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

3

4 Kuzmin Ruddy¹, Anstett Marie-Charlotte¹, Louâpre Philippe^{1*}

5

6 ¹ Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6 Boulevard

7 Gabriel, 21000 Dijon, France.

8

9 *Correspondence: Philippe Louâpre, Biogéosciences, UMR 6282 CNRS, Université

10 Bourgogne Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France.

11 E-mail address: philippe.louapre@u-bourgogne.fr

12 Abstract

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

27

28 Keywords

29 Trophic interaction, parasitism, WPS, performance, blackcurrant

30

31 Compliance with ethical standards

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

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

34 **Introduction**

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

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

59 observation). NB is richer in aroma than RN, contains different essential oils and has a
60 slightly delayed phenology (Kerslake et al. 1989; Le Quere and Latrasse 1990; Giongo et al.
61 2008; personal observation).

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

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

79 The study was conducted with a natural population of *P. pentagona* collected in Burgundy
80 (France) on NB and RN varieties. We specifically focused on females because they feed on
81 blackcurrant plants from the stage following crawlers to their death, making them more
82 sensitive to plant variety in comparison with males (non-feeding adult stage). Females are
83 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

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

126
127 On the 80 branch segments collected from the two blackcurrant varieties, a total of 14,248
128 females were found and inspected for parasitism.

129

Size of the WPS females

130 On each of the 80 branch segments collected from the field, we measured the body size and
131 the shield surface of the first five living females found (when lifting shields) for a total of 400
132 females. We measured the first well-developed anterior segment of each insect for its width
133

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

137

138 *Statistical analysis*

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

154

155 **Results**

156 *Density of shields and living females, proportion of parasitized scales*

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

159 RN (mean density = 15.26 shields.cm⁻², CI_{95%} = [12.38; 18.15]) ($F_{1;38} = 34.12$, $P < 0.001$; $d =$
160 1.21, CI_{95%} = [0.79; 1.71]; Figure 1A). The density of living females on NB (mean density =
161 5.33, CI_{95%} = [4.60; 6.06]) was higher than on RN (mean density = 2.25, CI_{95%} = [1.66; 2.83])
162 ($F_{1;38} = 34.12$, $P < 0.001$; $d = 1.52$, CI_{95%} = [1.08; 2.05]; Figure 1B). The density of living
163 females was positively correlated with the density of shields on the branch ($r = 0.8$, $t = 11.77$,
164 $df = 78$, $p < 0.001$). Among all shields found on the cuttings, the proportion of parasitized
165 scales was higher on RN (mean proportion = 0.03, CI_{95%} = [0.02; 0.04]) than on NB (mean
166 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;
167 1.02]; Figure 1C). Overall, NB bore 2.36 times more alive females than RN, which was
168 associated with parasitism reduced by almost half. The position of the cutting on the branch
169 (basal vs. middle sections) had no effect on the density of shields ($F_{1;38} = 4.08$, $P = 0.05$), the
170 density of living females ($F_{1;39} = 4.03$, $P = 0.05$), nor on the proportion of parasitized scales
171 ($F_{1;39} = 0.98$, $P = 0.33$) (Figure 1).

172

173 **Female size**

174 The body size of *P. pentagona* females depended on which blackcurrant variety they fed on:
175 females feeding on RN had a smaller first anterior segment (mean segment width = 0.99mm,
176 CI_{95%} = [0.97; 1.01]) compared to those feeding on NB (mean segment width = 1.13mm,
177 CI_{95%} = [1.11; 1.16]) (LMEM – $F_{1;38} = 32.39$, $P < 0.001$, Figure 2A). Their size was not
178 influenced by the position of the cutting on the branch (LMEM – $F_{1;335} = 0.04$, $P = 0.842$).
179 Shield surface depended on both first anterior segment width and blackcurrant variety
180 (LMEM – interaction term, $F_{1;334} = 18.66$, $P < 0.001$): shield surface increased faster with first
181 anterior segment width for females feeding on NB than for females feeding on RN (Figure
182 2B).

183

184 **Discussion**

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

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

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

209 defensive compounds, all impacting the size of *P. pentagona* and its vulnerability towards
210 their natural enemies (Price et al. 1980; Inbar and Gerling 2008, Wetzel et al. 2016). For
211 example, the effect of host plant variety on the ability of herbivores to avoid or resist
212 parasitoids has been thoroughly studied in vineyards – providing a similar case study to
213 blackcurrant cultivation where host plant varieties may be cultivated simultaneously in the
214 same plot. Grape variety has a strong impact on the immune function of the grape berry moth,
215 *Eupoecilia ambiguella* (Vogelweith et al. 2015), which affects the moths' propensity to be
216 parasitized by endoparasitoids (Moreau et al. 2010; Vogelweith et al. 2013). Natural enemies
217 (including parasitoids and predators) may thus represent a strong force that shapes the
218 abundance and spatial distribution of *P. pentagona* in mulberry trees (Hanks and Denno
219 1994). Habitats hosting abundant natural enemies are those on which *P. pentagona* survival is
220 low. It is thus possible that the two blackcurrant varieties differently attract local parasitoids,
221 among others *Encarsia spp.* and *Aphitys spp.* (Pedata et al. 1995; Rauleder 2011, personal
222 observations), resulting in a higher rate of parasitism on RN rather than NB.

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

231 Our results demonstrate that NB suffers a higher pressure exerted by *P. pentagona*
232 than RN in our experimental field, and, in addition, females infesting NB are less attacked by
233 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).

247

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360 **Figure legends**

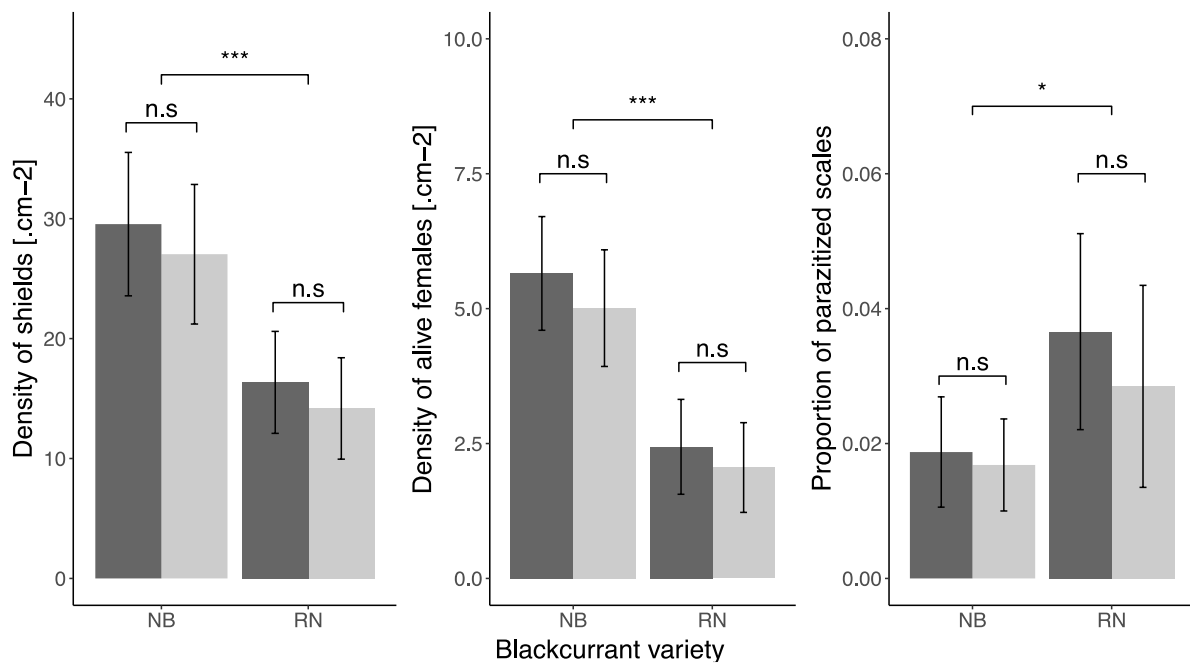
361 Figure 1. Comparison of (A) density of shields, (B) density of alive females, and (C)
362 proportion of parasitized scales of overwintering *P. pentagona* females feeding on ‘Noir de
363 Bourgogne’ (NB) and ‘Royal de Naples’ (RN) blackcurrant varieties in Burgundy. Females
364 were collected in the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

367

368 Figure 2. (A) First anterior segment width [cm] of *P. pentagona* for overwintering females
369 feeding on ‘Noir de Bourgogne’ (NB) and ‘Royal de Naples’ (RN) blackcurrant varieties in
370 Burgundy. (B) Relationship between shield surface and first anterior segment width of the
371 females (NB-black line and circles: $y = -2.11 + 3.73x$, $R^2 = 0.64$; RN-grey line and triangles: $y = -$
372 $0.79 + 2.47x$, $R^2 = 0.49$). Associated bars represent 95% confidence intervals of the means.
373 *** $P < 0.001$.

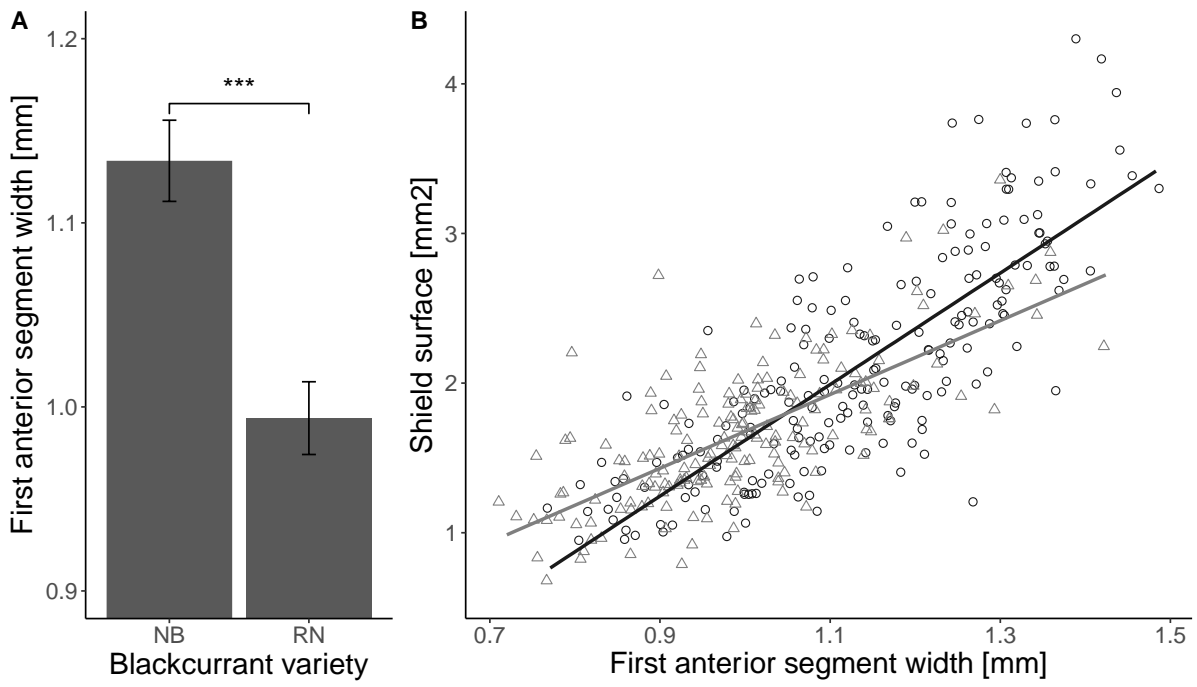
374 **Figures**

375 Figure 1



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377 Figure 2



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