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Unraveling the tripartite interactions among the woolly poplar aphid, its host tree, and their environment: a lead to improve the management of a major tree plantation pest?

Aurélien Sallé¹ · Sophie Pointeau¹ · Stéphanie Bankhead-Dronnet¹ · Catherine Bastien² · François Lieutier¹

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Abstract

• **Key message** For an optimal deployment of poplar resistance to the gall-inducing aphid *Phloeomyzus passerinii*, a laboratory susceptibility assay has been developed. The nature of aphid–tree interactions during compatible and incompatible situations has been studied in detail. This should help at identifying specific resistance markers and at testing effects of site conditions on tree–pest interactions.

• **Context** *P. passerinii* is a major pest of poplar plantations in Europe, and the plantation of resistant poplar genotypes is regarded as the best long-term management strategy for this pest. This requires a sound knowledge of the interactions among the pest, its host and their environment.

• **Aims** Here, we review the recent advances aiming at developing an optimal deployment of host resistance versus *P. passerinii*.

• **Results** Investigations on aphid–host interactions demonstrated that *P. passerinii* induces pseudogalls within the bark of susceptible hosts. This results in a reduction of starch bark content during aphid outbreaks, which could be involved in tree death. The constitutive level of starch in the bark could be related to the tolerance level of trees. A susceptibility test has been designed for poplar genotypes, discriminating three categories of susceptibility depending on tree’s ability to totally or partially inhibit pseudogall induction. The test still has several limitations however. It neither takes into account the large level of individual genetic diversity of the aphid in France, nor the environmental modulation of tree resistance and tolerance, while water deficit and fertilization could potentially affect these parameters.

• **Conclusion** The hypotheses drawn regarding the processes leading to tree death or resistance should help at identifying resistance markers, and at testing effects of site conditions on tree–pest interactions.

Keywords *Phloeomyzus passerinii* · *Populus* · Gall · Resistance · Tolerance

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Contribution of the co-authors AS supervised the experiments on tree–pest interactions and wrote the paper.

SP contributed to the population genetics studies and tree–pest interactions.

SBD supervised the population genetics studies.

CB provided insights on the evaluation and management of tree susceptibility.

FL coordinated the research project.

All the authors have edited and approved the manuscript.

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1 Introduction

Forest plantations are often composed of few species, planted at regular spaces, in even-aged stands (Stanturf and van Oosten 2014). When the objective is to maximize wood production, the plantation can be intensively managed with planned silvicultural practices including fertilization, irrigation, weeding, and pruning (Stanturf et al. 2001; Cardias Williams and Thomas 2006; Stanturf and van Oosten 2014). Poplar cultivation often falls within this category and poplar stands are sometimes considered as agricultural crops (Stanturf and van Oosten 2014). They cover more than 8 million ha in the world. Most of them are located in China (7.6 million ha) and Europe (800,000 ha), especially in France (236,000 ha), Hungary (109,000 ha), Spain (105,000 ha), and Italy (101,000 ha) (Stanturf and van Oosten 2014). Poplars are easy to propagate, to plant, and are fast-growing trees with high growth rates when planted in appropriate sites (Heilman 1999; Stanturf and van Oosten 2014). Plantations mostly aim at producing wood, pulp, paper, and biofuel but might also serve for phytoremediation and carbon sequestration purposes. Harvest cycles could be very short depending on the application, ranging from a few years for pulp production to 10 to 20 years or longer for solid wood products (Heilman 1999; Stanturf and van Oosten 2014). Most stands are monoclonal and poplar plantations may be seen as mosaics of monoclonal blocks at the landscape level (Stanton et al. 2014). The breeding of elite genotypes are facilitated by easy vegetative propagation, and breeding programs rely on 12 species, either Eurasian or North American, and hybrids (Stanturf and van Oosten 2014). The traits targeted by selection are mostly related to wood quality, silviculture and disease resistance, i.e., the ability of the plant to prevent or reduce damage by parasites (Stanton et al. 2014; Stanturf and van Oosten 2014).

In Europe, only a handful of genotypes, mostly belonging to the *P. x canadensis* hybrid (*Populus nigra* x *Populus deltoides*), dominates in the plantations. For instance in France, 10 genotypes represent approximately 70% of the cutting production (Paillassa 2013). This reduced genotypic diversity at both the stand and landscape levels, together with the intensification of silvicultural practices, make poplar plantation particularly prone to diseases and pests problems (Charles et al. 2014; Ostry et al. 2014). Among these pests, *Phloeomyzus passerinii* (Signoret), the woolly poplar aphid (WPA), is regarded as a major threat to poplar plantations in Europe (Charles et al. 2014; Sallé and Battisti 2016).

P. passerinii is a primary pest, colonizing vigorous trees (Sallé and Battisti 2016). Since no significant damage have been reported from natural forests, it is considered a plantation pest causing massive mortality in the stands of susceptible poplar genotypes (Charles et al. 2014; Sallé and Battisti 2016). Currently, population control is mostly achieved

through mineral oil or insecticide spraying, like Karate Xpress® for instance (Charles et al. 2014; Sallé and Battisti 2016). Outbreaks generally start in the upper third of mature trees, i.e., trees close to their expected full height and canopy size. Since this is an area difficult to reach, insecticide application is performed by misting. However, this could result in significant environmental issues, especially considering that poplar stands are generally located in alluvial areas. Although numerous insects have been found preying on the WPA, they do not seem to significantly control its populations and biological control is not currently considered an efficient control strategy (Vidotti 1960; Arzone 1987; Raspi 1996, 2005; Charles et al. 2014; Sallé and Battisti 2016). For now, the best alternative to chemical control is probably the selection and deployment of resistant poplar genotypes. This idea is supported by field and laboratory observations indicating an important individual variability in resistance among wild and cultivated poplar genotypes (Allegro et al. 1996; Sadeghi et al. 2007; Pointeau et al. 2011; Charles et al. 2014). The plantation of resistant genotypes is regarded as the best long-term strategy, for both environmental and economic issues, to manage major pests and disease in plantation forests (Ostry et al. 2014). This strategy has been considered in poplar improvement programs for many years. In Europe for instance, together with high yielding, genotypes have been selected for their resistance to bacterial canker and leaf rust (Ostry et al. 2014).

Developing a pest management strategy relying on host resistance might be achieved with empirical observations of pest performance and host damage, in field and laboratory conditions. However, for an optimal deployment of host resistance in time and space, a sound knowledge of the tripartite interactions among the pest, its host and their environment would be required. Although the WPA is a primary pest, causing significant damage to poplar stands since almost a century, until recently only few studies have been conducted on this insect, mainly in Italy and Iran (see section 2). However, intensive studies have been developed in France following dramatic damage extension at the end of the 1990s. Indeed, once damage has started and spread in France, only a few elements of the aphid biology have been described, and almost nothing was known on the interactions with its host plant. For instance, the WPA was reported to feed on cortical parenchyma and to inject salivary toxins, but there was no histological or biochemical data supporting these assertions (Charles et al. 2014). This basic knowledge of the pest biology was sufficient though to build laboratory or nursery tests of susceptibility, i.e., assessments of potential damage level caused by the WPA, in Italy and Iran. However, these tests suffered from several limitations, related to knowledge gaps in the aphid biology and ecology, particularly in the nature of interactions with the host-tree. There were three main gaps. Firstly, the genetic diversity and the genetic structure of the pest populations were unknown. Secondly, several components of the

interactions between the WPA and its host tree were unclear. The feeding strategy of the aphid, and the resistance and tolerance mechanisms of the trees, i.e., their ability to resist or to sustain damage without fitness reduction (Stowe et al. 2000), had never been investigated. As a consequence, the processes leading to tree's death were not known (Charles et al. 2014). Finally, the impact of the environment on the interactions had never been assessed.

To improve the WPA management in France, several investigations have been conducted to fulfill these different gaps. In this review we aim at presenting the achievements and limitations of these investigations and how they could contribute to the development of a management strategy based on a rational and sustainable use of host resistance and/or tolerance. More specifically, we intend to illustrate the usefulness of detailed studies of pest-host-environment interactions to propose means or novel leads, to improve pest management in plantation forests. This review has been arranged into four sections. At first, in section 2, it presents what was known on the biology and ecology of the WPA before its damage starts to extend in France. The section 3 refers to the initial evaluation of tree-pest interactions and their components, in particular the genetic diversity and structure of the pest populations. The section 4 presents the in-depth analysis of compatible interactions between a susceptible genotype and the pest. Finally, the section 5 presents the potential resistance mechanisms, the parameters related to tolerance, and their environmental modulation. The manuscript ends with a discussion on research prospects.

2 Overview of the pest biology and damage

The WPA is the only known species within the Phloeomyzinae sub-family (Hemiptera: Aphididae) (Blackman and Eastop 1994; Nieto-Nafria and Mier-Durante 1998). A phylogeny reconstruction using the data previously described by Ortiz-Rivas and Martinez-Torres (2010), and based on two nuclear genes, long wavelength opsin and elongation factor-1 alpha, showed that the sub-family Phloeomyzinae was closely related to the Lachninae sub-family (Poiteau 2011). This suggests that the WPA occupies a basal position within the Aphididae family. The WPA has a Palaearctic distribution, but has also been introduced in Northern and Southern America (Smith 1974; Ortego et al. 2004). Aphid colonies develop only on poplars, on the trunk or main branches, where they produce an abundant white woolly wax. The insect reproduces by cyclical parthenogenesis. Grayish or greenish apterous parthenogenetic females can be observed all year round (Fig. 1(1)). They are viviparous and produce nymphs with an intrinsic rate of natural increase at 25 °C reaching up to 24% on a susceptible host genotype (Poiteau 2011). In autumn, sexual winged morphs can occur

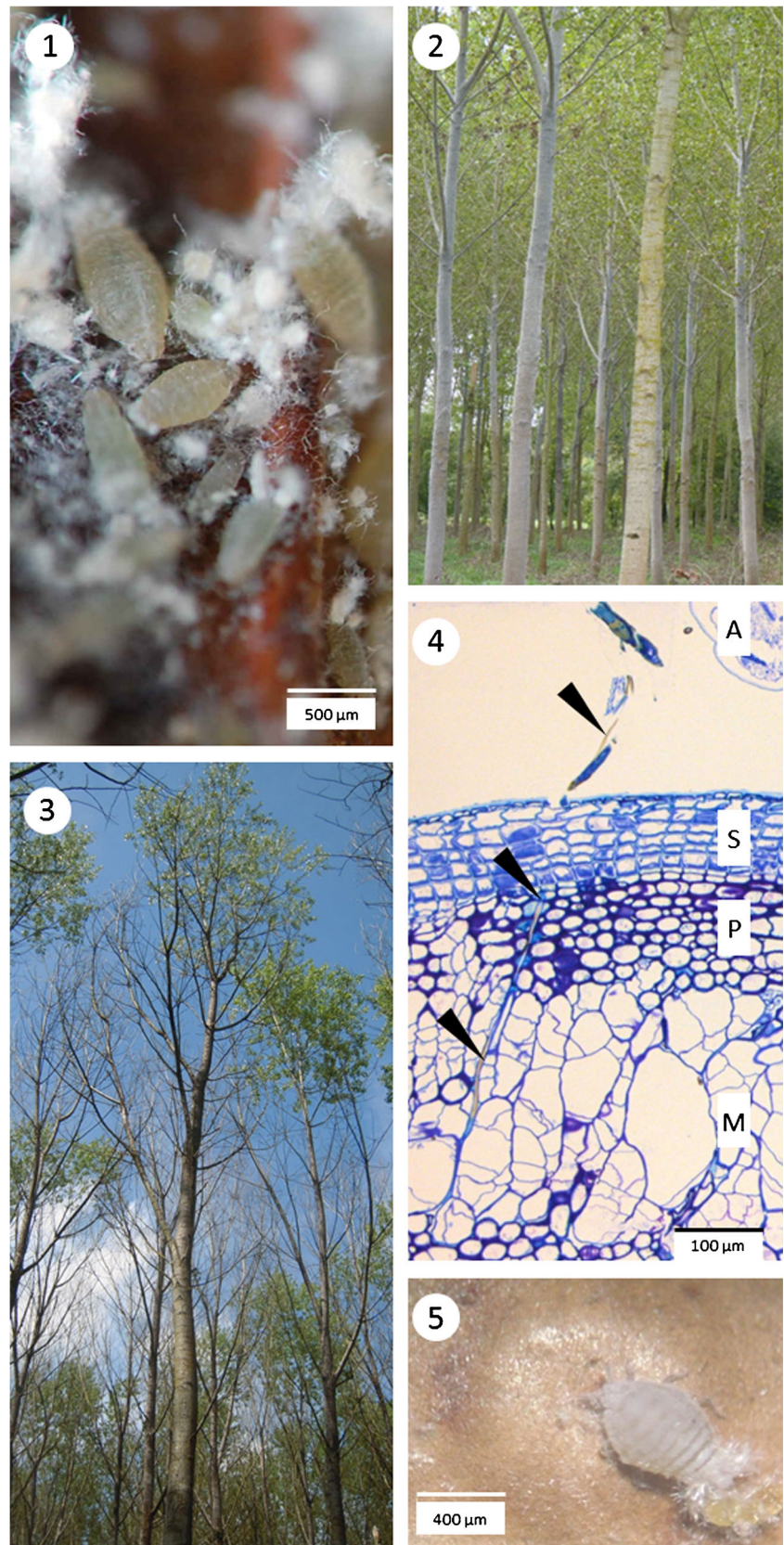
and produce eggs through sexual reproduction (Arzone and Vidano 1984; Blackman and Eastop 1994; Vala et al. 2011). While many aphid species alternate host plants to complete their life cycle, the WPA has only been reported on *Populus* species, and is therefore considered a monoecious species. Several species and hybrids of poplars can be colonized: *Populus nigra* L., *P. deltoides* (Bartr.) Marsh., *P. suaveolens* Fisher, *P. ciliata* Wall., *P. maximowiczii* Henry, *P. tremuloides* Michx., and *P. x canadensis* Michx. (Habib and Ghani 1970; Smith 1974; Blackman and Eastop 1994). The species has been described for the first time in 1875 in France (Signoret 1875), but was reported as a pest several decades later, in several countries of the Mediterranean Basin (Sallé and Battisti 2016). The first outbreaks were reported in 1934 in Italy (Della Beffa 1936) and in 1940 in Spain (Aparisi 1971). Damage occurred in Iran in 1980 (Rajabi Mazhar et al. 2003). In France, damage was reported more recently, in 1996 in the southwest of the country (Maugard 1996). Since then, most poplar plantation areas in France were drastically affected (Baubet and Goudet 2010) (Fig. 2). Damage was particularly recorded from stands of I-214, Triplo and Dorskamp genotypes, three of the most planted poplar genotypes in the 2000s (Baubet 2007; Paillassa 2013).

Damage arises following outbreaks, which occur mostly in mature stands, when tree circumference is above 90 cm (Maugard and Baubet 2004; DSF 2006). Trunks can be covered with aphid colonies and turn blackish due to sooty molds development on aphid honeydew (Fig. 1(2)). The main symptoms are observed in spring following the outbreak. Barks cracks and necroses, together with dark exudations, appear on formerly infested trunks. The most striking consequence of an infestation is the absence of bud break on some or all of branches of the canopy (Sallé and Battisti 2016) (Fig. 1(3)). This results in reduced growth and sometimes massive mortality. Following an outbreak, up to 70% of a susceptible stand, generally close to harvest age, can be killed (Maugard and Baubet 2004). Killed trees are generally vigorous, and damage is often reported in fertile stands. This species is therefore considered a primary pest of poplar plantations (Charles et al. 2014; Sallé and Battisti 2016).

3 Evaluation of tree-pest interactions and their components

A pest management based on host resistance firstly requires the evaluation of the susceptibility level of tree genotypes, and more specifically of plant and/or pest-related parameters or traits associated with resistance or susceptibility. For this, it is necessary (i) to perform a susceptibility assessment to screen the existing tree genotypes and (ii) to evaluate the genetic diversity and population structure of the pest.

Fig. 1 1–Apterous parthenogenetic females and nymphs of *Phloeomyzus passerinii*. 2–Outbreak in a poplar stand. Note the grayish trunks of the infested trees in front, on the left, covered by aphid colonies. 3–Infested tree, in the spring following an outbreak, with a reduced canopy. 4–Resin embedded cross section (5 μm) of bark of a susceptible poplar genotype infested by *P. passerinii*. Black arrows indicate aphid stylets and their pathway. *A* aphid, *S* suber, *P* unmodified cortical parenchyma of poplar bark, *M* modified poplar tissues with thin-walled, hypertrophied cells. 5–Apterous parthenogenetic female feeding on a modified bark tissues of a stem cutting. Note the slight swelling of bark tissues



3.1 Building a susceptibility assay

The best evaluation of plant genotype susceptibility to a pest is generally provided by field surveys which can integrate performance of local pest populations, tree resistance and tolerance, and effect of environmental conditions. However, field tests in uncontrolled environments can lead to high experimental errors, while tests conducted under controlled conditions, in a laboratory or a greenhouse can easily and quickly provide reproducible results (Russell 1978). In the case of WPA, early assessments of susceptibility cannot be made under field conditions because outbreaks must occur to see damage and then damage can only be assessed on mature trees. In addition, since outbreaks are unpredictable events, assessments for genotypes that are planted over a small area or in a specific region would be even more difficult. Laboratory or nursery assays are then required. The evaluation of host

susceptibility to a pest can rely on host response and/or pest performance (e.g., Goundoudaki et al. 2003; Puterka et al. 2006; Ennahli et al. 2009). In the latter situation, the evaluation is rather related to host suitability for the pest, like for instance the adequacy of plant tissues with nutritional requirements and optimal development of the insect, than to actual host susceptibility, i.e., the extent of damage caused by the pest to the host. Considering that suitability should enhance pest performance and the resulting damage, it could be related to susceptibility. Nonetheless, since host response to aphid infestation is not evaluated, this approach does not allow taking into account the ability of the host-plant to tolerate pest attacks, through compensation or other means. For instance, under field conditions, similar colonization by the WPA can lead to different outcomes for the trees, depending on their physiological status (see section 5.2). For practical issues, since the symptoms expression on plant is delayed and

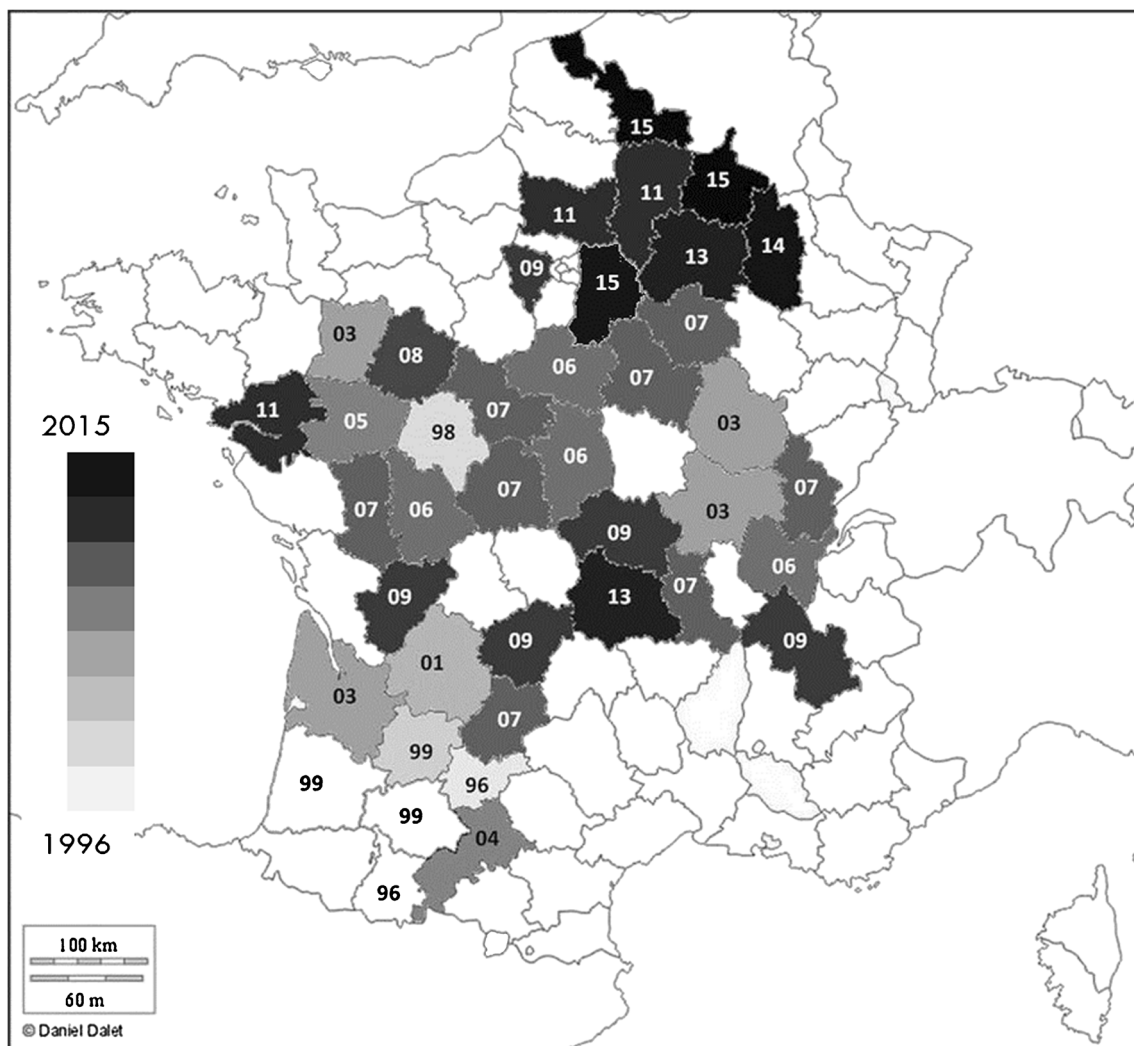


Fig. 2 Map of France showing the progressive expansion of outbreaks of *Phloeomyzus passerinii* in the different French departments. Numbers in the departments indicate the first year of outbreak observation. This map

has been built with the database of the French forest health service (DSF). The DSF is performing field observations on pests and pathogens affecting the vitality of forest stands since 1989

requires a high infestation density, the susceptibility assays for the WPA rely on pest performance.

First assays to evaluate susceptibility of various genotypes of *P. x canadensis*, *P. nigra*, *P. deltoides* and *P. alba* were conducted in Italy and Iran on one-year-old cuttings and 3- to 6-year-old trees, respectively (Lapietra and Allegro 1990; Allegro et al. 1996; Rajabi Mazhar et al. 2003; Karahroodi et al. 2006; Sadeghi et al. 2007). The number of aphids, or colony surface area after a delay of infestation (several weeks on cuttings or months on trees), were used to build a resistance index for each poplar genotype and gave valuable information on different poplar species and/or genotypes. However, at least for the Italian assays, several discrepancies were observed between the test results and field observations (Allegro et al. 1996). For instance the evaluation led to “false positive” genotypes, considered as susceptible in the assays but on which few damage had been recorded in field conditions. In addition, the origin of aphid populations used in the assays was never taken into account.

Based on these preliminary results, a detailed physiological and behavioral investigation of aphids was performed on different poplar genotypes in France (Pointeau et al. 2011). The susceptibility assays were based on pest response to host genotype. First-instar nymphs were laid on 1-year-old cuttings of candidate poplar genotypes and the ability of nymphs to settle on these cuttings was evaluated. Settled nymphs were then left to develop, to reach the imaginal instar and to reproduce, and their fecundity was estimated. Susceptibility was consequently assessed through two insect-related parameters: establishment and multiplication capacities (Pointeau et al. 2011). When the test was performed with a large set of genotypes, belonging to *P. x canadensis*, *P. nigra*, *P. deltoides*, *Populus trichocarpa* Torr. & A. Gray ex Hook., and *Populus x interamericana* Brockh., the two parameters varied in a continuous way (Pointeau et al. 2011; Sallé et al. 2015). Yet the tree genotypes could be arranged in three categories: not susceptible (i.e., with no or low aphid establishment), partially susceptible (i.e., with aphid establishment but reduced aphid multiplication), and susceptible (i.e., with both aphid establishment and good aphid multiplication) (Sallé et al. 2015). Reference genotypes for each of these three categories were selected from (i) repeated laboratory assays, and (ii) field observations among genotypes planted over large areas, and therefore potentially exposed to different aphid populations, with repeated reports of susceptibility or resistance. For standardization purposes, during each assay comparisons were made with these reference tree genotypes to decide in which category the assessed genotypes would fall. In addition, the assays were performed with an aphid lineage, i.e., a monoclonal aphid colony from a known origin, or identified population. Field observations and experiments, using the same lineage, supported the predictions of aphid performance made with the laboratory assay

(Pointeau et al. 2011). The susceptibility of 25 commercialized poplar genotypes (belonging to *P. x canadensis*, *P. x interamericana*, *P. nigra*, *P. deltoides*, and *P. trichocarpa*) has been assessed, and most of them were categorized as “not susceptible” or “partially susceptible” (Pointeau et al. 2011; Sallé et al. 2015).

Such laboratory assays, although more convenient than field observations, i.e., more rapid and cost-effective, still suffer from several limitations. For instance, tree-related responses to aphid infestation are not evaluated. The ability of the host-tree to tolerate an aphid infestation is then not taken into account, as well as the environmental effects (see sections 5.2 and 5.3). In addition, the susceptibility of tree genotypes is evaluated but not their resistance level. The assay can guarantee that, at least with the tested aphid lineage and under the test conditions, the WPA can settle and proliferate on susceptible genotypes. Therefore, there is a likelihood that outbreak can occur under field conditions on these genotypes. Nonetheless for the not susceptible tree genotypes, a failure to settle and develop with the tested aphid lineage and under the test conditions do not guarantee that it cannot occur under field conditions, making the interpretation of the results somewhat difficult to generalize beyond the experimental conditions. Hence, generalization to field conditions should be made with caution. Moreover, the recorded parameters can be sometimes variable among assays, especially the multiplication capacities of the aphids. This might be related to the aphid population, the physiological status of cuttings or to another fluctuating environmental parameter. It suggests that assay conditions require more standardized conditions and can still be improved. So far however, among the genotypes that have been assessed several times, sharp variations in the susceptibility level among assays or with field recordings have been observed only once, with Dorskamp, a *P. x canadensis* genotype. This genotype indeed exhibits contrasting susceptibility levels in laboratory assays, being sometimes reported as “susceptible” or “not susceptible.” This variable susceptibility is however also observed under field conditions, stands of this genotype being heavily damaged in some regions while totally unaffected in others (Sallé et al. 2015).

Finally, this assay only considers the performance of an individual insect since aphids originate from a monoclonal colony. However, an assay based on insect-related parameters requires a good knowledge of how these parameters might vary among insect populations. This is particularly relevant for aphid-plant interactions in which the outcome of the interaction can be highly dependent on aphid biotypes—plant genotypes combinations, different biotypes having sometimes completely different host ranges (Peccoud et al. 2009; Kanvil et al. 2014). To take into consideration the possible occurrence of pest populations with different levels of aggressiveness, it is necessary to unravel the pest genetic variability and population structure.

3.2 Genetic diversity of the WPA

The WPA can reproduce either asexually, with parthenogenetic females, or sexually. Having both reproductive modes confers to aphids in general an adaptive response to environmental changes (Simon et al. 2010). The proportion of sexual reproduction versus parthenogenesis, and how environment could modulate it, is still unknown in the WPA. Moreover, neither dispersal range nor processes involved in dispersal have been investigated yet. However, both reproductive modes and dispersal are critical issues to consider since they can sharply affect aphid genetic diversity at the tree, stand and region scales, which, in turn, could modulate the adaptability of the pest to resistant hosts. Population genetic studies offer a powerful approach to gain information about genetic diversity, long-distance movements, and population structure on a wide variety of organisms. The level of WPA genetic diversity was first assessed on parthenogenetic females collected in 35 localities from France, Spain, and Italy where aphid outbreaks were common. A total of 25 multilocus genotypes (MLGs), which are unique combinations of alleles across all tested marker microsatellite loci, were found (Pointeau 2011; Pointeau et al. 2012a). Two complementary population genetic studies relying on several hundreds of genotyped aphids are currently under analysis, at different spatial scales: Europe, French regions, poplar stands, and tree levels. Samples were collected in stands of susceptible genotypes (mostly I-214). A high number of MLGs has been found and suggests a large level of individual genetic diversity (Pointeau et al. unpub. data; Bankhead-Dronnet et al. unpub. data). An analysis of their spatial distribution showed that the diversity is heterogeneously distributed among regions, even among poplar stands of the same poplar genotype distant from a few kilometers within regions, suggesting the existence of different aphid lineages (Pointeau et al. unpub. data; Bankhead-Dronnet et al. unpub. data). Such studies should also help understanding the contribution of sexual and/or asexual reproductions in WPA populations' composition and dispersal.

In parallel, tree susceptibility assays were performed using aphid lineages obtained from four parthenogenetic females collected from different French regions and genetically characterized by distinct MLGs (Bankhead-Dronnet et al. unpub. data). The establishment and multiplication capacities of the aphids were tested on three genotypes of *P. x canadensis* (a susceptible, a partially susceptible reference genotype, and Dorskamp). A low but significant lineage effect was detected on the aphid multiplication ability on the Dorskamp genotype, with an intrinsic rate of natural increase fluctuating from 0.32 to 0.38 depending on lineage, while it varied from 0.34 to 0.36 for the partially susceptible genotype and from 0.37 to 0.41 for the susceptible one. The lack of aphid lineage effect on the two other tree genotypes, further confirms their value as reference for susceptibility assays. However, the results still raise the

problem of taking into account the population genetic variability of the pest encountered in field conditions.

The simple assessment of host susceptibility does not require a sound knowledge of plant-pest interactions. However, further investigations regarding the feeding strategy of the pest and host-plant response during compatible and incompatible interactions might provide useful information. Here, we will consider that a compatible interaction occurs when a pest is able to successfully feed and reproduce on its host-plant, while in incompatible interactions host resistance hamper or prevent the nutrition and development of the insect (Giordanengo et al. 2010; Hogenhout and Bos 2011). Investigating how these interactions take place from both the insect and plant perspectives could help to infer how breeding and silvicultural practices might improve the management of tree pests based on host resistance. Moreover, because they result in tree weakening or death, it is particularly relevant to understand how compatible interactions take place.

4 In-depth analysis of compatible interactions

Understanding how compatible interactions take place is a prerequisite to understand the processes leading to incompatible interactions. It should therefore precede or be concomitant with the unveiling of resistance mechanisms. In a plant-pest system, the analysis of compatible interactions implies to understand the feeding strategy of the pest and its consequences for the host at different scales, i.e., from cells or tissue to the entire tree level (Giordanengo et al. 2010). Knowing in detail the feeding strategy of a pest is of prime importance since it is frequently related to the type of damage inflicted to the host-plant. Most aphids feed on sap and, as they rarely transmit phytoviruses to trees (Blackman and Eastop 1994), they mostly affect their host growth and reproduction through resource depletion, due to sap consumption and sometimes photosynthesis reduction (Zvereva et al. 2010). However, some species also perform complex host manipulations, leading for instance to gall induction in host tissues (Wool 2004). Host manipulation often aims at improving the nutritional value of plant tissues by turning them into mobilizing sinks of carbohydrates and/or nitrogen compounds, drawing nutrients from the surrounding tissues (Price et al. 1987; Schönrogge et al. 2000; Koyama et al. 2004; Schoonhoven et al. 2006; Suzuki et al. 2009). This may have dramatic outcomes on the allocation of nutrients in the tree, at the tissue or organ levels (Abrahamson and McCrea 1986; Fay and Hartnett 1991). In addition, gall induction may lead to tissue or organ misshaping or abortion, thereby affecting basic plant functions. For instance, the galls induced in the inner bark of apple trees by *Eriosoma lanigerum* (Hausmann) can interrupt sap flow (Brown et al. 1991).

Feeding strategy is also a critical factor affecting the impact of environmental constraints on plant-herbivore interactions (Larsson 1989). For instance, for sap-sucking insects, the plant stress hypothesis predicts that an intermediate water deficit should enhance their performance, by improving the nutritional value of the host-plant (Larsson 1989; Tariq et al. 2012). However, host-manipulating herbivores, like gall-inducing insects, are predicted to be adversely affected by water deficit, mostly because the reduction in plant growth, due to water shortage, impairs the initiation and growth of the manipulated tissues (Larsson 1989; Koricheva et al. 1998; Huberty and Denno 2004). Because the mouthparts and feeding site of the aphid are quite concealed, the feeding strategy of the WPA was unraveled only recently. Combined anatomical, histological, and behavioral approaches confirmed that the WPA feeds within the cortical parenchyma, and does not feed on sap, because of the short size of its mouthparts (Pointeau et al. 2012b). Further histological analyses of bark tissues of an infested susceptible *P. x canadensis* genotype, I-214, indicated that the WPA induces a reaction tissue, with cells multiplication and enlargement (Dardeau et al. 2014a) (Fig. 1(4)). This reaction tissue shares similarity with galls but, since it appeared more like a misshaping of cortical parenchyma than like a novel organ, it was referred to as a pseudogall, also called an open gall (Dardeau et al. 2014a). On trees, this tissue modification is invisible macroscopically. However, on 1-year-old stem cutting with thin bark tissues, a slight swelling of bark tissues can be seen where aphids feed (Fig. 1(5)). The hypothesis of a manipulation of tree cortical tissues by the insect was supported by physiological and behavioral investigations, showing that aphid development and feeding behavior were improved on infested tissues of I-214 (Dardeau et al. 2014b). Compared to unaffected bark tissues, infested tissues accumulate free and protein-bound amino acids, while starch reserves are depleted within the pseudogall and in the surrounding parenchyma (Dardeau et al. 2014a, 2015b). This suggests that the benefits of pseudogall induction for the aphid are an improvement of the nutritional value of host tissues, through nutrients mobilization by the manipulated host tissue.

The fact that the WPA is a gall-inducing insect and not a sap-sucker has several outcomes on the potential processes involved in host damage. It does not totally rule out the potential involvement of unknown salivary toxins injected within host tissues. Nonetheless, since the aphid mouthparts do not reach sap flow, it raises the question of how an infestation can trigger systemic effects, like an absence of bud break, while the aphids developed on the trunk. In addition, no necrosis has been observed in the feeding sites. The uncovering of this feeding strategy raises hypotheses on the origin of host damage. Firstly, the development of modified tissues in the bark may affect sap circulation. Nonetheless, the pseudogall is superficial and apparently does not significantly interfere with

the underlying phloem (Dardeau et al. 2014a). Secondly, the nutrient mobilization by the numerous pseudogalls induced during outbreaks could significantly alter nutrient allocations within infested trees, and in turn affect host growth and survival (Dardeau et al. 2014a, b). This latter hypothesis still needs to be validated but is supported by the results of a field survey performed in stands of a susceptible *P. x canadensis* genotype, I-214, infested by the WPA. Aphid infestation significantly reduced starch and protein contents in autumn in the bark of 12 to 13-year-old trees, this reduction being related to the infestation duration for starch (Sallé et al. 2018). Moreover, starch content in autumn, and to a lesser extent in spring, correlated with (i) the proportion of crown exhibiting bud break in the following spring, and (ii) the subsequent radial increment in the following autumn (Sallé et al. 2018). In addition, the trees exhibiting the lowest starch content in the bark in autumn did not survive to the infestation (Sallé et al. 2018).

5 Potential resistance and tolerance mechanisms and their environmental modulation

Plant defense can be arranged in two categories, resistance and tolerance (Stowe et al. 2000; Schoonhoven et al. 2006). Resistance gathers mechanisms aiming at preventing or reducing damage to the plant, through repellent or antibiotic structures or compounds for instance. On the contrary, tolerance refers to the ability of a plant to sustain tissue loss without fitness reduction (Stowe et al. 2000). There is often a trade-off between these two components, which can be negatively correlated genetically, although exceptions exist (Strauss and Agrawal 1999; Stowe et al. 2000).

5.1 Resistance mechanisms

The fact that the WPA is a gall-inducer has specific implications concerning the nature and location of resistance mechanisms. The most commonly described resistance mechanism to gall-inducing insects is the hypersensitive reaction (HR), characterized by a biosynthesis and an accumulation of chemical defensive compounds, like reactive oxygen species or phenolic compounds, together with the formation of a necrotic lesion surrounding the damaged tissues (Heath 2000; Fernandes and Negreiros 2001; Stuart et al. 2012). This resistance mechanism is also frequently encountered in plant-pathogen interactions, and aims at isolating the aggressor from the living host tissues to stop its development (Agrios 1997). The HR can totally inhibit gall differentiation and lead to a rapid death of the gall-inducer (Fernandes et al. 2003). Besides the HR, resistance can also result from an inability of the aggressor to achieve a successful manipulation of host

metabolism (Höglund et al. 2005, 2012). Höglund et al. (2015) demonstrated that willow resistance to a gall midge was rather due to a lack of induced susceptibility than to an induced HR. Likewise, in some plant–gall-inducer systems, resistance is related to a failure in the manipulation of plant hormones concentrations (Matsukura et al. 2012; Tokuda et al. 2013).

To unveil the resistance mechanisms affecting the establishment and development of WPA, comparative studies have been performed with reference *P. x canadensis* genotypes, one susceptible (I-214) and two resistant genotypes, one affecting the establishment of the aphid (Brenta), the other its development and multiplication (I-45/51). The comparisons were performed at two different timing of the interaction corresponding to (i) the settlement phase, i.e., when the induction of the pseudogall begins, and (ii) the multiplication phase, when the aphid feeds on a manipulated host tissue and reproduces. Behavioral investigations indicated that, during the settlement phase, resistance mechanisms interfered with aphid probing, probably through stimuli located at the bark surface and in the parenchyma (Pointeau et al. 2013). Similar investigations performed during the multiplication phase showed that aphids feeding on a resistant host genotype on which they experienced a reduced development had an altered probing behavior and a reduced host acceptance (Dardeau et al. 2014b). Complementary histological and biochemical approaches demonstrated that tree resistance impeded gall formation with lignin deposition (Dardeau et al. 2014a, 2015a). Lignification occurred even in the susceptible genotype but was restricted to localized parts of the pseudogall, whereas it was more intense and more extended in the resistant genotypes. The intensity of lignin deposition varied according to resistance level of the host-plant. In the host genotype preventing aphid settlement, lignification and accumulation of phenolic compounds, like tannins and flavanols, was rapid and very intense compared to the other, less resistant genotypes. As a consequence, no pseudogall differentiation occurred (Dardeau et al. 2014a). In the host genotype allowing aphid settlement but affecting its development and fecundity, a pseudogall was induced, but lignification occurred throughout the pseudogall, which was consequently disorganized (Dardeau et al. 2014a). The occurrence of lignified cell walls throughout the pseudogall, and its disorganization, may explain the altered probing behavior of the aphid and its reduced host acceptance observed in that case (Dardeau et al. 2014b). Also congruent with an impaired development of the pseudogall, the infested bark tissues of the same resistant poplar genotype did not significantly accumulate free and protein-bound amino acids (Dardeau et al. 2015b).

It must be mentioned however that these detailed resistance studies focused mostly on two reference resistant genotypes, affecting either aphid settlement or its development and fecundity, compared to a single susceptible genotype. Other mechanisms might be involved and uncovered if a wider array of

resistant poplar genotypes was investigated. Moreover, the two resistance categories, defined by the susceptibility assays, may overlay different mechanisms. Therefore, generalization should be made with caution.

5.2 Tolerance

An infestation by the WPA can strongly reduce starch content of bark tissues in mature trees (see section 4, Sallé et al. 2018). Starch bark content turned out to be, among the monitored nutrients (i.e., starch, soluble sugars, proteins and amino acids), the best indicator of subsequent radial increment and tree survival following an infestation (Sallé et al. 2018). A survey performed in two stands of I-214, with 12- to 13-year-old trees, showed that the initial, constitutive, bark starch content differed between stands, indicating a significant environmental modulation of this trait (Sallé et al. 2018). Both stands were infested the same year by the WPA, with similar infestation levels, and infestation reduced bark starch content in both stands (Sallé et al. 2018). Nonetheless, trees with higher constitutive starch content still exhibited higher starch content and lower damage level after infestation (Sallé et al. 2018). This suggests that, within a genotype and at an individual level, promoting starch reserves in trees might provide them a higher likelihood to survive and to recover after an aphid infestation. More generally, genotypes exhibiting a high constitutive level of starch in their bark would also have a higher tolerance to WPA outbreaks. These results suggest that tolerance could be an interesting component of WPA management, at the individual level in stands of susceptible poplar genotypes, and among genotypes potentially colonized by the pest.

5.3 Environmental modulation

Evaluating environmental effects on plant–pest interactions is of prime importance. Environmental factors may indeed overcome genotype-related influence for some resistance traits, and genotype x environment interactions frequently occur (e.g., Osier and Lindroth 2006). Field observations reported increased damage of the aphid on fertile stands and during water stress (Maugard and Baubet 2004; pers. comm.). The impact of fertilization and water shortage, on the poplar–WPA interaction has been assessed by comparing their effects on a susceptible genotype, I-214, and a genotype affecting aphid multiplication, I-45/51 (Dardeau et al. 2015a, b). The experiments were performed under controlled conditions, with rooted cuttings. Complex interactions between environmental constraints and host-genotypes have been found. The range of the considered fertilization regimes did not significantly enhance the development of WPA colonies. Infestation induced an accumulation of amino acids in infested bark tissues, but, interestingly, the effect of fertilization on the amino acid

content of bark tissues was less pronounced in infested cuttings than in control ones. The accumulation of amino acids during infestation in the susceptible infested genotype decreased when fertilization increased, suggesting plasticity in host manipulation by the aphid (Dardeau et al. 2015b).

To consider the effect of water constraint, three levels of water shortage were tested on rooted cuttings: mild, intermediate, and high. Both intermediate and high water shortage negatively affected the growth of aphid colonies on the susceptible host genotype (Dardeau et al. 2015a). However, mild water shortage enhanced aphid growth on the resistant host genotype, suggesting that it triggered a release in resistance mechanisms, probably in the lignification process (Dardeau et al. 2015a). It did not dramatically affect the interactions between the WPA and the resistant genotype, i.e., the aphid growth was still reduced compared to the susceptible genotype. Nonetheless this significant genotype \times environment interaction suggests that water supply could modulate the susceptibility level of some poplar genotypes under field conditions.

In addition to a modulation of tree resistance or susceptibility traits, environment may also modulate the tolerance level of poplars to the WPA. Stand characteristics influence growth-related parameters of poplars and could also in turn affect their carbohydrate reserves, a trait apparently related to tree tolerance to the WPA (see sections 4 and 5.2). For I-214, starch content in the bark can vary depending on stand conditions and might be negatively correlated with tree growth (see section 5.2 and Sallé et al. 2018). This could explain why damage is more intense in fertile stands. It should be noted however that the hypothetical negative relationship between growth and starch reserves relies on a comparison between two sites only. Nonetheless, an extended sampling with more sites, various environmental conditions, and planted with several different poplar genotypes would allow to easily test this hypothesis. If confirmed, it would imply that site conditions and silvicultural practices could be manipulated to mitigate the outcome of a WPA outbreak on stand damage and survival.

6 Conclusion and research prospects

The investigations carried out during the last decade allowed to unravel different aspects of the tripartite interactions among the WPA, poplars and their environment. From this, a susceptibility test has been built and used to screen for susceptibility to the WPA of several commercialized poplar genotypes. Highlighting the nature of WPA–poplar interactions also gave interesting leads to understand the processes involved in tree death, summarized in the Fig. 3. Nonetheless, several issues still need to be addressed to achieve a successful and sustainable management of the WPA in poplar plantations.

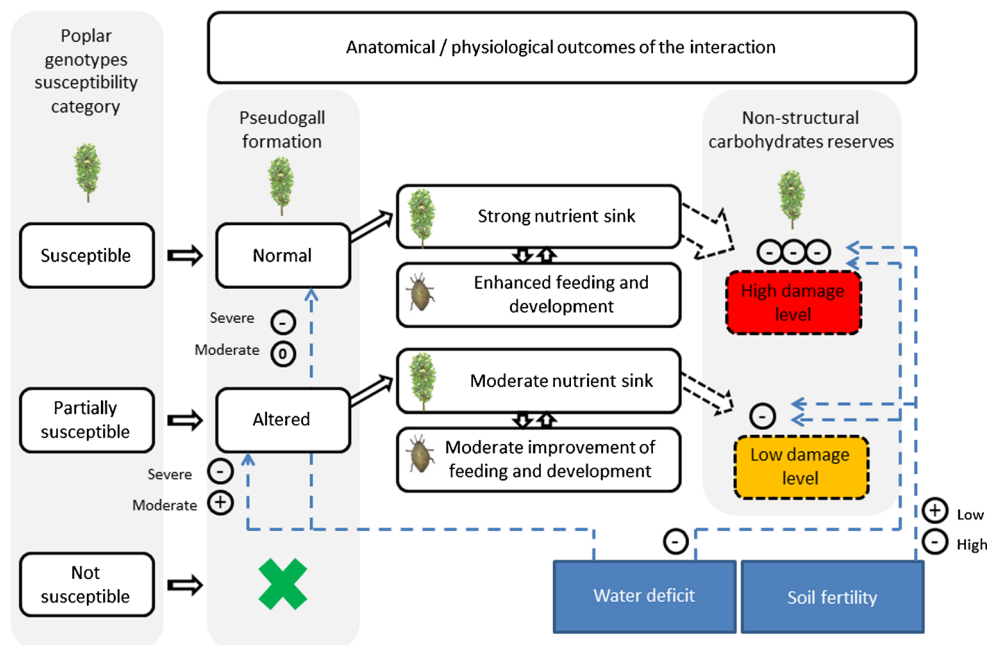
6.1 Fine characterization of the WPA–poplar interactions and their outcomes

The nature of the modifications induced in the host-tree by the aphid during both compatible and incompatible interactions should be further clarified. Ultrastructural, biochemical, and molecular investigations on the manipulated plant tissues could give a better understanding of the nature and function of the modified tissues: are they turned into nutritive tissues accumulating nutrients, with characteristic features like enlarged nuclei, fragmented vacuoles, and increased number of cellular organelles (Bronner 1992), or into tissues favoring aphid feeding and development through other means? A detailed metabolomic analysis, during both compatible and incompatible interactions, would for instance allow detecting how secondary metabolites, in particular phenolic compounds like flavonoids and salicinoids, could interfere with host acceptance and gall differentiation during incompatible interactions. Histochemical investigations have indicated a different pattern of accumulation of these compounds during compatible and incompatible interactions, but the specific involvement of these compounds in tree resistance is still unknown (Dardeau et al. 2014b; Sallé unpub. Data). Likewise, a detailed monitoring of early events during the onset of compatible and incompatible interactions could be performed. In particular, monitoring the accumulation of phytohormones involved in stress signaling, like jasmonic acid, ethylene and salicylic acid, and phytohormones potentially involved in the manipulation of host tissue and metabolism, like auxins and cytokinins, would allow pointing out the key processes involved in either the success or failure of plant manipulation as in other plant-gall-inducer systems (e.g., Tokuda et al. 2013).

In addition, complementary information should be obtained on the physiological outcomes of plant manipulation for the host-tree. The role of starch content in the bark, which still needs to be confirmed though, might prove useful for damage predictions in infested poplar stands. Regarding this, monitoring carbohydrates and nitrogen compounds allocation, storage, and dynamics within different tissues of a tree during an outbreak, would also confirm the hypothesis of host resource depletion by the aphid. Starch bark content might also serve as a predictor of tolerance level in stands of susceptible genotypes and could help to uncover site conditions that could mitigate it. The genetic determinism of this trait is still unknown though and potential genotypes \times environment interactions need to be investigated. For this, a survey of constitutive starch bark content in different poplar genotypes, growing under different site conditions, might prove useful.

From the aphid standpoint, a better characterization of the processes involved in pseudogall induction might also prove useful for management purposes. Two key components could

Fig. 3 Graphical summary of the interactions between *Phloeomyzus passerinii* and poplars, and their modulation by environmental factors. Dashed arrows indicate hypothetical interactions inferred from controlled conditions or field observations (see text for details). +, - and 0 signs indicate positive, negative and null effects of abiotic factors on pseudogall formation and non-structural carbohydrates, respectively



play a role during gall induction: the behavior of the gall-inducer and the composition of the secretions injected into the host-plant (Giron et al. 2016). An in-depth analysis of aphid behavior during gall induction would be necessary. Regarding this, the electrical penetration graphs, already used to study the probing behavior of the WPA (Poiteau et al. 2012b, 2013; Dardeau et al. 2014b), could help unraveling the intracellular probing behavior of the aphid associated with pseudogall induction. In addition, biochemical, proteomic, and transcriptomic investigations on the composition of aphid saliva could help identifying the effectors involved in host reprogramming and their targets in host genome or receptors (Giron et al. 2016).

6.2 Genetic control of resistance mechanisms and population structure of the pest

For breeding purposes, and concomitantly with a better characterization of the interactions between the WPA and poplar species and hybrids, deciphering the genetic determinism of resistance and exploring individual genetic variation would be highly desirable. For investigations on *Populus* various genetic, genomic, and biochemical tools are available (Jansson and Douglas 2007), and would allow the search for specific resistance markers at the genetic level. For instance, it would help avoiding the plantation over wide areas of poplar genotypes sharing similar resistance genes, which could favor a rapid genetic adaptation of the pest. Different genetic determinisms have been found for resistance to gall-inducing insects. In the well-studied *Mayetiola destructor* (Say) - wheat system, a gene-for-gene interaction, similar to what occurs in several plant-pathogen interactions, has been

uncovered (Stuart et al. 2012). Similarly, in the *Dasineura marginemtorquens* Bremsi-willow system a major QTL was found to be associated with resistance (Höglund et al. 2012).

Recently, two parental linkage maps have been obtained from a segregating controlled cross-mating between a resistant parent *P. deltoides* and a susceptible parent *P. nigra* (Carletti et al. 2016). The susceptibility to the WPA of the 131 progenies has been assessed with laboratory assays and three QTLs related to resistance have been identified, one major (44% of the variance explained) and two with a minor effect (17 and 9% of the variance explained, respectively) (Carletti et al. 2016). Several putative candidate resistance genes are present in the confidence interval of the QTLs, and include a Nicotiana Protein Kinase 1-like protein kinase, Leucine Rich Repeat protein kinases and zinc finger proteins (Carletti et al. 2016). Yet, their involvement in resistance mechanisms still needs to be clarified.

As a complement, it would be necessary to have deeper insights into poplar genotypes x WPA interactions, and to unravel the diversity of resistance mechanisms involved in the interaction. Exploring resistance mechanisms deployed in natural populations, which have co-evolved with the aphid, could be fruitful. To estimate for instance the likelihood of resistance breakdown, detailed knowledge on dispersal capacity and on the proportion of local WPA populations engaging in sexual reproduction would be necessary. Landscape genetics investigations could be carried out to fulfill this gap by improving our understanding of how geographical and environmental features structure genetic variation (Manel et al. 2003). For instance, information would be provided on how spatial heterogeneity of poplar plantations may influence WPA populations' gene flow and reproduction.

6.3 The WPA as a model for tree–insect interactions

Due to their rapid growth, their easy vegetative propagation and genetic transformation, the small size of the genome and the large genomic resources available, poplars are considered as model plants for tree physiology, wood formation, and response to abiotic and biotic stresses (Brunner et al. 2004; Cronk 2005; Jansson and Douglas 2007; Ralph 2009). It is therefore a relevant model for studying tree–herbivore interactions (Major and Constabel 2006; Philippe and Bohlmann 2007; Ralph 2009). Most the studies have dealt with defoliators, like the forest tent caterpillar, *Malacosoma disstria* Hübn., or the gypsy moth, *Lymantria dispar* L., among others (Major and Constabel 2006; Ralph 2009). A few studies focused on other feeding guilds, including gall-inducing insects like *Pemphigus* aphids inducing galls on petioles (Ralph 2009; Richardson et al. 2016). Nonetheless, several characteristics of the WPA would make it an interesting and original model species for the study of tree–herbivore interactions. This aphid ecology is atypical compared to the other Aphididae. It occupies a basal position in the phylogeny of this group and exhibits an unusual probing behavior and feeding strategy. Therefore, it would be a key chain link to study the evolutionary history of aphids. The development of manipulated tissues is quite slow, which allows studying the sequential events of gall differentiation. In addition, compared to other plant-manipulating insects, the rearing is easy and colonies can be maintained all year round on poplar cuttings, under controlled conditions. It feeds within the bark of its host, and relatively little attention has been paid in general to the resistance mechanisms deployed in broadleaved trees versus pests attacking these tissues (Paine 2002; Lieutier 2004). Lastly, the impact of pseudogall induction on nutrient allocations within the host tree, and the potential consequences it may have on tree survival, would make this insect an interesting tool to study the interactions between reserves and mortality in trees. For instance, this interaction could be used to test the controversial relationship between carbon starvation and tree mortality (Parker and Patton 1975; Sala et al. 2010).

6.4 Conclusion

Building a laboratory susceptibility assay, although still not fully reliable, has contributed to early discrimination among susceptible, non-susceptible and partially susceptible *Populus* genotypes, helping poplar growers to make a selection among available tree genotypes. Understanding the feeding strategy of the WPA, and the nature of the interactions between the aphid and its host-tree, has allowed making assumptions regarding (i) the impact of aphid infestation on colonized trees, (ii) the processes leading to tree death and (iii) the processes underpinning tree resistance. This would help to identify specific resistance markers. In addition, since hypotheses have

now been drawn regarding the processes leading to tree death or resistance, it should be possible to test, under field conditions, how the environment, in particular silvicultural practices, could modulate tree–WPA interactions. As a consequence, unraveling the tripartite interactions among the woolly poplar aphid, its host tree, and their environment will certainly help to improve the management of WPA in poplar plantations.

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