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White peach scale *Pseudaulacaspis pentagona* (Targ.) (Hemiptera: Diaspididae) is affected by host plant variety in a blackcurrant orchard

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Abstract

The White Peach Scale (WPS) *Pseudaulacaspis pentagona* (Homoptera: Diaspididae) is one of the most damaging armored scale insects as it is a pest of various crops, including ornamental plants and fruit trees. In France, *P. pentagona* has become one of the main threats towards blackcurrants (*Ribes nigrum* L.), especially in Burgundy, the Loire Valley and the Rhône-Alpes where the cultivation of blackcurrants is not only an emblematic and cultural activity but also an important economic one. We determined the direct effect of blackcurrant varieties on the infestation rate, female's size and parasitism of *P. pentagona*. Our study was conducted in a Burgundy (France) natural population of *P. pentagona* developing on two blackcurrant varieties 'Noir de Bourgogne' and 'Royal de Naples'. This field study showed that females WPS feeding on 'Noir de Bourgogne' were more numerous, had a larger body, a larger shield, and were less parasitized compared to females feeding on 'Royal de Naples' at the same site. However, the high scale density and the low parasitism rate found overall on the two varieties question the potential gain for a possible pest management based on the change of the varieties used in blackcurrant orchards.

Keywords

Trophic interaction, parasitism, WPS, performance, blackcurrant

Compliance with ethical standards

Conflict of interest - The authors declare that they have no conflict of interest.

Ethical note - All experiments complied with French laws on animal experimentation.

Introduction

White Peach Scale (WPS), *Pseudaulacaspis pentagona* Targioni Tozzetti (Homoptera: Diaspididae), is a cosmopolitan pest originating in Eastern Asia. It is now present in 110 countries on every continent, from tropical to temperate regions (García Morales et al. 2016). Due to its wide host plant spectra (reported on 221 host plant genera), *P. pentagona* is one of the most damaging armored scale pests for various crops, including ornamental plants and fruit trees (Bennett 1956; Bennett and Brown 1958; Hanks and Denno 1993b; Kreiter and Marro 1997; Kreiter et al. 2002; García-Morales et al. 2016). In France, it has become one of the main threats to blackcurrant cultivation (*Ribes nigrum* L.), especially in Burgundy, the Loire valley and the Rhône-Alpes regions where blackcurrant production is an emblematic activity as well as an important economic activity. In the years following infestation, blackcurrants experience a decrease in plant vigor, defoliation and the subsequent death of infested plants and orchards – probably due to intense sap collection by *P. pentagona* when female density is high (Yasuda 1979; Dalstein et al. 2016).

Using several varieties of a species in the same agricultural plot may improve crop productivity and quality, or may reduce vulnerability to disease and environmental fluctuations (Jarvis et al. 2008; Kotowska et al. 2010). By contrast, the vast majority of blackcurrant cultivators follow a monoculture regime system with usually a very few varieties per orchard. Moreover, farmers commonly use cuttings from a single clone for the whole orchard, which results in low genetic diversity. In Burgundy, the variety ‘Noir de Bourgogne’ (NB) is mostly planted in association with the variety ‘Royal de Naples’ (RN), with a usual ratio of about 5 to 1. NB produces berries with a very high organoleptic quality, but requires cross-pollination with RN for a good yield. RN was selected as a pollen donor since it crosses nicely with NB without affecting NB’s organoleptic properties. These two varieties have different phenological, horticultural and nutritional qualities (Giongo et al. 2008; personal

observation). NB is richer in aroma than RN, contains different essential oils and has a slightly delayed phenology (Kerslake et al. 1989; Le Quere and Latrasse 1990; Giongo et al. 2008; personal observation).

Herbivorous pests such as scale insects may be influenced by the host plant species and/or variety, which may results in different life histories through phenotypic plasticity, or in some cases, local adaptations depending on the host plant they feed on. For example, there is abundant evidence that differences between host plants (between or within species) affect morphology, longevity, fecundity, and resistance against the natural enemies of phytophagous insects (Awmack and Leather 2002; Moreau et al. 2017; Giron et al. 2018). This is particularly expected in scale insects such as *P. pentagona* because of their sedentary lifestyle (Gullan and Kosztarab 1997). For example, *P. pentagona* females exhibit typical local adaptations to their host plant, and individuals raised on their native host plant survive longer than those raised on a non-native host plant (Hanks and Denno 1993a, b).

The aim of this study was to determine the direct effect of blackcurrant variety on the infestation rate, size and parasitism of *P. pentagona*, in order to compare the pressure exerted by this pest on blackcurrant orchards. These data are crucial in blackcurrant orchards because a specific phytophagous pressure exerted on the variety of economic interest would change blackcurrant cultivation. Indeed, an hypothetic infestation rate higher one variety than on another should lead growers to modify the variety of economic interest, or the variety used as pollen donor.

The study was conducted with a natural population of *P. pentagona* collected in Burgundy (France) on NB and RN varieties. We specifically focused on females because they feed on blackcurrant plants from the stage following crawlers to their death, making them more sensitive to plant variety in comparison with males (non-feeding adult stage). Females are thus the most critical sex damages blackcurrant orchards.

84

85 **Materials and methods**86 ***Field sampling***

87 In April 2018, we collected overwintering *P. pentagona* females from blackcurrant (*Ribes*
88 *nigrum* L.) in Burgundy, France. In order to reduce geographical and climatic effects,
89 individuals were sampled in a three-hectare blackcurrant orchard, with the two varieties
90 planted alternately (one shrub of RN every five shrubs of NB) in Marey-Les-Fussey, France
91 (N-47°07'30", E-4°51'01"). For each variety, one branch (45-136 cm in length), cut at the
92 base of each shrub, was collected from 20 shrubs, following the following stratified sampling
93 procedure: 12 branches were collected from shrubs randomly selected within the first and the
94 last rows of crops, and 8 branches were collected from shrubs randomly chosen within the
95 three central rows of the orchards. These branches were put in a flower vase with fresh tap
96 water, and maintained in a climate room at 22 °C and under a natural photoperiod.
97 Observations were made within a maximum period of 2 days after cutting to avoid
98 dehydration of the samples. A total of 40 branches were collected within 4 days of sampling.
99 For each branch, observations were made on two cuttings (h=2 cm in length) taken at 10 cm
100 (basal section) and 25 cm (middle section) from the base of the cutting in order to control for
101 factors other than blackcurrant variety (e.g. microclimatic condition, plant tissue quality). In
102 order to calculate densities (number of individuals / surface of the cutting), the diameters of
103 each cutting (R at the top and r at the bottom) were recorded. The surface S of each cutting
104 was approximated by the lateral surface of a truncated cone (without the sections) with the
105 following equation:

106
$$S = \pi \times (R + r) \times \sqrt{h^2 + (R - r)^2}$$

107 A total of 80 branch segments were collected and inspected.

108

Density of shields and alive females, proportion of parasitized scales

Females WPS develop under protective shields that may accumulate on several layers year after year. Some young larvae stay and secrete their shield while still under the mother shield instead of migrating along the branch, thus leading to shield overlapping since dead mothers decay and disappear. We estimated the density of females' shields as the number of apparent overlapping shields divided by the surface of the cutting. The density of living females was estimated by carefully lifting each shield with fine pliers under a stereomicroscope (Nikon SMZ1500, X20) to count only the females alive when collected from the field (orange-colored and turgescient, without any indication of parasitism). The density of scales and living females was estimated by dividing the number of items by the surface of each cutting. The proportion of parasitized scales was estimated by dividing the number of scales exhibiting indications of parasitism (e.g. an emergence hole, larvae inside or outside of the female body) by the total number of shields found on each cutting. This metric underestimates the parasitism rate occurring at a certain time in the field, but since it is impossible to determine the generation of an scale, it is not possible to estimate the accumulation of shields from generation to generation makes it impossible to estimate. Indeed, the moment at which an individual has been parasitized (i.e. every shield exhibiting indication of parasitism) cannot be identified.

On the 80 branch segments collected from the two blackcurrant varieties, a total of 14,248 females were found and inspected for parasitism.

Size of the WPS females

On each of the 80 branch segments collected from the field, we measured the body size and the shield surface of the first five living females found (when lifting shields) for a total of 400 females. We measured the first well-developed anterior segment of each insect for its width

and the surface area of the shield under a stereomicroscope (Nikon SMZ1500, X20) with software Image J 1.49. Unfortunately, it was not possible to estimate female fecundity because eggs are continuously laid during the adult stage (Hanks and Denno 1993b).

Statistical analysis

All statistical tests were completed using R-CRAN (Version 3.4.3, R Core Team 2017). For each cutting, we calculated (i) the density of shields, (ii) the density of alive females, and (iii) the proportion of parasitized scales. These metrics were compared between the two blackcurrant varieties by using analysis of variance (ANOVA) with Linear Mixed-Effects models (package lme). The models included the blackcurrant varieties (NB, RN) and the position of the cutting on the branch (basal, middle) as fixed factors, and branch as a random factor (Pinheiro et al. 2018). When testing for differences between female mortality, we also included the female density as covariate in the model in order to test for a plausible effect of the density on mortality. To highlight significant differences among groups, Cohen's *ds* with their bootstrapped confidence intervals (CI_{95%}, 10 000 iterations) were calculated and reported (Nakagawa and Cuthill, 2007). These standardised measures of effect size allowed us to quantify the overall effect of the blackcurrant variety on the measured traits. The relationship between female width and shield surface was analyzed with a Linear Mixed-Effects Model, with female width as a covariate, blackcurrant varieties and position of the cutting as fixed factors, and branch as random factor.

Results

Density of shields and living females, proportion of parasitized scales

Blackcurrant variety influenced the density of *P. pentagona* shields: on average, the density of shields was higher on NB (mean density = 28.29 shields.cm⁻², CI_{95%} = [24.29; 32.29]) than on

RN (mean density = 15.26 shields.cm⁻², CI_{95%} = [12.38; 18.15]) ($F_{1;38} = 34.12$, $P < 0.001$; $d = 1.21$, CI_{95%} = [0.79; 1.71]; Figure 1A). The density of living females on NB (mean density = 5.33, CI_{95%} = [4.60; 6.06]) was higher than on RN (mean density = 2.25, CI_{95%} = [1.66; 2.83]) ($F_{1;38} = 34.12$, $P < 0.001$; $d = 1.52$, CI_{95%} = [1.08; 2.05]; Figure 1B). The density of living females was positively correlated with the density of shields on the branch ($r = 0.8$, $t = 11.77$, $df = 78$, $p < 0.001$). Among all shields found on the cuttings, the proportion of parasitized scales was higher on RN (mean proportion = 0.03, CI_{95%} = [0.02; 0.04]) than on NB (mean proportion rate = 0.018, CI_{95%} = [0.01; 0.02]) ($F_{1;38} = 5.95$, $P = 0.02$; $d = 0.6$, CI_{95%} = [0.20; 1.02]; Figure 1C). Overall, NB bore 2.36 times more alive females than RN, which was associated with parasitism reduced by almost half. The position of the cutting on the branch (basal vs. middle sections) had no effect on the density of shields ($F_{1;38} = 4.08$, $P = 0.05$), the density of living females ($F_{1;39} = 4.03$, $P = 0.05$), nor on the proportion of parasitized scales ($F_{1;39} = 0.98$, $P = 0.33$) (Figure 1).

Female size

The body size of *P. pentagona* females depended on which blackcurrant variety they fed on: females feeding on RN had a smaller first anterior segment (mean segment width = 0.99mm, CI_{95%} = [0.97; 1.01]) compared to those feeding on NB (mean segment width = 1.13mm, CI_{95%} = [1.11; 1.16]) (LMEM – $F_{1;38} = 32.39$, $P < 0.001$, Figure 2A). Their size was not influenced by the position of the cutting on the branch (LMEM – $F_{1;335} = 0.04$, $P = 0.842$). Shield surface depended on both first anterior segment width and blackcurrant variety (LMEM – interaction term, $F_{1;334} = 18.66$, $P < 0.001$): shield surface increased faster with first anterior segment width for females feeding on NB than for females feeding on RN (Figure 2B).

Discussion

Our field study showed that females WPS feeding on ‘Noir de Bourgogne’ were more numerous, had a larger body size, a larger shield, and were less parasitized compared to females feeding on ‘Royal de Naples’ at the same site. In armored scale insects, host plant quality is a key determinant of their life history. For example, orange tree varieties influence the fecundity of two diaspidid species: *Lepidosaphes beckii* and *Parlatoria pergandii* (Boyero et al. 2007). Until now, a similar effect on fecundity has only been shown for *P. pentagona* between individuals developing on different host plant species. Erkiliç and Uygun (1997) showed differences in the life tables of WPS reared in the laboratory on peach, potato and squash; they demonstrated that host plant species affected longevity, development time and fecundity. Here, we demonstrated that the variety of the same host plant species, *Ribes nigrum*, influences *P. pentagona* performance in field conditions.

Intrinsic characteristics of the blackcurrant varieties may explain the observed differences in parasitism, body and scale size of *P. pentagona*. Kerslake et al. (1989) showed that NB and RN buds have distinct chemotypes based on molecules such as, among others, δ -elemene, γ -elemene, allo-aromadendrene, and two unknown sesquiterpene hydrocarbons. Some of these molecules could have a direct effect on *P. pentagona* female’s size and mortality, as both varieties host a different number of females, especially living females. It is thus possible that RN resists *P. pentagona* attacks better than NB. This has already been shown for other blackcurrant varieties which are known to express different resistance levels to insect pests and fungal diseases as shown, for example, against white pine blister rust *Cronartium ribicola* (Pluta and Broniarek-Niemiec 2000) or the big bud mite *Cecidophyopsis ribis* (Łabanowska and Pluta 2010).

Intrinsic differences between the two varieties may also explain the observed different parasitism rate. This difference may indeed involve host plant nutritional quality or toxic

defensive compounds, all impacting the size of *P. pentagona* and its vulnerability towards their natural enemies (Price et al. 1980; Inbar and Gerling 2008, Wetzal et al. 2016). For example, the effect of host plant variety on the ability of herbivores to avoid or resist parasitoids has been thoroughly studied in vineyards – providing a similar case study to blackcurrant cultivation where host plant varieties may be cultivated simultaneously in the same plot. Grape variety has a strong impact on the immune function of the grape berry moth, *Eupoecilia ambiguella* (Vogelweith et al. 2015), which affects the moths' propensity to be parasitized by endoparasitoids (Moreau et al. 2010; Vogelweith et al. 2013). Natural enemies (including parasitoids and predators) may thus represent a strong force that shapes the abundance and spatial distribution of *P. pentagona* in mulberry trees (Hanks and Denno 1994). Habitats hosting abundant natural enemies are those on which *P. pentagona* survival is low. It is thus possible that the two blackcurrant varieties differently attract local parasitoids, among others *Encarsia spp.* and *Aphitys spp.* (Pedata et al. 1995; Rauleder 2011, personal observations), resulting in a higher rate of parasitism on RN rather than NB.

Faced with these two varieties of different quality for *P. pentagona*, our results may suggest a specific apparent preference for NB rather than RN. However, there is no evidence in the literature of an active behavioral preference of *P. pentagona* females for a given profitable host plant, presumably because of its very limited dispersal ability at larval stage and its sedentary lifestyle when adult (Beardsley and Gonzalez 1975). Differences in chemotypes and/or phenology are thus likely to be more influential on survival and susceptibility to parasitoids of females settled on each of the two varieties, compared to unlikely different attraction/repellant levels between the blackcurrant varieties.

Our results demonstrate that NB suffers a higher pressure exerted by *P. pentagona* than RN in our experimental field, and, in addition, females infesting NB are less attacked by local parasitoids than RN. Thus, our study reveals a trend in blackcurrant cultivation,

234 especially for NB, the variety of economic interest in Burgundy, which suffers a higher pest
235 pressure in comparison with RN. To select and to use specific plant varieties should be a
236 valuable pest management strategy which manipulates natural enemies to produce beneficial
237 long-term results (Bottrell et al. 1998). However, the very high density of *P. pentagona*
238 females and the low parasitism rate we found in our experimental field constrain the
239 establishment of a rapid and efficient biological control of *P. pentagona*. Moreover, we
240 sampled *P. pentagona* females during one year only, which limits the generalization of our
241 results to the entire blackcurrant cultivation. Future researches should test for the effect of
242 soil, agricultural practices and climatic conditions on the trend we revealed here. For example,
243 environmental temperature and precipitation pattern are key ecological factors that may affect
244 the trophic relationship between blackcurrant varieties, *P. pentagona* females and their related
245 parasitoids, as it is the case for many other biological systems (see for example, Ball 1980,
246 Jeffs and Lewis 2013, Jamieson et al. 2012).

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Figure legends

Figure 1. Comparison of (A) density of shields, (B) density of alive females, and (C) proportion of parasitized scales of overwintering *P. pentagona* females feeding on ‘Noir de Bourgogne’ (NB) and ‘Royal de Naples’ (RN) blackcurrant varieties in Burgundy. Females were collected in the basal (darkgrey) or the middle (lightgrey) segment of a blackcurrant branch. Associated bars represent 95% confidence intervals of the means. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Figure 2. (A) First anterior segment width [cm] of *P. pentagona* for overwintering females feeding on ‘Noir de Bourgogne’ (NB) and ‘Royal de Naples’ (RN) blackcurrant varieties in Burgundy. (B) Relationship between shield surface and first anterior segment width of the females (NB-black line and circles: $y = -2.11 + 3.73x$, $R^2 = 0.64$; RN-grey line and triangles: $y = -0.79 + 2.47x$, $R^2 = 0.49$). Associated bars represent 95% confidence intervals of the means. *** $P < 0.001$.

374 **Figures**375 **Figure 1**

376

377 Figure 2