



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

Ruddy Kuzmin¹, Marie-Charlotte Anstett¹, and Philippe Louâpre^{1,*}

¹ Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France.

* Corresponding author: philippe.louapre@u-bourgogne.fr

With 2 figures

Abstract: The White Peach Scale (WPS), *Pseudaulacaspis pentagona* (Hemiptera: 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 has economic importance. We determined the direct effect of blackcurrant varieties on the infestation rate, female body size, and parasitism rate 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 WPS females 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 both varieties brings into question the benefits of a pest management strategy based on the change of the varieties used in blackcurrant orchards.

Keywords: Trophic interaction, parasitism, WPS, performance, blackcurrant

1 Introduction

White Peach Scale (WPS), *Pseudaulacaspis pentagona* Targioni Tozzetti (Homoptera: Diaspididae), is a cosmopolitan pest originating in Eastern Asia. It has between 2 to 5 discrete generations per year depending on the regions. The females lay between 70 and 100 eggs, and the sex-ratio is usually even (Hanks & Denno 1993b). The species 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 spectrum (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 & Brown 1958; Hanks & Denno 1993b; Kreiter & 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). Previous observations showed that two primary parasitoids are present in this blackcurrant orchard in Burgundy, belonging to the *Aphytis* and *Encarsia* genera.

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, usually with 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 & 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 result 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 & 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 & 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 & 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. Higher rates of infestation on one variety may 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 egg hatching to their death, making them more sensitive to plant variety in comparison with males (with non-feeding immature and adult stages).

2 Materials and methods

2.1 Field sampling

In April 2018, we collected overwintering *P. pentagona* females from blackcurrant (*Ribes nigrum* L.) in Burgundy, France. In order to reduce geographical and climatic effects, individuals were sampled in a three-hectare blackcurrant orchard, with the two varieties planted alternately (one shrub of RN every five shrubs of NB) in Marey-Les-Fussey, France (N-47°07'30", E-4°51'01").

For each variety, one branch (45–136 cm in length), cut at the base of each shrub, was collected from 20 shrubs, following a stratified sampling procedure: 12 branches were collected from shrubs randomly selected within the first and the last rows of crops, and 8 branches were collected from shrubs randomly chosen within the three central rows of the orchards. These branches were put in a flower vase

with fresh tap water, and maintained in a climate-controlled room at 22 °C and under a natural photoperiod. Observations were made within a maximum period of 2 days after cutting to avoid dehydration of the samples. A total of 40 branches were collected within 4 days of sampling. For each branch, observations were made on two cuttings (h = 2 cm in length) taken at 10 cm (basal section) and 25 cm (middle section) from the base of the cutting in order to control for factors other than blackcurrant variety (e.g. microclimatic condition, plant tissue quality). In order to calculate densities (number of females / surface of the cutting), the radii of each cutting (R at the bottom and r at the top) were recorded. The surface S of each cutting was approximated by the lateral surface of a truncated cone (without the sections) with the following equation:

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

A total of 80 branch segments were collected and inspected.

2.2 Density of shields and living females, proportion of parasitized scales

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 while dead mothers decay. 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 living females when collected from the field (orange-colored and turgescient, without any indication of parasitism). The densities of scales and living females were estimated by dividing the number of items by the surface of each cutting. When parasitoids emerged, they leave an empty scale and it is not possible to determine if they emerged recently or not. We thus calculated a parasitism rate summarizing several generations as 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.

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

2.3 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 larger cephalothorax 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 & Denno 1993b).

2.4 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 living 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). We also included the scale density as covariate in the model in order to test for a plausible effect of the density on female viability. To tease out significant differences among groups, Cohen's d s with their bootstrapped confidence intervals (CI_{95%}, 10 000 iterations) were calculated and reported (Nakagawa & 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 cephalothorax width and shield surface was analyzed with a Linear Mixed-Effects Model, with cephalothorax width as a covariate, blackcurrant varieties and position of the cutting as fixed factors, and branch as random factor.

3 Results

3.1 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]; Fig. 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]; Fig. 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 = 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]; Fig. 1C). Overall, NB bore 2.36 times more living females than RN, which was associated with parasitism reduced by almost half. The position of the cutting on the branch (basal vs. middle sections)

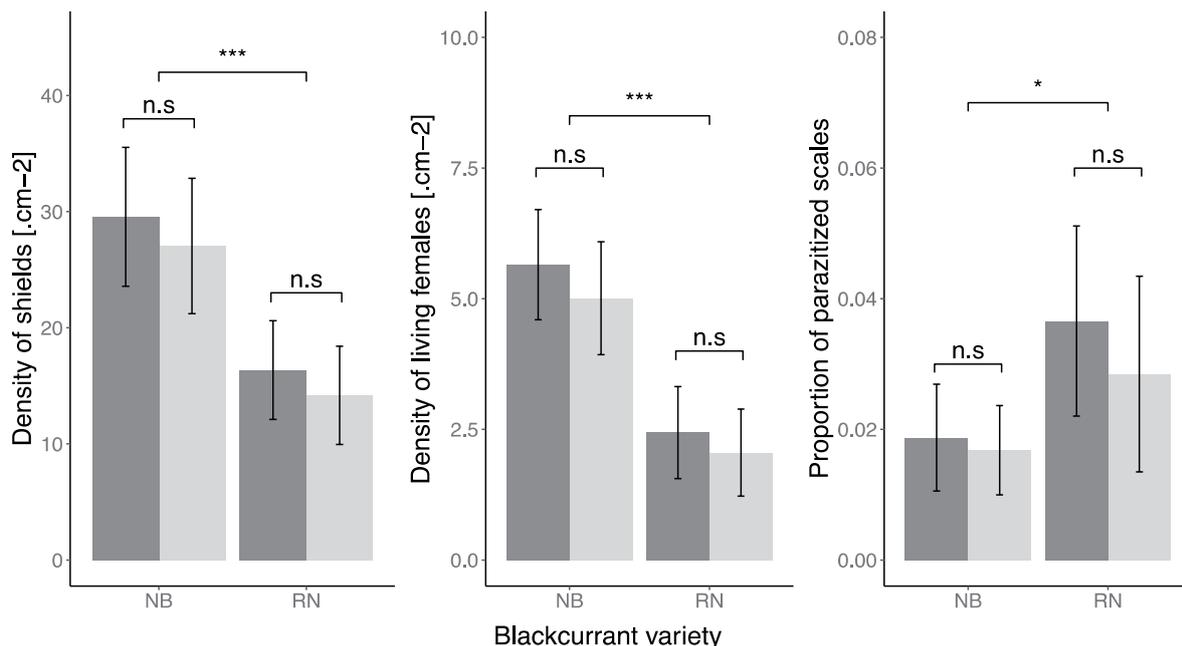


Fig. 1. Comparison of (A) density of shields, (B) density of living females, and (C) proportion of parasitized scales of overwintering *P. pentagona* females feeding on 'Noir de Bourgogne' (NB) and 'Royal de Naples' (RN) blackcurrant varieties in Burgundy. Females were collected in the basal (darkgrey)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

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 ($F_{1;39} = 0.98$, $P = 0.33$) (Fig. 1).

3.2 Size of the WPS females

The body size of *P. pentagona* females depended on which blackcurrant variety they fed on: females feeding on RN had a smaller cephalothorax (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 – $F_{1;38} = 32.39$, $P < 0.001$, Fig. 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 cephalothorax width and blackcurrant variety (LMEM – interaction term, $F_{1;334} = 18.66$, $P < 0.001$): shield surface increased faster with cephalothorax width for females feeding on NB than for females feeding on RN (Fig. 2B).

4 Discussion

Our field study showed that WPS females 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 & Uygün (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* size and parasitism rate 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.

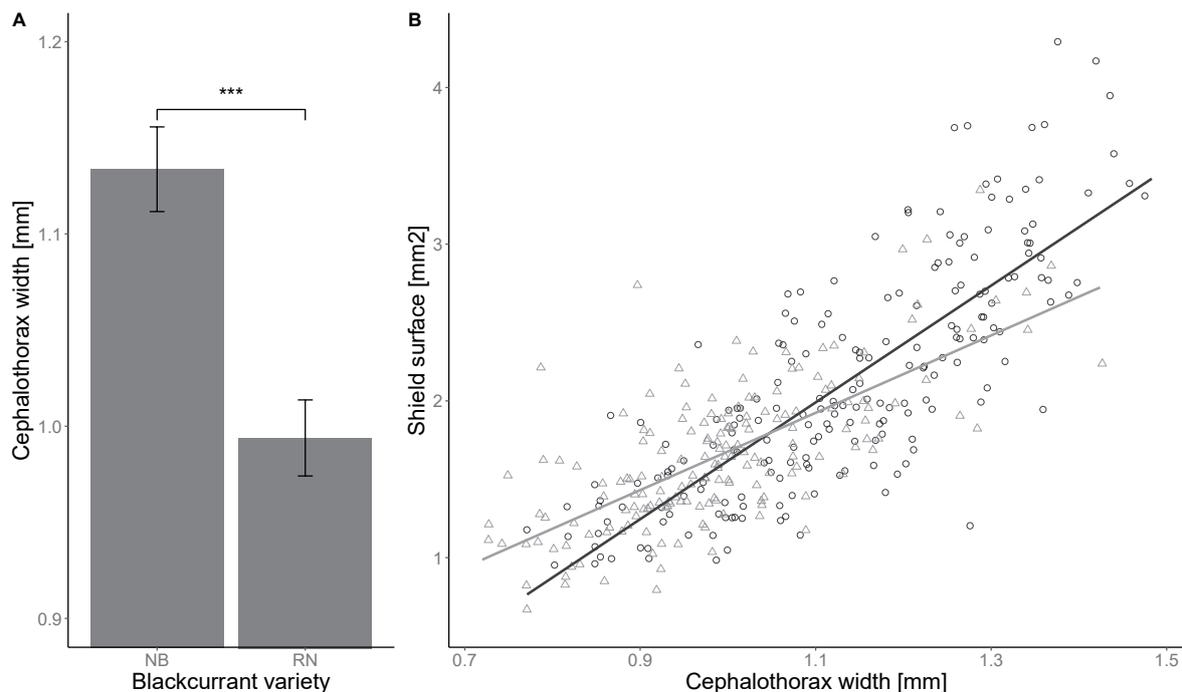


Fig. 2. (A) Cephalothorax width [mm] of *P. pentagona* for overwintering females feeding on ‘Noir de Bourgogne’ (NB) and ‘Royal de Naples’ (RN) blackcurrant varieties in Burgundy. (B) Relationship between shield surface and cephalothorax width of the females (NB-black line and circles: $y = -2.11 + 3.73x$,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

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 & Broniarek-Niemiec 2000) or the big bud mite *Cecidophyopsis ribis* (Łabanowska & Pluta 2010).

The differences between the two varieties may also explain the different parasitism rates observed. 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 & 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* (Hanks & 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, *Encarsia spp.* and *Aphitys spp.* (Pedata et al. 1995; Rauleder 2011, personal observations) among others, resulting in a higher rate of parasitism on RN rather than NB.

Faced with these two varieties of unequal quality for *P. pentagona*, our results 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 & 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/repellent 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, especially for NB, the variety of economic interest in Burgundy, which suffers a higher pest pressure in comparison with RN. To select and to use specific plant varieties should be a valuable pest management strategy which manipulates natural enemies to produce beneficial long-term results (Bottrell et al. 1998). However, the very high density of *P. pentagona* females and the low parasitism rate we found in our experimental field constrain

the establishment of a rapid and efficient biological control of *P. pentagona*. Moreover, we sampled *P. pentagona* females during one year only, which limits the generalization of our results to the entire blackcurrant cultivation. Future research should test for the effect of soil, agricultural practices and climatic conditions on the trend we revealed here. For example, environmental temperature and precipitation patterns are key ecological factors that may affect the trophic relationship between blackcurrant varieties, *P. pentagona* females and their related parasitoids, as is the case for many other biological systems (see for example, Ball 1980, Jeffs & Lewis 2013, Jamieson et al. 2012).

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.

Acknowledgements: This project was funded by Le Fonds Européen Agricole pour le Développement Rural (FEADER RBOU160118CR0260011 “Pérenité et développement de la filière cassis en Bourgogne”) and the Région Bourgogne-Franche-Comté in association with “Les acteurs du cassis”. We thank Manon Leon de Treverret for her technical support, Paul Simon who gave us access to his blackcurrant orchards, Fabrice Ecalte (Chambre d'Agriculture 21), Olivier Lenoir, three generations of the Family Lenoir, and all other blackcurrant growers for kindly sharing their knowledge on past and present blackcurrant cultivation and encouraging this study. We also thank colleagues met at the XVth International Symposium on Scale Insect Studies Meeting (Zagreb, Croatia, June 17-20, 2019), especially Dr. Paul Amouroux, who helped us identify *P. pentagona*.

References

- Awmack, C. S., & Leather, S. R. (2002). Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, 47(1), 817–844. <https://doi.org/10.1146/annurev.ento.47.091201.145300>
- Ball, J. (1980). Development and fecundity of the White Peach Scale at two constant temperatures. *The Florida Entomologist*, 63(1), 188–194. <https://doi.org/10.2307/3494672>
- Beardsley, J. W. J., Jr., & Gonzalez, R. H. (1975). The biology and ecology of armored scales. *Annual Review of Entomology*, 20(1), 47–73. <https://doi.org/10.1146/annurev.en.20.010175.000403>
- Bennett, F. (1956). Some parasites and predators of *Pseudaulacaspis pentagona* (Targ.) in Trinidad, B.W.I. *Canadian Entomologist*, 88(12), 704–705. <https://doi.org/10.4039/Ent88704-12>
- Bennett, F., & Brown, S. (1958). Life history and sex determination in the Diaspine Scale, *Pseudaulacaspis pentagona* (Targ.) (Coccoidea). *Canadian Entomologist*, 90(6), 317–324. <https://doi.org/10.4039/Ent90317-6>

- Bottrell, D. G., Barbosa, P., & Gould, F. (1998). Manipulating natural enemies by plant variety selection and modification: A realistic strategy? *Annual Review of Entomology*, 43(1), 347–367. <https://doi.org/10.1146/annurev.ento.43.1.347>
- Boyer, J. R., Ruiz-López, R., Rodríguez, N., Vela, J. M., Moreno, R., & Pascual, F. (2007). Varietal influence of orange trees on armoured scale insect fecundity (Hemiptera: Diaspididae). *International Journal of Pest Management*, 53(3), 217–225. <https://doi.org/10.1080/09670870701289114>
- Dalstein, M. C., Guigneault, P., & Kreiter, P. (2016). Management of *Pseudaulacaspis pentagona* in French blackcurrant. In: Fernandez G., Hummer K. (eds) *Acta Horticulturae*, Proc. XI Int. Rubus and Ribes Symp. pp. 445–450
- Erkiliç, L. B., & Uygun, N. (1997). Development time and fecundity of the white peach scale, *Pseudaulacaspis pentagona*, in Turkey. *Phytoparasitica*, 25(1), 9–16. <https://doi.org/10.1007/BF02981474>
- García-Morales, M., Denno, B. D., Miller, D. R., Miller, G. L., Ben-Doc, Y., & Hardy, N. B. (2016). ScaleNet: A literature-based model of scale insect biology and systematics. *Database (Oxford)*, 1–5. <https://doi.org/10.1093/database/bav118>
- Giongo, L., Grisenti, M., Eccher, M., ... Mattivi, F. (2008). Horticultural and nutritional qualities of white, red and black currants. In: *Acta Horticulturae*, Proc. XI Int. Rubus and Ribes Symp. pp. 167–171 <https://doi.org/10.17660/ActaHortic.2008.777.23>
- Giron, D., Dubreuil, G., Bennett, A., ... Pincebourde, S. (2018). Promises and challenges in insect-plant interactions. *Entomologia Experimentalis et Applicata*, 166(5), 319–343. <https://doi.org/10.1111/eea.12679>
- Hanks, L. M., & Denno, R. F. (1994). Local adaptation in the armored scale insect *Pseudaulacaspis Pentagona* (Homoptera, Diaspididae). *Ecology*, 75(8), 2301–2310. <https://doi.org/10.2307/1940885>
- Hanks, L. M., & Denno, R. F. (1993a). Natural enemies and plant water relations influence the distribution of an armored scale insect. *Ecology*, 74(4), 1081–1091. <https://doi.org/10.2307/1940478>
- Hanks, L. M., & Denno, R. F. (1993b). The White Peach Scale, *Pseudaulacaspis pentagona* (Targioni-Tozzetti) (Homoptera: Diaspididae): Life history in Maryland, host plants, and natural enemies. *Proceedings of the Entomological Society of Washington*, 95, 79–98.
- Inbar, M., & Gerling, D. (2008). Plant-mediated interactions between whiteflies, herbivores, and natural enemies. *Annual Review of Entomology*, 53(1), 431–448. <https://doi.org/10.1146/annurev.ento.53.032107.122456>
- Jamieson, M. A., Trowbridge, A. M., Raffa, K. F., & Lindroth, R. L. (2012). Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology*, 160(4), 1719–1727. <https://doi.org/10.1104/pp.112.206524>
- Jarvis, D. I., Brown, A. H. D., Cuong, P. H., ... Hodgkin, T. (2008). A global perspective of the richness and evenness of traditional crop-variety diversity maintained by farming communities. *Proceedings of the National Academy of Sciences of the United States of America*, 105(14), 5326–5331. <https://doi.org/10.1073/pnas.0800607105>
- Jeffs, C. T., & Lewis, O. T. (2013). Effects of climate warming on host-parasitoid interactions. *Ecological Entomology*, 38(3), 209–218. <https://doi.org/10.1111/een.12026>
- Kerslake, M. F., Latrasse, A. G., & Quéré, J. (1989). Hydrocarbon chemotypes of some blackcurrant cultivars. *Journal of the Science of Food and Agriculture*, 47(1), 43–51. <https://doi.org/10.1002/jsfa.2740470106>
- Kotowska, A. M., Cahill, J. F., Jr., & Keddie, B. A. (2010). Plant genetic diversity yields increased plant productivity and herbivore performance. *Journal of Ecology*, 98(1), 237–245. <https://doi.org/10.1111/j.1365-2745.2009.01606.x>
- Kreiter, P., Coquelet, C., & Thaon, M. (2002). La cochenille blanche du mûrier, principal ravageur des cassissiers en Région Rhône-Alpes. *Bulletin mensuel de la Société linnéenne de Lyon*, 71, 251–225. <https://doi.org/10.3406/linly.2002.13399>
- Kreiter, P., & Marro, J.-P. (1997). La cochenille du mûrier présente aussi dans la moitié nord de la France, importants foyers sur les arbres d'ornement. *Phytoma – La défense des végétaux*, 491, 58
- Łabanowska, B. H., & Pluta, S. (2010). Assessment of big bud mite (*Cecidophyopsis ribis* Westw.) infestation level of blackcurrant genotypes in the field. *Journal of Fruit and Ornamental Plant Research*, 18, 283–295.
- Le Quere, J.-L., & Latrasse, A. (1990). Composition of the essential oils of blackcurrant buds. *Journal of Agricultural and Food Chemistry*, 38(1), 3–10. <https://doi.org/10.1021/jf00091a001>
- Moreau, J., Desouhant, E., Louâpre, P., ... Thiéry, D. (2017). How host plant and fluctuating environments affect insect reproductive strategies? *Advances in Botanical Research*, 81, 259–287. <https://doi.org/10.1016/bs.abr.2016.09.008>
- Moreau, J., Villemant, C., Benrey, B., & Thiéry, D. (2010). Species diversity of larval parasitoids of the European grapevine moth (*Lobesia botrana*, Lepidoptera: Tortricidae): The influence of region and cultivar. *Biological Control*, 54(3), 300–306. <https://doi.org/10.1016/j.biocontrol.2010.05.019>
- Nakagawa, S., & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: A practical guide for biologists. *Biological Reviews of the Cambridge Philosophical Society*, 82(4), 591–605. <https://doi.org/10.1111/j.1469-185X.2007.00027.x>
- Pedata, P. A., Hunter, M. S., Godfray, H. C. J., & Viggiani, G. (1995). The population dynamics of the white peach scale and its parasitoids in a mulberry orchard in Campania, Italy. *Bulletin of Entomological Research*, 85(4), 531–539. <https://doi.org/10.1017/S0007485300033034>
- Pinheiro, J., Bates, D., Debroy, S., et al. (2018). nlme: Linear and Nonlinear Mixed Effects Models, R package version 3. 1–137
- Pluta, S., & Broniarek-Niemiec, A. (2000). *Field evaluation of resistance to white pine blister rust of selected blackcurrant genotypes in Poland* (pp. 567–569). HortTechnology.
- Price, P. W., Bouton, C. E., Gross, P., McPherson, B. A., Thompson, J. N., & Weis, A. E. (1980). Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, 11(1), 41–65. <https://doi.org/10.1146/annurev.es.11.110180.000353>
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Rauleder, H. (2011). Antagonisten und prädatoren der maulbeerschildlaus *Pseudaulacaspis pentagona* (Targioni - Tozzetti, 1886)(Homoptera: Diaspididae) in Baden-Württemberg. *Erwerbs-Obstbau*, 53(2), 51–58. <https://doi.org/10.1007/s10341-011-0129-4>

- Vogelweith, F., Dourneau, M., Thiéry, D., Moret, Y., & Moreau, J. (2013). Geographical variation in parasitism shapes larval immune function in a phytophagous insect. *Naturwissenschaften*, *100*(12), 1149–1161. <https://doi.org/10.1007/s00114-013-1119-1>
- Vogelweith, F., Moreau, J., Thiéry, D., & Moret, Y. (2015). Food-mediated modulation of immunity in a phytophagous insect: An effect of nutrition rather than parasitic contamination. *Journal of Insect Physiology*, *77*, 55–61. <https://doi.org/10.1016/j.jinsphys.2015.04.003>
- Wetzel, W. C., Kharouba, H. M., Robinson, M., Holyoak, M., & Karban, R. (2016). Variability in plant nutrients reduces insect herbivore performance. *Nature*, *539*(7629), 425–427. <https://doi.org/10.1038/nature20140>
- Yasuda, S. (1979). Microscopic observations on the external morphology of *Pseudaulacaspis pentagona* Targioni and on the portion of mulberry tissues inserted with the stylet. *Japanese Journal of Applied Entomology*, *23*(2), 61–68. <https://doi.org/10.1303/jjaez.23.61>

Manuscript received: 2 January 2019

Revisions requested: 26 February 2020

Modified version received: 12 March 2020

Accepted: 16 March 2020