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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.

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#### Introduction

Insect pests represent a severe threat to crop production, being responsible for an estimated yield loss of

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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 plantpest 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

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