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ORIGINAL PAPER

Berry skin resistance explains oviposition preferences of *Drosophila suzukii* at the level of grape cultivars and single berries

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Abstract

Drosophila suzukii (Matsumura) is an invasive species, which is able to attack intact ripening fruit and has become a serious pest in the Americas and Europe. However, susceptibility toward *D. suzukii* varies strongly within and between grapevine cultivars. The aim of our study was to differentiate between berry parameters influencing oviposition of *D. suzukii* in grapevine with two complementary approaches. We investigated the influence of berry skin resistance, total soluble solids (a sugar related parameter), acidity and volatile acidity on grape susceptibility; in the first approach at the cultivar level in a field survey, and in the second approach at the single berry level in a laboratory choice experiment. Both approaches revealed that berry skin resistance explained oviposition decidedly better than chemical composition of the berries did: Soft skinned cultivars and berries received significantly more eggs than hard skinned cultivars and berries. These findings suggest a major role of berry skin resistance in the susceptibility of grapevine toward *D. suzukii*. The cultivar approach identified the cultivars Dornfelder, Trollinger (= Vernatsch, Schiava), Portugieser, Roter Elbling and Cabernet Dorsa to be susceptible, whereas Dakapo, Lemberger (= Blauer Limberger) and Riesling showed no oviposition by *D. suzukii*. Nevertheless, parameters like previous damage, climate, environment and plant protection may have an additional impact.

Keywords Spotted wing drosophila · Pest insect · Susceptibility · Viticulture · Penetration force

Key message

- We differentiated the role of chemical composition and berry skin resistance for susceptibility of grapevine to *Drosophila suzukii.*
- Differences in oviposition among grapevine varieties in the field and differences in oviposition among single berries in the laboratory were both best explained by berry skin resistance.
- The cultivars Dornfelder, Trollinger, Portugieser, Roter Elbling and Cabernet Dorsa were more susceptible than Dakapo, Lemberger and Riesling.
- Breeding and cultivation should aim at a firm and intact berry skin to avoid *D. suzukii* damage.

Introduction

Drosophila suzukii (Matsumura) is an invasive species from Asia, which has become a serious agricultural pest of soft fruits in the Americas and Europe over the last 10 years (Asplen et al. 2015; Schetelig et al. 2018). It has a wide range of hosts including blackberries, blueberries, cherries, raspberries and strawberries, as well as grapevine (Lee et al. 2015). In contrast to the native fruit fly *Drosophila melanogaster*, which oviposits only in overripe, decaying fruit, *D. suzukii* is able to lay its eggs in fresh healthy fruit because of its serrated ovipositor (Atallah et al. 2014; Hamby et al. 2016). The developing larvae damage the fruit directly, and wounds from oviposition can facilitate secondary pathogen

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colonization, damaging the fruit indirectly (Ioriatti et al. 2018).

In European viticulture, *D. suzukii* was associated with considerable damage in Northern Italy in 2012, in Southwest Germany in 2014 and in France since 2014 (Delbac et al. 2017). Consequently, research focused on parameters influencing the susceptibility of grapes to this pest. Environmental parameters like climate or composition of the landscape indirectly affect infestation via their influence on the presence of the fly in the environment (Kinjo et al. 2014; Kraus et al. 2018; Pelton et al. 2016; Tochen et al. 2014, 2016; Wang et al. 2016). In addition, berry-related parameters have been investigated with respect to their role in grape susceptibility toward *D. suzukii*. Ioriatti et al. (2015) showed that *D. suzukii* oviposition increases from veraison until harvest, along with increasing sugar content and decreasing acidity and berry skin resistance. They concluded that berry skin resistance is a critical component of host selection in *D. suzukii*. Large-scale monitoring of *D. suzukii* oviposition in numerous grape cultivars in Switzerland revealed differences in susceptibility between grape cultivars (Kehrli et al. 2017). Some red cultivars seemed to be especially susceptible and showed a critical level of infestation before harvest. The authors hypothesized that berry skin resistance was responsible for these differences. Moreover, various studies showed wounded grapes to be more susceptible to *D. suzukii* than intact berries (Grant and Sial 2016; Ioriatti et al. 2015; Linder et al. 2014; Pelton et al. 2017). Thus, it can be expected that pre-damaged grapes have a higher risk of infestation than healthy grapes.

The aim of our study was to differentiate between berry parameters influencing oviposition of *D. suzukii* in grapevine. We used two complementary approaches in order to combine the realistic conditions of field surveys and the more controlled conditions of laboratory trials. To exclude possible confounding variables that vary between vineyards, we used data from 13 different grape cultivars that were grown in the same vineyard under standardized conditions. Previous studies have focused on variation in berry-related parameters over time within a limited number of varieties (Baser et al. 2018; Ioriatti et al. 2015). The novelty of our approach is that it allows direct comparisons of berry-related parameters between multiple cultivars. Temporal patterns are out of the scope of our study. In our field experiment, oviposition and berry parameters were measured from different subsets of multiple berries per cultivar. This is a destructive approach that precludes examining one-to-one relationships of explanatory variables and oviposition on single berries (Lee et al. 2015). Thus, we took a complementary approach to investigate effects of the same parameters on oviposition at the level of single berries. In this second approach, we conducted a laboratory choice experiment and measured oviposition, TSS and berry skin resistance on the same berry. For both approaches, we hypothesize that oviposition of *D. suzukii* increases with decreasing berry skin resistance. Moreover, we expect oviposition to be influenced by chemical composition of the berry like TSS, acidity or rot parameters.

At the beginning of berry ripening, growers often walk a fine line between harvesting immediately, and applying insecticides against *D. suzukii*. In this study, we try to identify threshold levels of berry parameters that can be used for risk prediction in a future decision support system for an integrated management of *D. suzukii*.

Materials and methods

Cultivar approach

In this approach, data come from an assortment of different grapevine cultivars in one vineyard next to JKI in Siebeldingen, Germany (49°13′03.0″N 8°02′49.7″E; one row of 25 plants per cultivar). We included the following 13 cultivars in the analysis: Acolon, Cabernet Dorsa, Cabernet Sauvignon, Dakapo, Domina, Dornfelder, Grauburgunder (=Pinot gris), Lemberger (=Blauer Limberger), Portugieser, Roter Elbling, Riesling, Trollinger (=Vernatsch, Schiava), Weissburgunder (=Pinot blanc). All cultivars were treated with the same soil tillage, fertilization and plant protection, which comprises only fungicide and no insecticide application (detailed plant protection schedule: Table S1, supplementary material). This setting allowed us to investigate the effect of different grapevine cultivars with their different berry parameters on *D. suzukii* oviposition. The location of all cultivars within the same vineyard allows us to exclude possible confounding factors such as the presence of field margins containing wild *D. suzukii* hosts like for example blackberry, which is thought to attract D. *suzukii*. We focused on the time when oviposition occurred, which was at or after harvest in most cultivars (2–5 weeks depending on cultivar). For each cultivar, we assessed oviposition of *D. suzukii*, chemical composition of the berries (by analyzing parameters of the juice) and berry skin resistance weekly for 6 weeks around the harvest (calendar week 39–44; 21.9.–26.10.2015). For oviposition of *D. suzukii*, we counted the number of eggs in 50 randomly selected healthy berries under a stereo microscope (Stemi 2000, Carl Zeiss AG, Oberkochen, Germany). To determine the chemical parameters, 50 randomly selected berries were blended and centrifuged and their juice was analyzed (Sigma 6K15, Sigma Laborzentrifugen GmbH, Osterode am Harz, Germany; 10 min, 20 °C, 10000 rpm). From the supernatant, we determined the following parameters related to berry ripening: TSS [°Oechsle], tartaric acidity [g/L] and volatile acidity [g/L] by Fourier-transform infrared spectroscopy

(FTIR; WineScan FT 120, FOSS, Hillerød, Denmark). To determine berry skin resistance, we sampled 25 berries without visible skin damages per cultivar and date. We measured the resistance of the berries skins on the lateral side of the berry by using a Universal Testing Machine TAxT2i Texture Analyzer (Stable Micro System, Godalming, Surrey, UK) as described in Letaief et al. (2008). Hereby, the maximal penetration force [N] that a needle probe (P/2 N, ø at tip 0.3 mm) moving at 1 mm/s needed to puncture the berry skin is assessed.

Statistics We performed all analyses using the open source program R (R Core Team 2017). We used $n = 75$ samples (13 grapevine cultivars times 6 weeks minus three missing samples) to investigate the relationship between oviposition and berry parameters. As oviposition data were not normally distributed, we $\log_{10}(X+1)$-transformed them. As it is well known that oviposition increases during the ripening process (Hamby et al. 2016; Ioriatti et al. 2015; Lee et al. 2015), we did not investigate temporal patterns. We fitted linear mixed models with sampling date as random factor and the berry parameters described above as fixed factors using the nlme package (Pinheiro et al. 2017). As some of the tested fixed factors are strongly correlated (e.g., TSS and acidity), we tested each fixed factor individually and estimated the quality of the respective model based on the Bayesian Information Criterion (BIC, Dormann 2013) and performed permutation tests of the best model to check for its robustness using the function PermTest in the pgirmess package (Giraudoux 2017).

For illustration, we performed linear models with oviposition and berry parameters averaged across sampling dates. We also analyzed the relationship between oviposition and the independent variables for the six sample dates separately using linear models. We used diagnostic plots to identify overly influential data points according to Cook's distance (> 1) and performed an analysis without these points, to test the robustness of the results. In the results, the analysis with all data points is given (Dormann 2013).

Berry approach

The second approach was a controlled laboratory choice experiment, and the parameters were measured on the single berry level. Berries from six different cultivars were exposed to *D. suzukii* in mesh cages (56 × 58 × 92 cm, PAPA Papillon, Bern, Switzerland) in six trials in 5 weeks around harvest (17.8.–22.9.2017). We placed 60 berries per cage and two cages per trial date. Experiments were performed in a climatic chamber with 23 °C, 75% relative humidity and a photoperiod of L16:D8 h. Berries came from the cultivars Dornfelder, Spätburgunder, Calandro, Regent, Reberger, and a cultivar under development (Breeding number: 884-58-998) from six vineyards surrounding the JKI in Siebeldingen, Germany (49°13′05.8″N 8°02′47.2″E). All vineyards were treated with similar soil tillage, fertilization and plant protection (detailed plant protection schedule: Table S2, supplementary material). The experimental procedure was as follows: After cropping of the berries, berry skin resistance was instantly measured for each berry. Then, berries were placed on individually marked Petri dishes (∅ 5.5 cm) plated with water soaked cotton pads to avoid desiccation of flies. The perforation of the berry skin (caused by skin measurement device) was placed toward the cotton pad so that flies had no access to the wound. To control for spatial influence, we randomly placed the berries (on the individual marked Petri dishes) on a prepared coordinate system. Finally, 120 adult females and 30 adult males of *D. suzukii* were added to the cage with the berries for 12 h. After completion of the experiment, berries were checked for eggs under a stereo microscope (Stemi 2000, Carl Zeiss AG, Oberkochen, Germany) and TSS was measured for each berry with a digital refractometer in Brix (PAL-BX/ACID2, Atago CO., LTD, Tokyo, Japan) and converted in °Oechsle.

Drosophila suzukii flies were obtained from a laboratory rearing of the JKI in Dossenheim, Germany and originated from collection of wild specimen in the area of this research institute (49°26′57.6″N 8°38′21.7″E) during October 2013. We maintained the flies in rearing cages with mesh side panels (30 × 30 × 30 cm, Bugdorm-1, Megaview, Taiwan) with Drosophila cornmeal diet (1.2 L water, 25 g agar, 30 g wheat germ, 25 g corn meal, 25 g brewer's yeast, 22.5 g apple pulp, 50 g sugar, 2.5 g ascorbic acid, 2.5 g Wesson's salt, 1.125 g Vanderzant vitamin mixture, 0.75 g methyl-4-hydroxybenzoate, 0.75 g benzoic acid and 2 ml formaldehyde (3,7%)) as described in Bellutti et al. (2018). The climatic chamber was set to 23 °C, 75% relative humidity and a photoperiod of L16:D8 h.

Statistics We performed all analyses using the open source program R (R Core Team 2017). We used $n = 718$ berries to investigate the relationship between oviposition and berry skin resistance as well as TSS across 6 grapevine cultivars for 6 weeks around harvest. As oviposition data were not normally distributed, we $\log_{10}(X+1)$-transformed them. We fitted linear mixed models with cage as random factor and berry skin resistance and TSS as fixed factors using the nlme package (Pelton et al. 2017). Model robustness was checked with permutation tests using the pgirmess package (Giraudoux 2017).

For illustration, we divided berries into berry skin resistance classes (with the following class limits: 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0 and 1.1 N) and TSS classes, respectively (with the following class limits: 40°, 50°, 60°, 70°, 80°, 90°, 100° and 110° Oechsle), and graphically displayed the relationship between mean number of eggs per berry and the referring class for both parameters.

Results

Cultivar approach

Across the 13 grape cultivars, berry skin resistance as well as tartaric acidity had a significant effect on oviposition of *D. suzukii*, whereas TSS and volatile acidity had no effect on oviposition (Table 1). Oviposition decreased with increasing berry skin resistance and tartaric acidity (Fig. 1). However, comparison of the models on the basis of the BIC revealed that berry skin resistance explained oviposition distinctly better than chemical composition (Δ BIC > 24, Table 1). The effect of berry skin resistance on oviposition was also significant in five out of six sampling dates: Oviposition was significantly higher on cultivars with a low penetration resistance (soft skinned cultivars) than on cultivars with a high penetration resistance (Fig. 2).

Berry approach

At the individual berry level, berry skin resistance was again the best predictor of *D. suzukii* oviposition, with egg numbers increasing with decreasing berry skin resistance across six cultivars (lme: $n = 718$, $t = -6.82$, $p < 0.0001$). In contrast, TSS was not correlated with oviposition on berry level (lme: $n = 718$, $t = -0.85$, $p = 0.40$). Dividing the berries into classes of berry skin resistance and TSS, respectively, illustrates this relationship very clearly: Infestation decreases with increasing berry skin resistance class (Fig. 3A), whereas no such pattern was found for TSS (Fig. 3B).

Discussion

Both experiments suggest a major role of berry skin resistance for *D. suzukii* oviposition in grape vine. This is in line with previous research from different fruits. Ioriatti et al. (2015, for grapevine), Baser et al. (2018, for table grapes), Burrack et al. (2013, for blackberries, blueberries, raspberries and strawberries) and Kinjo et al. (2013, for blueberries) found similar results and conclude that berry skin resistance (or similar parameters like fruit firmness) is a major driver of host selection in *D. suzukii.*

Table 1 Effects of the tested berry parameters on *D. suzukii* oviposition across 13 grapevine cultivars: parameters of the linear mixed ‘models for $n = 75$ samples with calendar week as random factor

Berry parameter	*t* value	*p* value	BIC
Berry skin resistance	− 8.09	< 0.0001	84.7
TTS	− 1.13	0.26	139.6
Tartaric acid	− 5.69	< 0.0001	109.6
Volatile acid	− 0.19	0.85	131.2

Previous studies showed sugar parameters to be relevant for *D. suzukii* oviposition as well (Baser et al. 2018; Burrack et al. 2013; Ioriatti et al. 2015; Kinjo et al. 2013). However, these studies investigated oviposition during the grape ripening period, concluding that only ripe berries were affected. In contrast, our study compared oviposition between and not within different cultivars with their given berry parameters, and focused on fully ripe berries, all of which had a high albeit considerably differing sugar content (Fig. 1B). When given the choice between different grapevine cultivars within the same vineyard and between berries within a cage, the flies chose soft berries with low acidity, but did not distinguish between different sugar contents.

While berry skin resistance played a dominant role for *D. suzukii* oviposition in our study, other parameters can play a role in different environments and cultivars. Andreazza et al. (2016) investigated 18 vine genotypes in Brazil and found that berry skin resistance alone cannot account for differences in susceptibility. They concluded that chemical parameters must be important for *D. suzukii* oviposition. Moreover, various studies show pre-damaged grapes to be more susceptible to *D. suzukii* than intact berries (Grant and Sial 2016; Hoffman 2015; Ioriatti et al. 2015; Jarausch et al. 2017; Linder et al. 2014; Pelton et al. 2017). In fact, the vineyard studied here was pre-damaged by wasp feeding and by Powdery Mildew (*Erisiphe necator)* and we performed measurements beyond the harvest date including the transition from ripe to overripe (and decaying) grapes, thereby increasing infestation. Another vineyard of Dornfelder with a better general state of health located 2 km away from our study orchard showed low infestation levels at the same time. Thus, the results of our field survey may be specific to situations with pre-damaged berries. Further, factors like microbial contamination of clusters may be the final elicitors for egg laying (Hamby and Becher 2016). However, in the berry approach we included berries without any visible damages from healthy looking vineyards, suggesting an important role of berry skin resistance for *D. suzukii* oviposition independent of pre-damage.

For field surveys, factors unrelated to berry properties may be important for *D. suzukii* infestation as they influence the presence of the fly in the environment. *D. suzukii* was shown to be temperature and humidity dependent (Kinjo et al. 2014; Kraus et al. 2018; Tochen et al. 2014, 2016) and seasonal conditions consequently influence population densities, e.g., mild winters were related to high population densities in Germany in 2014 (Asplen et al. 2015). Moreover, wild hosts and adjacent natural habitats were hypothesized to affect *D. suzukii* population density and thereby to also affect infestation rates (Arnó et al. 2016; Diepenbrock et al. 2016; Elsensohn and Loeb 2018; Kenis et al. 2016; Pelton

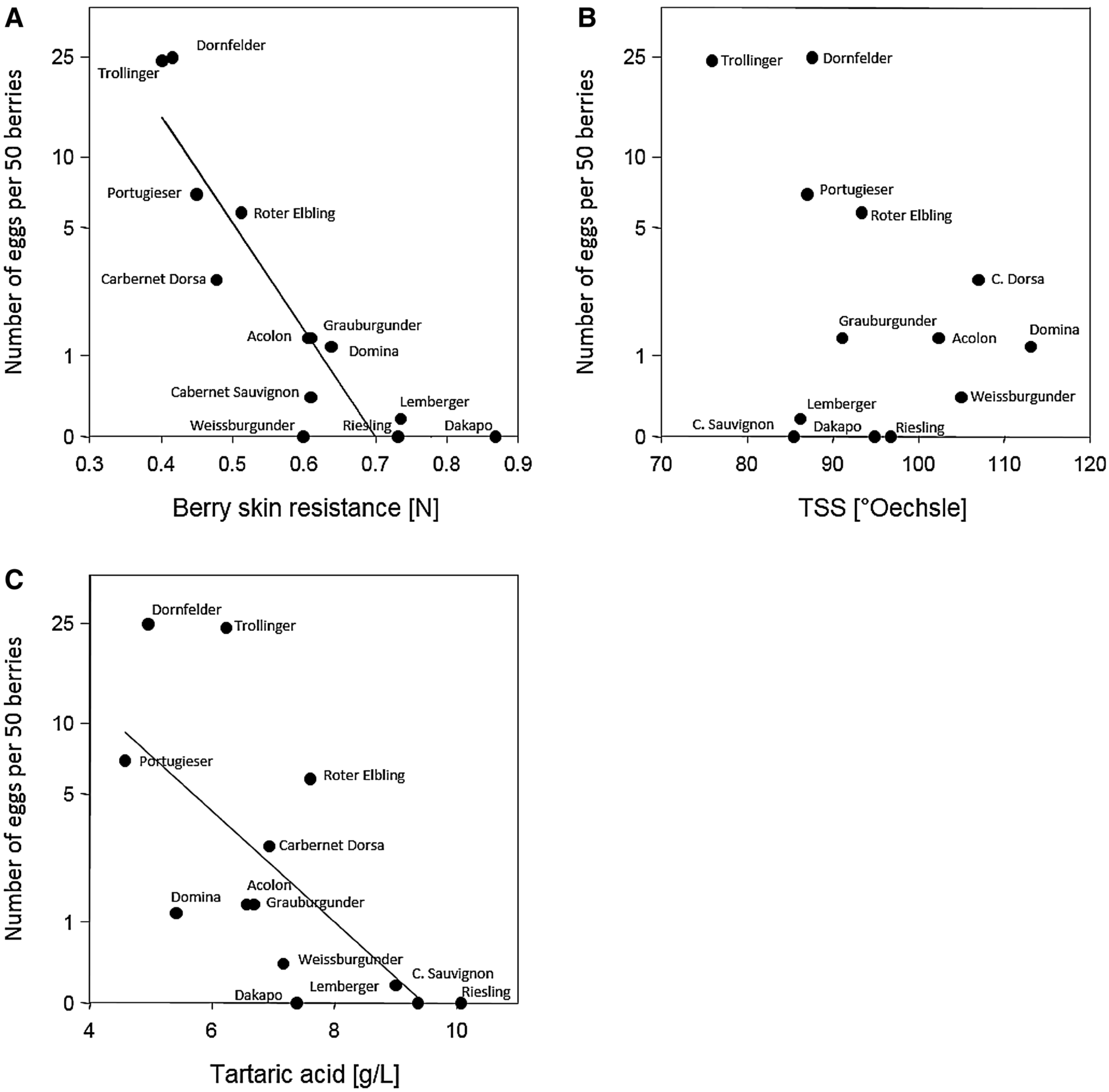

Fig. 1 Relationship between oviposition of *D. suzukii* and berry skin resistance (**A**), TSS (**B**) and tartaric acid (**C**) across 13 grapevine cultivars. Oviposition and berry parameter data were averaged across sampling dates. Oviposition decreased with increasing berry skin resistance (**A**; $n=13$, $t=-5.69$, $p=0.0001$) and tartaric acid (**C**; $n=13$, $t=-3.06$, $p=0.01$), but showed no significant relationship with TSS (**B**; $n=13$, $t=-1.51$, $p=0.16$). The international terms for the non-endemic cultivars are: Grauburgunder = Pinot gris; Trollinger = Vernatsch, Schiava; Weissburgunder = Pinot blanc; Lemberger = Blauer Limberger

et al. 2016; Wang et al. 2016). However, these additional factors were comparable across all cultivars in our field experiment and excluded in our laboratory approach. Thus, our results are independent of such possible confounding factors.

The cultivar approach revealed considerable differences in susceptibility between the investigated 13 cultivars (Figs. 1, 2). These correspond well with earlier observations and observations from other regions. In 2014, when serious damages associated with *D. suzukii* occurred in South West Germany, Trollinger and Dornfelder were the varieties for which the highest oviposition (up to 70% and 95% of berries) was found (C. Hoffmann, JKI Siebeldingen, Germany; unpublished data). These cultivars were the most susceptible in our study as well. Large-scale monitoring of *D. suzukii* oviposition in Baden-Württemberg from 2014 to 2015 (Staatliches Weinbauinstitut (WBI) Freiburg,

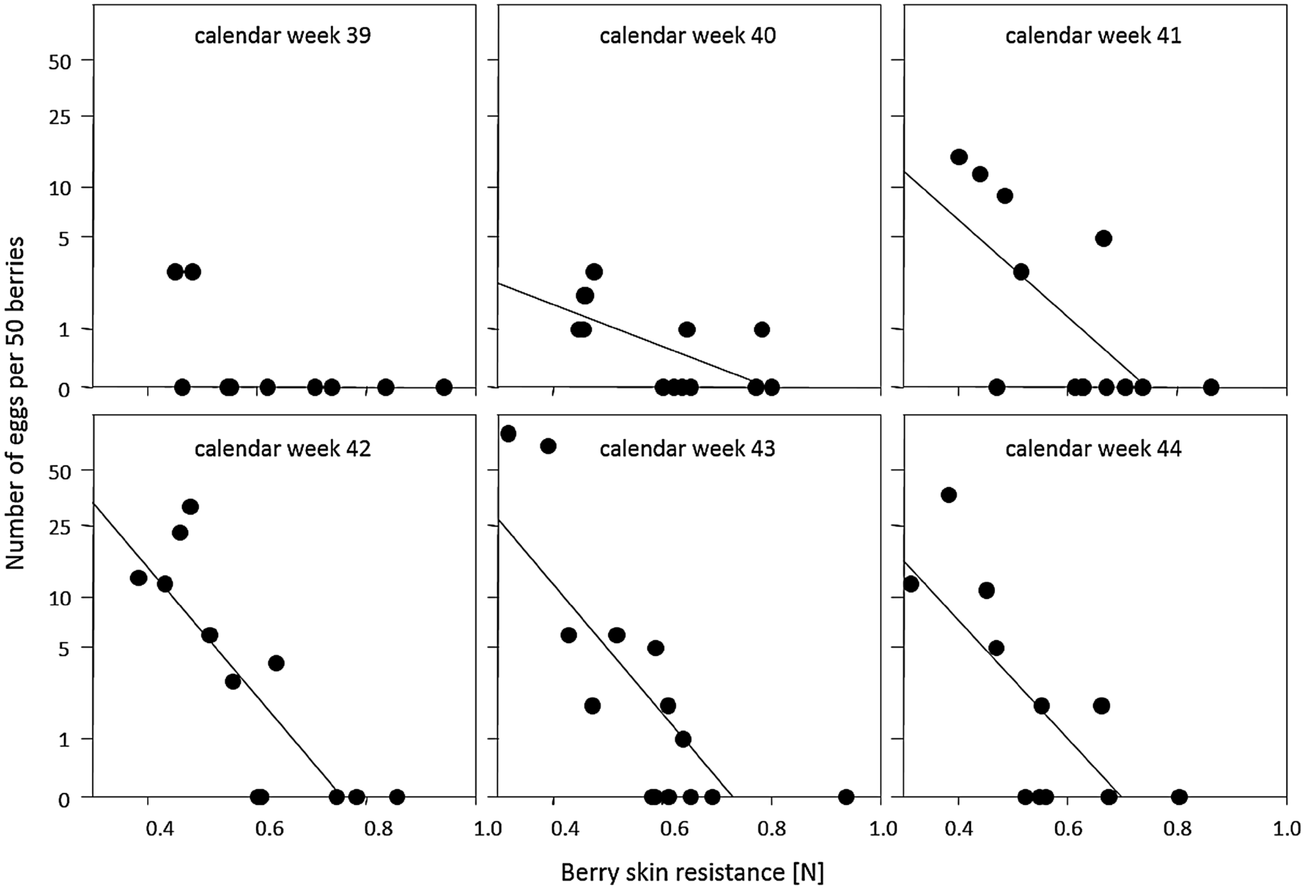

Fig. 2 Relationship of oviposition of *D. suzukii* and berry skin resistance across 13 grapevine cultivars at six different sampling dates. Oviposition decreased significantly with increasing berry skin resistance at five of the sampling dates (calendar week 39 ($p=0.12$, $t=-1.75$, $n=13$), 40 ($p=0.01$, $t=-2.90$, $n=13$), 41 ($p=0.01$, $t=-3.09$, $n=13$), 42 ($p=0.0009$, $t=-4.52$, $n=13$), 43 ($p=0.002$, $t=-4.06$, $n=13$) and 44 ($p=0.003$, $t=-3.88$, $n=13$))

Germany; unpublished data) identified Acolon, Cabernet Dorsa, Dornfelder, Portugieser and Trollinger as especially susceptible, whereas Grauburgunder, Weissburgunder and Riesling had little or no oviposition in the investigated vineyards, which largely accords with our data. Out of the 13 cultivars we investigated, the Swiss monitoring of *D. suzukii* oviposition (Kehrli et al. 2017) classified Dornfelder, Cabernet Dorsa and Acolon as highly susceptible, whereas Dakapo has no high oviposition risk, which is again in accordance with our data. Thus, the ranking that we identified seems to be also relevant in other regions. However, as strong infestation occurs only in certain years, there may be factors like pathogens or other damages of the berry skin that facilitate oviposition in those years. Hence, the preservation of the health of the berry skin might play an important role for avoiding *D. suzukii* oviposition. Integrated control strategies like timing of fertilization and soil tillage, efficient powdery mildew control and canopy management could indirectly influence berry skin resistance and thereby *D. suzukii* oviposition.

Our findings emphasize the role of berry skin as a physical barrier against *D. suzukii* infestation. Hence, this character should be considered for the breeding of cultivars with increased berry skin resistance. In fact, recent research (Hecht, A., JKI Siebeldingen, Germany; unpublished data) focuses on the genomic investigation of cross-bred populations with respect to berry skin resistance and thickness. The aim of such studies is the identification of the loci of these traits and the subsequent development of markers that allow for selection of genotypes with high berry skin resistance. Furthermore, berry skin resistance can be used as an indicator for general infestation risk. Although there was no clear threshold value where oviposition of *D. suzukii* begins, the probability of oviposition in general clearly decreased with increasing berry skin resistance. Thus, sensible cultivars for which frequent egg monitoring is recommended can be identified. Generally, the preservation of a firm, intact berry skin, is a key aspect to avoid *Drosophila suzukii* damage.

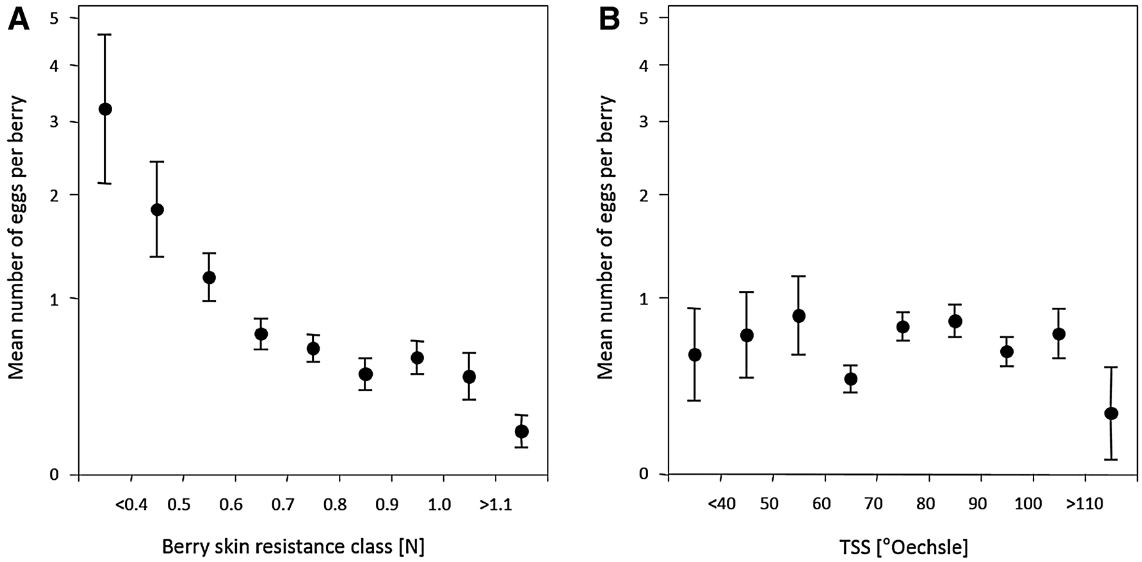

Fig. 3 **A** Decrease of *D. suzukii* oviposition with increasing berry skin resistance (lme: $n=718$, $t=-6.82$, $p<0.0001$) and **B** relationship between *D. suzukii* oviposition and TSS (lme: $n=718$, $t=-0.85$, $p=0.40$) both assessed under controlled laboratory conditions at the level of $n=718$ single berries. For illustration, berries were divided into berry skin resistance classes (**A**) and TSS classes (**B**): Oviposition is calculated as the average number of eggs of the berries of the referring class and is given with standard error

Author Contribution Statement

CH and BJ conceived and designed the field survey (cultivar approach). WE conceived and designed the laboratory choice experiment (single berry approach). GM and CH conducted the field survey. SA conducted the laboratory choice experiment. WE analyzed data and wrote the manuscript. WE and CH edited and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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