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Tree genotype modulates the effects of water deficit on a plant-manipulating aphid

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ABSTRACT

Successful plant manipulation by herbivores requires a reconfiguration of the primary and secondary metabolisms of the host-plant. Water deficit is generally predicted to negatively affect the development of gall-inducing insects, by impairing their ability to remodel the primary metabolism of their host. We assessed whether host genotype could modulate water deficit effects on a gall-inducing aphid, *Phloeomyzus passerinii*, developing on poplars, which are known to be among the most susceptible trees to water deficit. Stem-cuttings of two poplar genotypes, with a different resistance level to *P. passerinii*, were grown under three irrigation treatments, and subsequently infested with the same aphid clone. Plant growth parameters and aphid colonies development were recorded, and the development and organization of the pseudogall induced by the aphid was observed using histological investigations. The three irrigation treatments resulted in three levels of water deficit. Mean predawn leaf water potential reached −0.10, −0.49 and −0.75 MPa in the optimal, intermediate and low irrigation treatments respectively. In both genotypes, growth, architecture and photosynthesis were similarly affected. The severe water deficit reduced the development of aphids on both genotypes, which is in agreement with the general prediction for gall-inducing insects. Nonetheless, while the intermediate water deficit did not affect the development of aphids on the susceptible genotype, it enhanced their development on the resistant one. This latter observation contradicts the prediction for gall-inducing insects, but is in agreement with the plant stress hypothesis for sucking insects. The size of the pseudogall induced by the aphids in the bark of their host progressively diminished when water deficit increased. Lignification, believed to be an important component of poplar resistance to *P. passerinii*, also progressively decreased with water deficit. The involvement of physiological and architecture modifications due to water deficit on the development of aphids is discussed. The results demonstrate that host genotype can modulate water deficit effects on the development of a galling aphid, thereby compromising predictions on the outcome of droughts on stand resistance to plant-manipulating herbivores.

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1. Introduction

In different regions of the world, progressive increases in frequency and severity of droughts are expected during the upcoming century (Allen et al., 2010; Lindner et al., 2010; IPCC, 2013). This is a critical issue for plant-herbivore interactions as the availability of environmental resources can affect plants allocations to primary or secondary metabolisms. Water deficit is known to enhance or decrease both the nutritional value of plant tissues and their content in defensive compounds (Inbar et al., 2001; Pritchard et al., 2007; Gutbrodt et al., 2011; Walter et al., 2012), which in turn alter their resistance to herbivores (Koricheva et al., 1998; Huberty and Denno, 2004; Jactel et al., 2012). Deficit intensity can affect the outcome of a water shortage on plant resistance level (Larsson, 1989; Koricheva et al., 1998; Huberty and Denno, 2004; Banfield-Zanin and Leather, 2015a,b). For instance, the growth differentiation balance hypothesis states that any environmental factor limiting plant growth more than photosynthesis would enhance secondary metabolism, and consequently host resistance to herbivores (Loomis, 1932; Herms and Mattson, 1992; Stamp, 2003). As a result, a higher host resistance level is generally expected for intermediate values within a resource gradient (Herms and Mattson, 1992; Stamp, 2003). A parabolic relationship

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between water availability and host resistance, with higher resistance levels during a mild stress, has been observed in some studies (Christiansen and Glosli, 1996; Sallé et al., 2008), but not consistently though (Glynn et al., 2004; Hale et al., 2005; Tariq et al., 2012).

The impact of water deficit on plant-herbivore interactions may also depend on the feeding strategy of the herbivore (Larsson, 1989). For instance, according to the plant stress hypothesis, boring insects generally perform better on water stressed plants, while leaf-chewers are negatively affected (Larsson, 1989; Koricheva et al., 1998; Huberty and Denno, 2004). For sucking insects, the pattern is less clear since the effects of water shortage on insect performance might depend on both deficit intensity and frequency (Larsson, 1989; Huberty and Denno, 2004; Banfield-Zanin and Leather, 2015a,b). For herbivores performing host manipulation, like gall-inducers, the situation might be even more complex as, to achieve manipulation, these organisms generally have to alter both the primary and secondary metabolism of their host plant (Nyman and Julkunen-Tiitto, 2000; Matsukura et al., 2012; Body et al., 2013; Dardeau, 2014). The meta-analyses performed by Koricheva et al. (1998) and Huberty and Denno (2004) concluded that water deficit generally negatively affects the survival or colonization density of gall-formers. Nonetheless, several studies also indicated that although drought reduces gall size, it could sometimes have positive effects on galling success or gall densities, probably by altering resistance mechanisms (De Bruyn, 1995; Björkman, 1998, 2000). This suggests that drought could favor host plant manipulation in resistant hosts, in situations where water deficit affects the resistance mechanisms, while still allowing a reconfiguration of their primary metabolism by the herbivore.

The woolly poplar aphid, *Phloeomyzus passerinii* (Sign.), is a major pest of poplar stands in Europe, the Near East and Northern Africa, which following outbreaks can cause extended tree mortalities (Pointeau et al., 2011). This aphid feeds on the cortical parenchyma of poplar stems, where it induces pseudogalls, characterized by the multiplication of thin-walled hypertrophied cells, a depletion of soluble phenolic compounds and a peripheral lignification of cell walls (Pointeau et al., 2012; Dardeau et al., 2014a). The pseudogall differentiation enhances nymphal development and optimizes the feeding behavior of the aphids (Dardeau et al., 2014b). This aphid is therefore both a sucking insect and a gall-inducer. Poplar resistance to this insect is highly variable among poplar species and hybrids, and can affect aphid settlement, development and/or fecundity (Sadeghi et al., 2007; Pointeau et al., 2011, 2013). In resistant host genotypes, pseudogall formation can be totally or partially inhibited through processes involving apparently a fast and extended lignification of the manipulated host tissues (Dardeau et al., 2014a,b). Depending on its intensity, water deficit can have no or a negative effect on lignin deposition in wound periderms which differentiate in wounded tree bark (Puritch and Mullick, 1975; Biggs and Cline, 1986), and could therefore alter poplar resistance to *P. passerinii*. Poplars are fast growing trees, requiring high water availability to sustain a high productivity (Tschaplinski and Blake, 1989; Tschaplinski et al., 1994), and are among the least resistant tree species to drought (Bréda et al., 2006). Consequently global change, and the increase in drought occurrence and intensity in many geographic areas, is likely to affect poplar interactions with *P. passerinii*.

We investigated how water deficit influences the interactions of *P. passerinii* with its host tree. Our objectives were (i) to assess whether water deficit modified aphids' development and pseudogall differentiation, (ii) to investigate whether water deficit interacts with host resistance. For this, we have considered the effect of three different levels of irrigation on aphids' interactions with two poplar genotypes, with different resistance level to the aphid.

2. Materials and methods

2.1. Plants and insects

Stem-cuttings of I-214 and I-45/51, two of the most planted *Populus x canadensis* Moench. hybrids in France, were obtained in January 2012 from the experimental nursery of Guéméné Penfao (France). Previous experiments and field observations have indicated that I-214 is highly susceptible to *P. passerinii*, while I-45/51 negatively affects the development and fecundity of the aphid (Pointeau et al., 2011, 2013). *P. passerinii* develops a pseudogall in the cortical tissues of I-214 while the differentiation of the pseudogall is hampered in I-45/51 (Dardeau et al., 2014a), and host manipulation results in lower benefits for the aphid (Dardeau et al., 2014b).

Aphids originated from a colony established in October 2008 from an apterous parthenogenetic aphid collected in Reboursin (France). This clonal colony belongs to the most common haplotype that has so far been identified in France (Pointeau et al. unpublished results from combined analyses of three mitochondrial DNA fragments, Cytochrome oxidase I and II and Cytochrome b genetic fragments). The colony was maintained in a climate controlled chamber (21 ± 1 °C, 70 ± 10% RH and 16L:8D photoperiod), on I-214 stem-cuttings (Pointeau et al., 2011).

2.2. Plants cultivation and infestation

Cultivation and infestation were performed in a greenhouse (INRA Orléans, France), where temperature was controlled (20 ± 2 °C). The experiment was performed with 75 stem-cuttings (30 cm-long) for each poplar genotype, distributed over 80 m^2. The stem-cuttings were kept at 5 °C until they were planted in February 2012 in 12 L pots filled with quartz sand, under tap water irrigation. Irrigation was automated and regulated by a tensiometer to maintain the soil water content at field capacity. Seven weeks after planting 50 mL of a nutrient solution was manually applied to each plant. The nutrient solution was then applied twice a week, until the end of the experiment. The macroelements contained in the nutrient solution were (in mM) 268 NH_4NO_3, 77 K_2HPO_4, 37 $CaCl_2$, and 31 $MgSO_4$. The microelements were (in μM) 4834 H_3BO_3, 951 $MnSO_4$, 80 $ZnSO_4$, 33 $CuSO_4$, 11 Na_2MoO_4, and 14 $FeSO_4$.

Two weeks later (mid-April), the stem-cuttings of each genotype were randomly separated into three groups of 25 stem-cuttings, with different irrigation levels. The first group, with high water availability (HW), was kept at field capacity under automated irrigation until the end of experiment. Automated irrigation provided 300 ± 20, 305 ± 15 and 350 ± 20 mL of water per day and per stem-cutting in April, May and June respectively, following poplars needs. The second and third groups were manually irrigated every other day with water volumes calculated to follow the automated irrigation. The stem-cuttings of the second group, with an intermediate water availability (IW), received two thirds of the water volume provided by automated irrigation, while the third group, in which a low water availability was applied (LW), received only one third of this volume of water. Stem-cuttings of both genotypes were mixed and organized in 8 blocks for each water treatment with 5–8 individuals per block.

Five weeks after the beginning of the water shortage, 20 plants per modality were infested with aphids. Three apterous parthenogenetic females were placed at mid-height on the initial shoot of the stem-cuttings, under a gelatin capsule for 48 h. The establishment of aphids was then checked, and new infestations were performed until stem-cuttings had 6–10 established nymphs. This

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