Forest Ecology and Management 407 (2018) 23–30

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Tree-killing aphid dramatically reduces bark contents in carbohydrates and nitrogen compounds

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ARTICLE INFO

Keywords:
Gall
Phloeomyzus passerinii
Populus
Reserves allocation
Resources mobilization

ABSTRACT

Aphids can affect the growth or architecture of their host-trees, but rarely challenge their survival. Nonetheless, the woolly poplar aphid, *Phloeomyzus passerinii*, can kill healthy, mature poplars during outbreaks. Trees fail to open their buds and flush their leaves in the spring following a severe infestation. This insect develops on poplar trunks, where it induces galls which accumulate amino acids and deplete starch content in the bark tissues. Here, we hypothesized that an infestation may then reduce non-structural carbohydrates (NSC) and non-structural nitrogen compounds (NSNC) contents in the bark, and that the reduction would be positively correlated with the infestation duration. This would in turn compromise the spring reactivation of trees. Consequently we also hypothesized that the bark contents of NSC and NSNC could be positively correlated with the amount of branches exhibiting bud break in spring, and the subsequent radial growth. The bark contents of NSC and NSNC were quantified in autumn for poplars exhibiting different levels of infestation and located in two distant stands. In one stand, NSC and NSNC contents in the bark were also quantified in the following spring and the damage level in the crowns were evaluated. In both stands, the infestation dramatically reduced the NSC and NSNC contents in autumn, especially starch and protein contents. While the drop in protein content was not related to infestation duration, the starch content gradually decreased when infestation duration increased. The infestation effect on starch content was still detectible in spring, after reserves had likely been mobilized for the spring reactivation.

Starch content in autumn and spring was strongly positively correlated with crown health and radial increment. These results suggest that poplars infested by *P. passerinii* may die from carbon reserves deficiency, which would be an unprecedented situation for tree-aphid and tree-gall inducing insects interactions. Further experiments monitoring seasonal dynamics of NSC and NSNC reserves in different organs of infested trees should be conducted to validate this hypothesis. The results also suggest that the starch content in the bark of infested trees, in autumn, might be used as a predictor of tree decay by managers.

1. Introduction

Tree species growing under temperate climates frequently harbor populations of aphids (Aphidoidea: Aphididae) which can have deleterious effects on their hosts (Blackman and Eastop, 1994). When aphid abundance reaches a high level, feeding can cause a significant removal of nutrients (Dixon, 1971; Wood et al., 1987; Collins et al., 2001; Bertin et al., 2010). Alternatively the wounding or manipulation of tree tissues can dramatically alter their metabolism and anatomy, and ultimately compromise their initial function. For instance, galls induced by *Eriosoma lanigerum* (Hausmann) in the twigs or roots of apple trees can interfere with nutrients uptake and conduction of sap, resulting in the stunting or death of young trees (Brown et al., 1991). Likewise, infestations by *Elatobium abietinum* (Walker) or *Eulachnus* species can cause extensive defoliation of conifers (Murphy and Völkl, 1996; Straw et al., 2000).

In most situations aphid infestation reduces growth increment and timber yields (Straw et al., 2000; Collins et al., 2001), and occasionally modify tree architecture (Kurzfeld-Zexer et al., 2010). However, besides few species like *Cinara cupressivora* Watson and Voegtlin on cypresses (Day et al., 2003), aphids rarely kill mature, vigorous trees. In this regard, the woolly poplar aphid, *Phloeomyzus passerinii* (Signoret) is rather exceptional. This aphid develops on the trunks or main branches of mature poplars, and induces galls in the inner bark of its hosts, within the shallow tissues of the cortical parenchyma (Dardeau et al., 2014a, 2014b). During outbreaks, aphid colonies can cover most of the trunk

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http://dx.doi.org/10.1016/j.foreco.2017.10.029
Received 14 July 2017; Received in revised form 13 October 2017; Accepted 16 October 2017
Available online 21 October 2017
0378-1127/

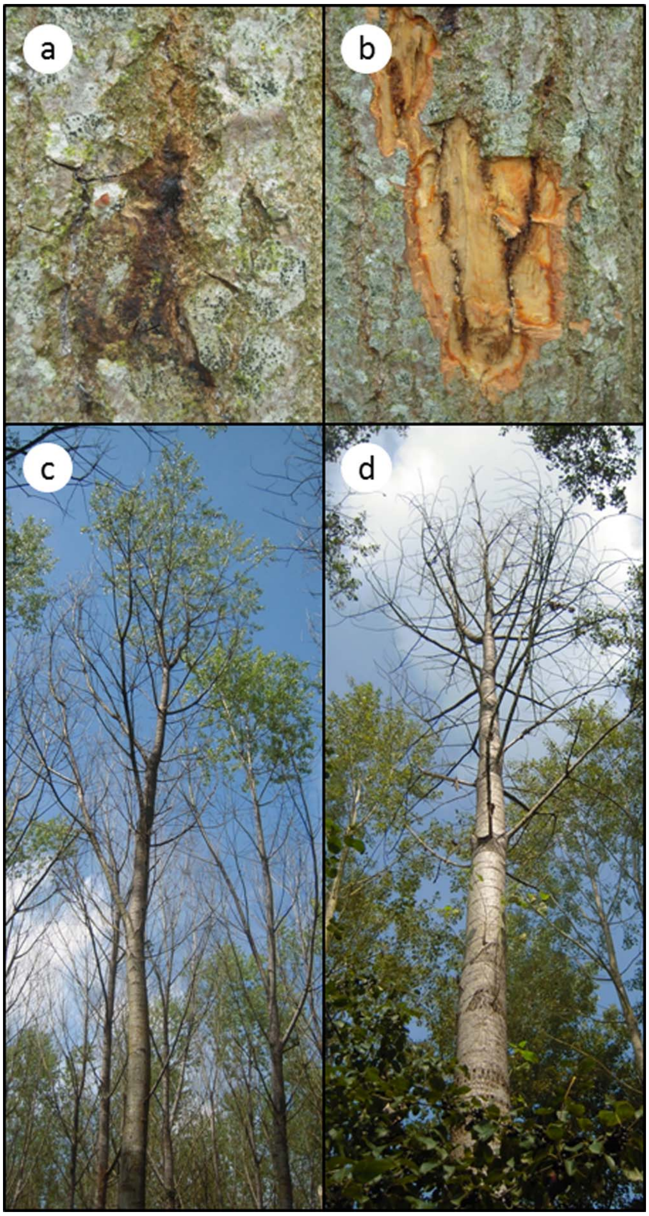

Fig. 1. Symptoms induced by an outbreak of *P. passerinii* on poplars in the stand located in Champdôtre. **a**: Dark exudation on the bark, **b**: localized necroses in an otherwise moist and live inner bark, **c** and **d**: crowns exhibiting a partial and total absence of bud break, respectively.

surface area of susceptible trees during several months. The spring following these outbreaks, bark necroses can be observed and bud breaking and leaf flush can be inhibited on a part or even the entire crown of infested trees, which may ultimately die (Sallé and Battisti, 2016; Fig. 1). As its outbreaks can trigger massive mortality in infested stands, *P. passerinii* is considered the most damaging pest of poplar plantations in Southern Europe, North Africa and the Near East (Sallé and Battisti, 2016).

Intense outbreaks, with massive trunk colonization by aphid colonies, do not systematically result in severe damage, like strong radial growth reduction or tree mortality (Sallé and Battisti, 2016). As a consequence, after such infestations poplar growers generally have to wait until spring, i.e. at least six months after the infestation, to evaluate the extent of damage in their stand using crown condition. Alternatively, they may immediately cut their trees in winter even though the stand may have tolerated the infestation. A good knowledge of the processes leading to growth reduction and/or tree death might then provide tools to predict the fate of trees following an outbreak, and help managers to rapidly plan tree cutting when necessary.

Tree death following outbreaks by *P. passerinii* has been attributed to the injection of salivary toxins into the tree (Charles et al., 2014). However, there is no demonstration that aphids actually inject toxins into their host-plants (Miles, 1999), and detailed histological investigations do not support this assertion, as no necrosis has been observed in the probing area (Pointeau et al., 2012; Dardeau et al., 2014a). An alternative hypothesis is that the aphid galls act as mobilizing sinks, drawing nutrients from the surrounding tissues, as is commonly observed in the interactions between gall-inducing insects and their host plant (Larson and Whitham, 1991, 1997; Dsouza and Ravishankar, 2014; Griesser et al., 2015). This is supported by the fact that bark tissues of rooted stem cuttings infested by *P. passerinii* accumulate protein-bound and free amino acids (Dardeau et al., 2015). In addition, starch granules disappear from the galled bark tissues and their vicinity during gall differentiation (Dardeau et al., 2014a).

Because it contains a large fraction of living parenchyma, bark can accumulate high contents of both carbohydrates and nitrogen compounds (Srivastava,1964; Cooke and Weih, 2005; Rennenberg et al., 2010). Although, at the tree level, the total amount of nutrients stored in the bark is generally low, compared to xylem for instance (Kozlowski, 1992; Barbaroux et al., 2003), bark tissues are considered to play a relevant role as storage organs (Srivastava,1964; Cooke and Weih, 2005; Rennenberg et al., 2010). Bark reserves can be mobilized in response to physiological needs of the tree, and therefore exhibit seasonal dynamics in winter deciduous broad-leaved trees, with maximum carbohydrate and nitrogen compounds contents in autumn, at the end of the growing season, and minimum contents in late spring, after bud break and leaf flush (Srivastava, 1964; Landhäusser and Lieffers, 2003; Cooke and Weih, 2005; Rennenberg et al., 2010).

During outbreaks of *P. passerinii*, when trunks are covered with aphid colonies, the mobilizing sinks induced by galls may significantly alter carbohydrates and nitrogen compounds content in the bark tissues. This could in turn limit the resource allocation to meet carbon and nutrient demands of buds in spring. As a comparison, severe defoliation by moths and galling by an aphid reduced subsequent leaf size and delayed bud burst in *Picea glauca* (Moench) Voss, as a result of local resources deficiencies (Quiring and McKinnon, 1999). In this regard, it can also be hypothesized that the longer the infestation is and/or the more extensive aphid colonies coverage is on a tree and the stronger the alterations in carbohydrate and nitrogen contents would be.

Here we present the results of an experiment testing the hypothesis that *P. passerinii* can significantly modify carbohydrate and nitrogen contents within the bark of mature poplars. More specifically, our objectives were firstly to assess whether an infestation by *P. passerinii* could reduce bark contents of non-structural carbohydrates and nitrogen compounds in mature trees. Secondly, we aimed at estimating whether an increase in infestation duration resulted in more pronounced reduction of non-structural carbohydrates and non-structural nitrogen compounds. Finally, we assessed whether a reduction of these contents was related to the level of crown damage.

2. Materials and methods

2.1. Biology of P. passerinii

Throughout the year apterous females can be observed within the bark crevices of mature trees, where they lay viviparous nymphs through parthenogenetic reproduction. In autumn sexual morphs, i.e. oviparous sexuales, may also occur and lay eggs in bark crevices of the trunk, which may overwinter. Outbreaks are unpredictable events during which massive colony development generally begins in the upper third of trunks, just below the crown, and aphid colonies then extend downwards. Outbreaks are often detected at the end of spring, but can also start later, until autumn. At the end of autumn, populations