared pots and randomly placed in a climate-controlled greenhouse at 60% RH, 16 L: 8 D, and 20 ± 1 °C at day and 14 ± 1 °C at night. Overhead lighting (sodium lamps, SON-T Philips, Eindhoven, The Netherlands) was supplied to ensure a minimum light intensity of 200 W/m^2 during the light period. After emergence, the best performing plant per pair was selected and the other clipped and removed in order to have six plants per pot of standardized dimension. Plants were watered three times per week, with quantities as required, before applying different irrigation regimes.

Water availability

Two weeks after sprouting, pots were assigned to two different irrigation regimes, well-watered and drought conditions, achieved by applying 300 mL and 150 mL water/week, respectively. The mentioned amounts of water were selected at the beginning of the water availability treatment in order to maintain steady leaf turgor (well-watered condition) and to allow the soil to dry until 70% of the plants showed wilting signs (drought condition without compromising plant survival). Individual pots were placed on 3 cm deep plastic dishes to retain any excess water.

Inorganic fertilization

Inorganic fertilizer was added in the form of Hoagland nutrient solution (Hewitt 1966) at two different levels: 0.3 g/pot (high fertilization) and 0.03 g/pot (low fertilization). These quantities reflect an amount of N–P–K inputs of c. 130–30–120 and 13–3–12 kg ha^{-1} for high and low fertilization treatment, respectively (see Appendix A in Supplementary material for the complete solution composition). Following normal farming practices, fertilizer was applied at plant sprouting (60%) and 4 weeks later (40%). Pots were randomly rearranged once before the aphid inoculation and not moved thereafter to not interfere with aphid growth.

Aphid material and plant harvest

S. avenae (F.) (Hemiptera: Aphididae) adults were obtained from the Laboratory of Entomology, Wageningen University, and reared in a growth chamber maintained at 20–22 °C, 16 L: 8 D. To support aphid population growth in the chamber, new spring wheat plants were added approximately every two weeks, and old plants were removed after the aphids had settled on the new plants.

Three weeks after sprouting (wheat growth stage 25, Tottman 1987), a single apterous adult aphid of standard size was carefully placed with a fine brush on the oldest leaf of each plant (6 aphids per pot). Pots were placed individually in gauze nets. In order to measure development time (number of days between birth and reproduction) and aphid fecundity (number of offspring produced per adult), clip cages were placed on one adult aphid per pot (MacGillivray & Anderson 1957). Once the adult aphid reproduced, only one neonate nymph was left inside the clip cage. The adult and the other nymphs (if present) were gently placed on another leaf. Clip cages were monitored daily and the nymph development time was scored for 11 days after the clip cage placement, the day by which most individuals had reproduced. Five days later, fecundity was measured (number of third-generation-offspring) and the clip cages removed. Aphids were counted on three different occasions, 10, 20 and 25 days after inoculation (number of aphids per plant) and were then removed from each pot with a soft brush (four weeks after inoculation, average wheat growth stage 60), collected, stored at 4 °C and then weighted to obtain the aphid fresh weight (total aphid biomass).

To better understand the effects of treatments on pest performance, measurements on plant material were also collected. After aphid removal, we recorded the growth stage of all infested plants, which were then harvested and separated into roots, shoots and ears. The roots were washed to remove soil residues. Subsequently, the plant material was dried at 60 °C for 24 h and weighed. The plant biomass (root, shoot and ear) refers to the total biomass per pot (6 plants). The effects of the treatments on the growth stage of infested plants are presented in Appendix B in Supplementary material.

Data analysis

Data were analyzed with linear mixed models with restricted maximum likelihood estimation method in the nlme package (Pinheiro, Bates, DebRoy, & Sarkar 2018). We investigated the effect of inorganic fertilization (high vs. low), soil fertility (high vs. low) and water availability (well-watered vs. drought conditions) and their interactions on aphid performance (development time, fecundity, number of aphids per plant and total aphid biomass) and plant growth (root, shoot and ear biomass). The model regarding the number of aphids per plant included also time (three counts) as fixed factor in interaction with the other treatments. The position of the pots in the greenhouse was included in all the models as random factor. Each treatment (eight in total) had 14 replicates. Development time, number of aphids per plant, total aphid biomass and root biomass were log-transformed to achieve normal distribution of model residuals. The analysis regarding aphid development time was based on data from 58 pots, fecundity on data from 94 pots (replicate loss was due to leaf damages caused by clip cages), those regarding total aphid biomass on 110 pots (aphid populations from two pots were damaged during final measurements) and those regarding number of aphids per plant on 112 pots. The analyses regarding plant biomass (root, shoot and ear) were based on data from 108, 112 and 107 pots, respectively (due to damages to plant structures during harvesting). Tukey multiple comparison test was applied to determine significant differences among treatments. The analyses regarding the number of aphids per plant and aphid total biomass reported very similar and consistent results. Only the latter are therefore presented in the main text (see Appendix C in Supplementary material).

Direct negative density-dependence is a mechanism strongly affecting aphid population dynamics (e.g. Agrawal, Underwood, & Stinchcombe 2004) and it can confound the effects of treatments on pest performance if density becomes high compared to available resources. In the present study, aphid populations showed a positive growth throughout the experiment in all treatment combinations, suggesting that the patterns observed in response to treatments were not driven by a limited carrying capacity of the plants (Appendix C in Supplementary material). All the analyses were performed using the R software, version 3.3.1 (R Development Core Team 2015)

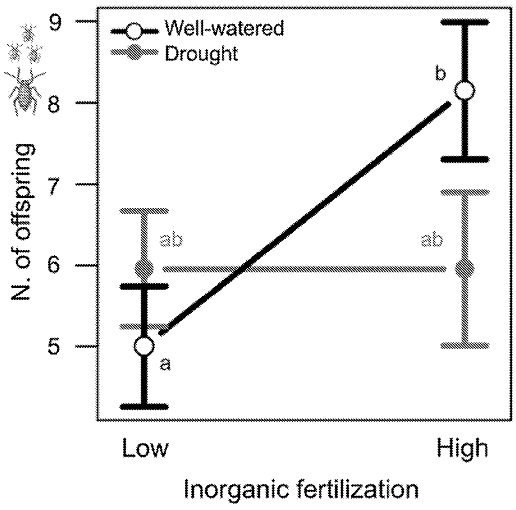

Fig. 1. Effects (mean ± SE) of inorganic fertilization and water availability on aphid fecundity (number of offspring per adult within five days from the start of reproduction). Different letters indicate significant differences among treatment combinations ($p < 0.05$, Tukey multiple comparison test).

Results

Inorganic fertilization reduced aphid development time (Table 2): nymphs developed 9% faster when high fertilizer inputs were delivered to wheat plants (11.0 ± 0.3 days, low fertilizer input; 10.0 ± 0.3 days, high fertilizer input; mean ± SE). High levels of soil fertility increased aphid fecundity (number of offspring per adult) by 44% compared to lower soil fertility levels. Inorganic fertilization also influenced aphid fecundity. However, its effect depended on water availability: high fertilization increased the number of offspring by 63%, but only under well-watered conditions (Fig. 1), whereas it did not affect fecundity under drought conditions. All three treatments affected the total aphid biomass. Fertilization positively influenced this variable. However, the increment in total aphid biomass owing to higher fertilizer inputs depended on soil fertility and water availability (Fig. 2). It was stronger at low levels of soil fertility compared to high soil fertility (Fig. 2A, 194 vs. 65% total biomass increase compared to low fertilization) and under well-watered conditions compared to drought (Fig. 2B, 163 vs. 57%, total biomass increase compared to low fertilization). The effects of treatments on aphid response variables for each treatment combination are presented in Appendix D in Supplementary material.

All treatments significantly affected plant growth (Fig. 3). Generally, plant biomass was increased by high levels of inorganic fertilization and soil fertility and reduced by drought. However, the effect of each treatment depended on the level of the others for all the plant parameters investigated (three-way interaction: fertilization × soil fertility × water availability). High levels of soil fertility partially compensated the decrease in root biomass due to low water availability. Inorganic fer-

Table 2. Results of linear mixed models testing the effect of inorganic fertilization (F; high vs. low), soil fertility (S; high vs. low) and water availability (W; well-watered vs. drought) and their interactions on aphid performance (development time, fecundity and total aphid biomass) and plant growth (root, shoot and ear biomass). Significant ($p < 0.05$) effects are highlighted in bold.

	Development time		Fecundity		Total aphid biomass	
Aphids	$F_{1,28}$	*p*	$F_{1,62}$	*p*	$F_{1,78}$	*p*
Fertilization	6.07	**0.020**	4.22	**0.044**	99.60	**<0.001**
Soil fertility	1.64	0.211	8.83	**0.004**	27.17	**<0.001**
Water availability	0.14	0.707	0.79	0.377	7.63	**0.007**
F × S	0.37	0.550	0.01	0.935	17.49	**<0.001**
F × W	1.26	0.271	4.43	**0.039**	15.26	**<0.001**
S × W	0.51	0.482	0.72	0.398	0.21	0.646
F × S × W	0.04	0.846	0.63	0.430	0.14	0.711

	Ear biomass		Shoot biomass		Root biomass	
Plants	$F_{1,75}$	*p*	$F_{1,80}$	*p*	$F_{1,76}$	*p*
Fertilization	0.24	0.625	17.37	**<0.001**	4.69	**0.033**
Soil fertility	0.57	0.454	26.84	**<0.001**	15.44	**<0.001**
Water availability	161.70	**<0.001**	803.46	**<0.001**	14.87	**<0.001**
F × S	0.48	0.491	5.55	**0.021**	1.60	0.210
F × W	9.99	**0.002**	7.41	**0.008**	5.29	**0.024**
S × W	0.65	0.422	9.07	**0.003**	1.30	0.259
F × S × W	4.30	**0.042**	9.54	**0.003**	4.12	**0.046**

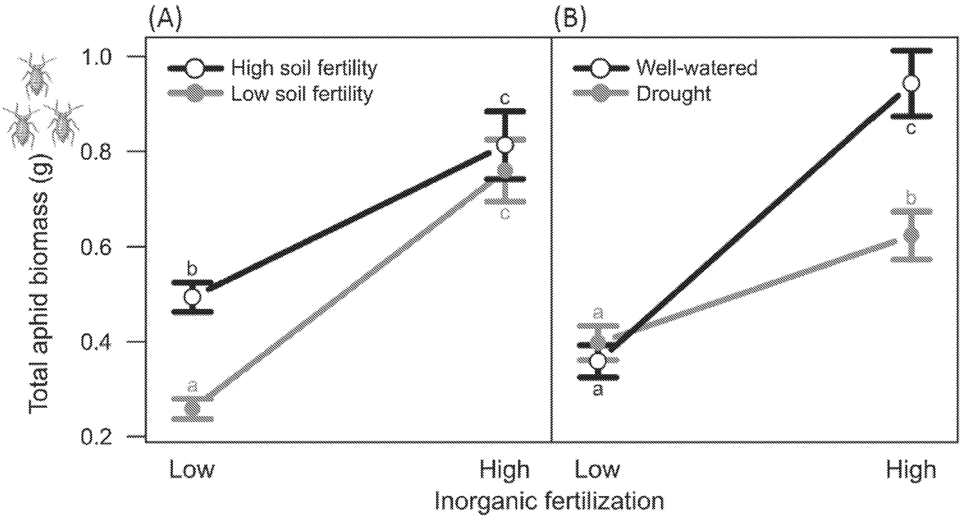

Fig. 2. Effects (mean ± SE) of inorganic fertilization, soil fertility and water availability on total aphid (fresh) biomass per pot. Interactions between fertilization and soil fertility (A) and between fertilization and water availability (B). Different letters indicate significant differences among treatment combinations ($p < 0.05$, Tukey multiple comparison test).

tilization influenced shoot biomass only in unstressed plants under low levels of soil fertility. High levels of soil fertility compensated the reduction in ear biomass owing to low fertilization in well-watered plants.

Discussion

We explored the combined effects of inorganic fertilization, soil fertility and water availability on the performance of the grain aphid. We found soil fertility and water availability to modify the positive effects of fertilizer inputs on aphid growth. Performance increase due to inorganic fertilization was stronger under low soil fertility levels and under well-watered conditions. Our study contributes to elucidate the responses of the aphid-wheat system to common soil management practices under variable climatic conditions.

High inorganic fertilizer inputs to wheat plants led to higher aphid performance, decreasing development time and increasing fecundity and total aphid biomass. As mentioned

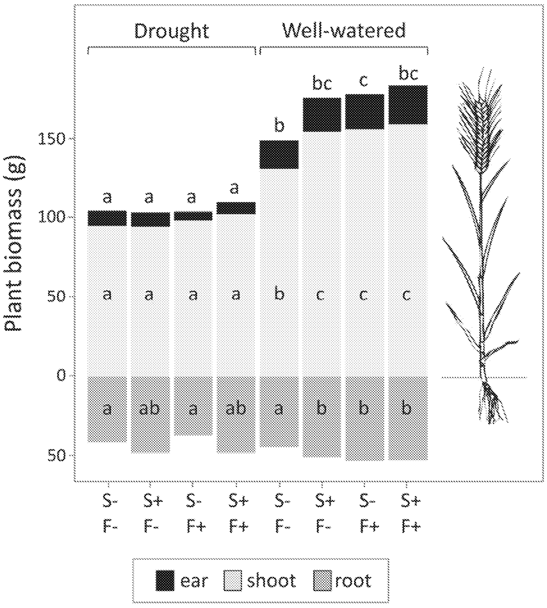

Fig. 3. Effects of treatments on infested plant biomass (roots, shoots, ears) at the end of the experiment; high (+) and low (−) levels of soil fertility (S), inorganic fertilization (F). Different letters indicate significant differences among treatment combinations ($p < 0.05$, Tukey multiple comparison test).

before, the positive effect of inorganic fertilization on growth of the aphid *S. avenae* via enhanced plant quality is well established (Pons & Tatchell 1995; Khan & Port 2008; Aqueel & Leather 2011). Nitrogen level in the diet of herbivorous invertebrates is known, for example, to be an important factor limiting their performance (Awmack & Leather 2002). However, we found that the effects of fertilization on aphid populations depended on the level of soil fertility and on water availability, confirming our third hypothesis. The increase in aphid performance owing to higher fertilizer inputs was stronger under low compared to high soil fertility. Under high fertilizer application aphid populations did not show any effect of soil fertility: aphids probably reached a biological limit in growth rate caused by high nutrient availability under both high and low soil fertility conditions (Douglas 2003; Douglas et al. 2006; Sauge, Grechi, & Poëssel 2010). Future studies exploring aphid responses to continuous gradients in both soil fertility and fertilizer input might shed light on the potential non-linear processes driving aphid population growth. At the low level of fertilization, the effects of soil fertility on aphid growth were more evident and similar to those of fertilization, but with smaller effect size (e.g. no effect on development time). Higher soil fertility increased fecundity and aphid biomass, indicating that the higher amount of nutrients in the soil supported plant growth, increasing aphid performance. Higher soil organic matter content is known, for example, to provide nitrogen to plants and to increase the availability of many micronutrients essential for crop growth (Kononova 2013) thereby improving the nutritional status of tissues and phloem, evidently favoring herbivores. We provide here evidence for the positive response of a sap-feeding pest to increased levels of soil fertility, levels that represent realistic values for conventional cropping systems. Nevertheless, aphid biomass at high level of soil fertility and low fertilizer input was still lower than under the high fertilization regime, suggesting that a shift from conventional to low input management in fertile soils might decrease pest performance. Moreover, under well-watered conditions, we found fertile soil to support levels of wheat biomass (root, shoot and ear) similar to those achieved under high inorganic fertilization, suggesting that, even if the increased nutrient availability favors aphid growth, it sustains plant development. Nevertheless, the present experimental set-up was designed to study aphid response to treatments. In order to fully understand their effects on plant performance (disentangling therefore the effect of treatments and aphids), we should have included control pots without aphids (doubling the number of total pots). We therefore cannot fully address this topic here.

As expected, water availability strongly influenced aphid growth, limiting the total aphid biomass at the high level of fertilization. This result is in line with previous findings showing lower aphid performance in response to plant water stress (Pons & Tatchell 1995; Sumner, Eikenbary, & Johnson 1986; Pineda et al., 2016; Rousselin et al. 2016). The prolonged drought condition probably limited the ability of aphids to access plant resources via reduced turgor and increased sap viscosity (Hale et al. 2003). At low levels of fertilization the effect of drought on aphid development was negligible, clearly showing that the limiting factor under those conditions was the lack of nutrients. Nevertheless, water stress strongly influenced plant performance as well. High levels of fertilization and soil fertility had in fact little effect on wheat biomass under drought conditions confirming that limited water availability can constrain nutrient uptake by wheat plants (Barraclough, Kuhlmann, & Weir 1989). However, plant biomass depended also on the growth stage: the low values of ear biomass under drought conditions, for example, are probably due to the slower development of the plants caused by limited water availability (see Appendix B in Supplementary material). Prolonged water stress might therefore blur the well-known relationships between inorganic fertilization and sap-feeding pests. Although drought can have severe negative impacts on winter wheat production (Eitzinger, Štastná, Žalud, & Dubrovsk 2003), yield losses directly attributable to pests might be limited compared to those inflicted under normal water availability conditions. Not surprisingly, high levels of soil fertility did not reduce the negative effect of drought on both aphid and plant growth, suggesting that soil structure, rather than nutrient availability, is critical in determining water availability to plants (Bot & Benites 2005).

Our study demonstrated that water availability and soil fertility modify inorganic fertilization effects on herbivore pest performance in cereals. Our findings suggest that current practices promoting soil fertility and associated ecosystem services such as biological pest control, carbon sequestration and flood regulation (Bommarco et al. 2013) do not have direct negative consequences on crop protection in conventional cropping systems. Moreover, the enhancement of soil fertility is also expected to improve aphid biological control. Healthy soils rich in organic matter have been shown in fact to sustain richer and more abundant communities of natural enemies, because of the improved soil environment and increased availability of alternative preys (Birkhofer et al. 2008). Moreover, organic fertilizers are expected to influence parasitoid performance through altered aphid fitness but their effects on final aphid control are still debated (Garratt, Leather, & Wright 2010; Garratt, Wright et al. 2010; Garratt et al. 2011). The identification and adoption of alternative (biological) strategies to control aphid populations is of primary importance considering that many aphid populations have developed resistance to common pesticides, resulting in widespread infestations (Foster et al. 2014). Our findings provide an insight into the potential consequences of adopting different soil fertility management strategies on aboveground pest performance in a world exposed to drastic climatic variability. However, more studies exploring the potential interactions between farming practices and abiotic conditions and their effects on pest dynamics are needed to develop more effective crop protection strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.05.010.

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