



Rosy apple aphid abundance on apple is shaped by vegetative growth and water status



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ABSTRACT

Regulated deficit irrigation, which is a common practice to cope with water scarcity, can impact plant-aphid interactions, and possibly lead to a reduction in the use of pesticides. To test the possible effect of water restriction on the apple tree-rosy apple aphid (*Malus domestica*-*Dysaphis plantaginea*) system, we performed a factorial experiment with two levels of water supply and two genotypes on artificially infested trees. Plant growth and aphid abundance were characterised during the entire infestation period at two scales of analysis: the apical shoot scale and the tree scale, and additional measures were performed to evaluate plant water status. Aphid abundance increased with plant vegetative growth at both scales of analysis, which is consistent with the Plant Vigor Hypothesis (i.e. with the fact that most of the phloem feeders prefer fast growing plants). At the tree scale, aphid abundance was lower on trees that underwent water restriction, but at the shoot scale, aphid abundance responded differently to water restriction depending on the tree genotype. Water restriction modified the relationship between aphid abundance and growth, thus indicating that host suitability for aphids was affected by different plant variables susceptible to water stress, among which growth. The different response patterns at the two scales of analysis highlight the importance of scale choice in the study of plant-insect interactions.

1. Introduction

Reducing the use of pesticides and coping with water scarcity are two of the main challenges in Mediterranean horticulture. The use of less drought susceptible plant varieties and the implementation of regulated deficit irrigation represent possible solutions to decrease water consumption in horticulture. Interestingly, due to cross tolerance mechanisms between abiotic and biotic stresses, the implementation of deficit irrigation can also reduce host plant suitability for pests and especially aphids (Foyer et al., 2016). Host plant suitability for aphids encompasses multi-aspects, which can be modulated by plant water status. The four main ones are (i) nutrition (or settlement) site availability, i.e. the number of growing apices (Forrest and Dixon, 1975), (ii) phloem nutritional quality, e.g. the secondary metabolites (Czerniewicz et al., 2011) and the amino acid profiles (Ryan et al., 2014), (iii) phloem accessibility (Mody et al., 2009) and (iv) phyllosphere micro-environment (Pangga et al., 2012). As the effects of water scarcity on host plant characteristics vary with stress timing, intensity, and

duration (Tariq et al., 2012), the published results on the effect of host plant water stress on aphid performance, are often contradictory. Water stress has been shown to have a positive (Archer et al., 1995; Mewis et al., 2012), a negative (Agele et al., 2006; King et al., 2006; Simpson et al., 2012) or no effect (Bethke et al., 1998; King et al., 2006; Mewis et al., 2012) on aphid performance. The plant genotype is also a factor that is expected to influence the plant-aphid interaction under water restriction. Yet, the studies evaluating the effects of drought stress on aphid performance on different plant genotypes generally considered genotypes contrasted for their resistance to the insect (Agele et al., 2006; Dardeau et al., 2015; Verdugo et al., 2015) rather than genotypes contrasted for their response to drought stress.

In the present work, the apple tree-rosy apple aphid system [*Malus domestica* Borkh. – *Dysaphis plantaginea* (Passerini)] was chosen as the study case, because apple trees are cultivated worldwide under a wide range of climatic conditions and also in semi-arid areas such as the Mediterranean basin. Moreover apple is the major deciduous fruit tree production worldwide (FAO, 2016). *Dysaphis plantaginea* is a major

Rosy apple aphid abundance is positively correlated to plant vegetative growth at both the shoot and tree scales. Water restriction has a negative impact on aphid abundance only at the tree scale.

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apple tree pest (Forrest and Dixon, 1975). It causes leaf roll (Forrest and Dixon, 1975), shoot and fruit deformations (Marchetti et al., 2009), and populations resistant to pesticides have already appeared (Delorme et al., 1999). Two apple genotypes with different drought response mechanisms were identified from a “Starkimson” × “Granny Smith” cross progeny (Lauri et al., 2016). The first genotype (referred to as DAG: Drought Avoidance Genotype) is characterised by drought avoidance strategy, with reduced stomatal conductance and photosynthesis under water deficit, growth being affected to a smaller extent. The second one (referred to as GCG: Growth Cessation Genotype) is characterised by a high percentage of shoots experiencing growth cessation under drought stress. We intend to use these contrasted genotypes to test how far the mechanism involved in drought resistance affects the apple tree – rosy apple aphid interactions, namely under water stress conditions whose effects on shoot growth may be modulated by the genotype. Other determinants of plant suitability to aphids, such as leaf water potential and gas exchange rates, may also be affected to a greater of lesser extent according to genotype. The related physiological traits, namely leaf temperature (Satar et al., 2008), turgor pressure (Verdugo et al., 2015), phloem sap soluble sugars content (Zehnder and Hunter, 2009) and viscosity (Sevanto, 2014) to which aphids are sensitive, could be modified in turn. The relationship between shoot growth and aphid performances may therefore be disentangled by water stress conditions.

Thus, aphid abundance has been positively correlated to vegetative growth at the shoot scale (Stoekli et al., 2008; Rousselin et al., 2016). Yet, the existence of a similar relationship at the tree scale remains unclear. Indeed, the susceptibility of tree organs to aphids may vary within the tree, between long and short shoots and between fruiting and non-fruiting shoots (Simon et al., 2011). This could affect the patterns of aphid dispersion within the crown. We will therefore consider simultaneously two study scales: the infested shoot and the whole tree, thus verifying if the relation between aphid abundance and growth still holds at the tree scale, and how far it is affected by water stress conditions.

To reach these goals, both apple genotypes were submitted to contrasted irrigation regimes, *i.e.* control vs deficit irrigation, and the aphid population monitored after artificial infestation as well as tree growth, leaf gas exchanges and leaf water potential. Gathered data were then analysed via hierarchical analysis of multiple regression to test how far the plant genotype and the irrigation treatment affected aphid density, possibly via an effect on the plant vegetative growth.

2. Material and methods

2.1. Experimental design and plants

The experiment was conducted in Avignon (southern France) under an 126 m² insect proof shelter (PEHD Cristal 500*600 µm mesh), insulated from the ground with a tarpaulin (PP 86gr UV stabilized), and treated with various chemicals to eliminate weeds, insects, culture auxiliaries and pests. This treatment was applied first on bare soil when the tunnel was built (2013) then repeated without herbicide every year (in February). The trees were therefore moved for two weeks to a nearby clean shelter which also allowed control of the tarpaulin status and manual weeding of the few plants that would have grown through. From 10/April/2015 until the end of the experiment (1/July/2015), the temperature under the shelter was recorded every 30 min using a Hobo® Pro V2 logger (U23-002, Onset®, Bourne, USA).

For each of the two apple genotypes DAG and GCG (described in introduction), 30 scions were whip grafted on M9 Pajam 2 on March 2014. They were grown in 12 L-pots filled with a medium consisting of 1:2 (v:v) perlite and potting soil (Florabella® Klasmann-Deilmann®). Two drippers per pot, each with a delivery rate of 2 dm³ h⁻¹ and connected to a different pipe, provided respectively tap water and an NPK fertilizer.

After one-year of growth, plants were hand-pruned in February 2015. Only the main axis (or trunk) was left with 15 non latent buds (*i.e.* meaning that the trunk was pruned back to less than 80 cm above the grafting point). Pruning wounds were protected with Phytopast®-G. The differentiation of the irrigation treatments started on 24/Apr/2015. The pots were covered with a white plastic sheet to avoid penetration of rain water. Two sets of 12 plants of each genotype were selected for their homogeneity, and subjected to two different watering treatments, denoted by W+ and W-. Plants assigned to the W+ treatment were daily irrigated until run-off and the plants assigned to the W- treatment received a halved water supply. The W- treatment was adjusted by reducing the duration of each of the two to four daily irrigation periods.

2.2. Aphid rearing and infestation

To ensure that individual aphids did not genetically differ in their intrinsic performance, a single clone of *D. plantaginea* (Dp15) was used for the infestation. The aphid colony was established from a single female collected on an apple tree ‘Ariane’ on 26/March/2015 in Avignon. Aphids were reared in the laboratory on the apple cultivar M9 susceptible to aphids, under parthenogenesis-inducing conditions: 20 °C ± 1 °C, 60–70% relative humidity and a 16-h-day cycle (Sauge et al., 1998). Five 7-days old wingless adult females were placed on one single current year axis (*i.e.* which had emerged on the trunk in early spring) per plant on 28/April/2015. The chosen axis for infestation was positioned in the apical position of the trunk. Aphids were then free to disperse all over the plant but could not move to the soil, being blocked by a glue barrier (Rampastop®, Protecta®) provided at the stem base, neither to a neighbouring plant since spacing was large enough to avoid canopy contact throughout the experiment.

2.3. Data collection

The infested trees were monitored weekly from the 30/April/2015 to the 01/July/2015 for vegetative growth and from the 04/May/2015 to the 01/July/2015 for aphid abundance. Vegetative growth was computed by counting the number of expanded leaves separately on each developing proleptic bud, or bud formed in 2014 whose development was delayed by dormancy (Wheat, 1980). Two types of vegetative proleptic structures were distinguished: (i) rosettes, which correspond to the expansion of the preformed leaves of the bud, and (ii) shoots, which correspond to a main axis resulting from the activation of the apical meristem (*i.e.* to the transformation of the rosettes into axes) and all its axillary structures. The diameter at the trunk base, considered as an accurate indicator of plant vigor and classically used as a covariable to explain interplant variability (Nesme et al., 2005), was measured at the start and at the end of the experiment. It varied by less than 12% within the tree populations sorted by genotype (April 4) and treatment combination (July 2). This variability was too small to affect the number of leaves or the aphid abundances, as shown by preliminary covariance analyses (data not shown) performed at shoot and tree scale. Aphid abundance was estimated by assigning to each proleptic structure (shoot or rosette) one class of infestation: C0 (no aphid), C1 (1–5 individuals), C2 (6–25), C3 (26–125), C4 (125–625) and C5 (more than 625) (Grechi et al., 2008; Rousselin et al., 2016). As a result, a total of 629 proleptic structures (an average of 13 per tree) were monitored, among which 55% were assigned to class C4 or C5 at the time of infestation peak.

During the same period, midday leaf water potentials were measured with a Scholander pressure bomb on eight sunny dates (*i.e.* approximately once a week according to the weather conditions) on a subsample of 3–6 randomly chosen trees per treatment, using a non-infested sun-exposed leaf near an apex. Simultaneously, leaf photosynthetic rate, leaf stomatal conductance, leaf transpiration and leaf temperature were measured on a non-infested sun-exposed attached leaf with an open gasometric system LCA-4 (ADC®, Hoddesdon, UK).

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