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# Potato varietal susceptibility to wireworms: feeding behaviour, fitness and semiochemical-based host selection

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## ABSTRACT

Wireworms (Agriotes sp.) represent a significant global threat in agriculture as soil-dwelling insect pests. Previous field observations have indicated varying susceptibilities of different potato varieties to wireworm attacks. In this laboratory study, we used three potato varieties known for displaying contrasted levels of susceptibility: Monalisa (high), Spunta (moderate) and Charlotte (low). We tested two groups of hypotheses: (1) wireworms display higher feeding activities when fed on a susceptible variety, which is also linked to faster larval development; (2) the most susceptible varieties are also the most attractive for wireworms, which can be explained by differences in their emissions of volatile organic compounds (VOCs), that guide larval foraging behaviour. Based on the results of our bioassays, we confirm our first hypothesis: wireworms feeding activity was higher on Monalisa tuber (i.e. longer galleries, lower weight gain of tubers), and these wireworms gained more weight and size than those that fed on the Charlotte variety, after 50 weeks of feeding. Based on our behavioural assays, we found that wireworms exhibit greater attraction towards Spunta tubers as opposed to those of Monalisa and Charlotte. The volatile collection analyses reveal a complex blend of 63 VOCs from potato tubers but do not suggest significant differences across the three varieties. The volatile profiles were however different between the two tuber phenological stages considered here. This study provides insights into the mechanisms of host detection and selection by wireworms.

## KEYWORDS

Elateridae, varietal selection, life history traits, GC-MS, chemical ecology

## INTRODUCTION

Wireworms, which are the larval stage of click beetles (Coleoptera: Elateridae), are polyphagous insect pests that cause significant damages to a wide range of plants, resulting in significant agricultural losses. They feed upon seeds and the underground parts of their hosts (Testa & Rusinek, 2021). Wireworm populations have been controlled using various plant protection chemicals as seed dressings, in combination with various tillage methods (Parker and Howard, 2001). However, non-specific insecticides have been progressively banned due to their high potential risks to the environment and human health (Gunasekara et al. 2007). At present, the lack of effective management methods could lead to an increase in attacks and economic losses associated with these insect pests. Various alternative methods have been applied to reduce click beetle and wireworm populations such as pheromone trapping, soil amendment with natural insecticides, repeated soil work, crop rotation or the use of resistant varieties (Poggi et al. 2021). Among these strategies, luring wireworms away from the crop during the host susceptibility period could be a promising and cost-effective specific sustainable solution.

Understanding the foraging and feeding preferences of wireworms could open new approaches to develop new effective integrated pest management (IPM) strategies. Like most belowground insects, wireworms use a diversity of olfactory cues to locate and select their host. Gradients of carbon dioxide indicate the presence of a potential food source (Johnson et al. 2012). After approaching the $CO_2$ emitter, the larva uses volatile organic compounds released by the plant in the rhizosphere to select a specific host (Barsics et al. 2014). Finally, the larva bites and tastes the root organs, and decides to stayi or leave based on the plant macromolecules, such as carbohydrates, lipids and proteins, present in the belowground tissues of potential host plants (Barsics et al. 2014).

Potato farming (*Solanum tuberosum*) is highly impacted by wireworms (Jansson and Seal 1994). In northern Europe, *Agriotes lineatus*, *Agriotes obscurus* and *Agriotes sputator* cause serious economic damages in agriculture (Vernon and Herk, 2022). Various studies have highlighted the preferences of wireworms for certain potato varieties regarding tuber injuries (Fasulati et al. 2019; Johnson et al. 2008; Jonasson & Olsson, 1994). The resistance of some varieties has been consistently associated with high levels of glycoalkaloid contents (α-solanine and α-chaconine) (Jonasson & Olsson 1994). In this study, we test the hypothesis that differences in damage levels observed in the field among different varieties of potato are associated with (i) their palatability and impact on larval development and/or (ii) their ability to attract larvae. We used three varieties that exhibited contrasting levels of wireworm attacks in the field: "Charlotte" (low susceptibility), "Spunta" (medium susceptibility) and "Monalisa" (hight susceptibility). These susceptibility levels were determined based on a survey of wireworm damages conducted among French farmers by Arvalis Institute over several years (unpublished data, Taupic project, 2020). The level of wireworm damages on each potato variety under controlled laboratory conditions was estimated. For each variety the palatability (over 15 days) and effect on wireworm life history traits (larval development) were estimated over a fifty-week period (replicates details in supplementary data). Then, the wireworms' attractiveness to each variety was assessed using dual-choice bioassays, and the volatile organic compounds released by the tubers (at two different physiological growing stages) were identified and quantified using dynamic volatile collection followed by gas chromatography.

## MATERIALS AND METHODS

**Wireworms and potatoes -** Insects were collected in spring 2022 by manual collection from two locations in Belgium: Gedinne (49.937727, 4.942047) and Gembloux (45.725833, 4.666111). The collection sites were chosen based on their organic cultivation history (maize and wheat) of at least two years. Species identification was carried out prior to behavioural tests

by molecular analysis in the ILVO institute (Dr Johan Witters) on a sample of 40 individuals from each collection site. Wireworms were identified as belonging to the species *Agriotes obscurus* and *A. lineatus* in both collection site. Thus, in all the tests carried out (2022-2023), a mixture of these two species from each collection site was used. The larvae were separated by development stage, and up to 10 individuals were placed in rearing boxes (500 ml – 11 × 11 × 6 cm) to reduce cannibalism. They were maintained in a soil-vermiculite mixture (1:1 v:v) at 65% water holding capacity (WHC) at room temperature (21 ± 1°C) and fed with germinating barley and wheat *ad libitum*. Prior to each behavioural test, larvae in stages L3-L8 were individually starved for 4-7 days in plastic boxes (5.8 × 4.4 × 4.5 cm) filled with vermiculite moistened at 65% WHC. To avoid physiological bias, larvae showing pre-moult (white transverse lines), moult or post-moult marks (white larvae) were systematically excluded from the bioassays, because their feeding activity is low during the moulting process, as noted by Furlan (2004).

Potato tubers of the Charlotte, Spunta and Monalisa varieties were collected from an open field organic culture in Britany region (France) in 2021, at tuber phenological stages BBCH 407 and BBCH 409 (Nemes et al. 2008). Potato tubers were gently washed with tap water and unpeeled in all experiments. The wash of tubers helped to prevent any potential side effects from soil odours.

**Feeding activity -** Wireworms feeding behaviour was evaluated for each potato variety using plastic boxes (500ml – 11 × 11 × 6 cm) sealed with a pierced lid and containing 50g of humidified vermiculite (65% WHC). In each box, one wireworm was placed in presence of one potato tuber (Organic certification, size 25). A total of 17 replicates per variety were performed, alongside 5 controls per variety (one potato tuber without wireworm). The bioassays were performed in the dark at 21±1°C. After fifteen days, wireworms located inside tubers were gently removed, and tuber injuries were measured as the number of bites and the number and

size of galleries. Wireworms and potato tubers were weighted at the beginning (day 0) and at the end (day 15) of the bioassay.

**Life history traits -** Wireworms (L1-L4 instars, Poidatz 2015) were individually placed in plastic boxes (500ml – 11 × 11 × 6 cm) with a pierced lid containing 50g of humidified vermiculite (65% WHC). They were allowed to feed on one potato variety for one year (one tuber, Organic certification, size 25). The vermiculite substrate was humidified every week and replaced once a month, while the tuber was replaced twice a month. The experiment was conducted in darkness and constant temperature (21±1°C) in a climate-controlled room. The body size (mm) and weight (mg) were measured every fifteen days for the first 6 months, then once a month for another 6 months.

**Dual-choice bioassays -** The attractiveness of potato tubers of each variety was assessed using a two-branch olfactometer (Barsics et al., 2014). It consisted of a glass tube (20 cm long, 3.2 cm internal diameter) filled with lightly packed humidified vermiculite (65% WHC). A central inlet (wide neck GL14) was used as the larval entry point, and the two extremities of the olfactometer were opened to allow connexion with two 500ml borosilicate jars (Duran, Belgium) on one lateral wide neck (GL45). In each jar, 100±1 g of potato tubers of Monalisa, Spunta, or Charlotte variety (Organic certification, size 25, washed and unpeeled) were introduced. The jars were then filled with lightly packed vermiculite humidified at 65% WHC, before being hermetically sealed and stored in total darkness at room temperature (21±1°C) for 48 hours to allow odours to diffuse. After this diffusion time, the lateral lid of the jar (GL45) was removed, and the inlet was covered with fine mesh (8 × 8 cm) to prevent wireworms from accessing the potato tubers. The inlet was then sealed with an apertured GL45 cap. Two jars were randomly connected (Spunta vs Monalisa, Monalisa vs Charlotte and Spunta vs Charlotte) to the two side openings of the olfactometer, and odours were allowed to diffuse for 30 minutes. A single wireworm was then introduced inside the olfactometer through its central opening.

The set up was darkened in a room regulated at 21°C, and the wireworm was given one hour to make a choice. At the end of the experiment, the larva position was recorded. Wireworms located at 3cm from the entry point were recorded as non-responding. The experiment involved 19 olfactometers running simultaneously, was repeated over a period of three days, with 4 sessions per day. Two technical repetitions were performed with five-month delay.

**Volatiles organic compounds produced by potato tubers -** Tubers were washed with tap water, air-dried overnight on the laboratory bench, and stored in the dark at +4°C. On the evening before each odour sampling day, the tubers were placed in the dark at room temperature. To sample the volatile organic compounds (VOCs), two tubers were placed in a 1L airtight glass chamber. After 2 hours of equilibration, the headspace air present in the glass chamber was sampled dynamically in the dark at ambient temperature (21±1°C). A flow of activated carbon filtered air (200 ml/min) was generated through a GilAir™ Plus suction pump (Gilian®, West Caldwell, USA) and VOCs were trapped on a hydrophobic TenaxTa/Carbograph tube (Markes International®, Llantrisant, UK) for a six-hour period. After sampling, a standard solution containing chlorobenzene (25ng, Sigma-Aldrich, USA) and longifolene (50ng, Sigma-Aldrich, USA) as internal standards were injected in each tube before being hermetically sealed and stored at +4°C. A control sample (empty glass chamber) was performed under the same conditions for each sampling day. At least one sample of each variety was taken for every sampling day. Four and five replicates were carried out for each variety at development stage 1 (BBCH 407) and 2 (BBCH 409), respectively. After each sampling, the tubers were peeled uniformly, and the peelings were dried (72 hours at 50°C) and weighed.

To analyse the VOCs samples we used a gas chromatograph (model Nexis GC-2030; Shimadzu®, Kyoto, Japan) coupled to a mass spectrometer (model QP2020 NX; Shimadzu®, Kyoto, Japan), with a thermodesorption injection on a TD30R module (Shimadzu®, Kyoto, Japan). Samples were desorbed at 280 °C for 8 minutes under a constant flow of carrier gas at

60 mL/min. The volatiles were recollected in a cryotrap set at -30 °C, then heated to 280 °C for 5 min before being separated on a capillary column (HP-5MS, 30m × 0.25mm ID, thickness 0.5µm; Agilent Technologies, Santa Clara, CA, USA) with helium as carrier gas set at a flow rate of 0.94 mL/min. A split ratio of 5 was set to optimise the analysis. The temperature program was identical for all samples: 40 °C for 3 min; 5 °C/min to 200 °C; 20 °C/min to 300 °C; and 300°C for 6 min to purge the column. The mass spectra were recorded in Electron Ionisation (EI) mode at 100 eV with a scanned mass ranged from 35 to 300 amu. Compound identification was carried out through comparison with reference mass spectrum databases (NIST17 and FFNSC3). Also, the injection of a C7-C30 saturated alkanes standard solution (25ng/µl, Sigma-Aldrich, USA) under the same chromatographic conditions allowed to calculate Kovats retention indices (RI). These RI were compared to those available in the literature to confirm identification. Only peaks above the limit of detection were considered. The VOC quantities were estimated by comparing surface area of peak of interest to those from internal standards. These estimated VOC quantities were then adjusted to the peeling dry weight, which is representative of the emission surface of each tuber.

**Statistical analyses -** All statistical analyses were performed with R (V 4.2.1). Regarding the feeding bioassays, the differences between the initial weight (iw) and final weight (fw) of wireworms and potato tubers, as well as the size of galleries (summed) in a same potato tuber were registered. If the conditions allowed it, a Kruskal-Wallis or an analysis of variance (ANOVA) and TukeyHSD were performed to assess how varieties impacted on the variation of weight of wireworms and on the size of galleries. Similarly, to test the impact of varieties on the injuries caused by wireworms, differences of weight of potatoes were determined by Mann-Whitney-Wilcoxon test (package “vegan”). For the analyse of the variation of wireworm weight, one out-layer was removed. Graphs were realised with “ggplot2”. Then, the effect of the different potato varieties on wireworms’ fitness (weight and size) over a 50-week period

was evaluated using general linear mixed effects models (glmer, package “emmeans”, “lme4”, “multcomp”). Two models were calculated with weight and size as response variables. Each model was calculated with the interaction of potato variety and days as fixed factor. Individuals were included as random factors to account for the individual variability among all weeks of measurements. Pairwise contrasts of slopes were made using the “emtrends” function. A binomial general linear mixed model (GLMM) was fitted to assess whether attraction or rejection was observed in wireworm for one or another potato variety during the dual-choice bioassays. The models were calculated with the number of choices for one variety as response variable and the intercept as the fix effect. The possible impact of test date on insect choice was tested by including it as a random factor in the models (R packages “lme4” and “glmertree”). Finally, to compare the VOC profiles between the tubers of the two development stages and the three varieties, PermManova (Permutational Multivariate Analysis of Variance) were carried out using Euclidean distance matrices and 999 permutations ("adonis" function of the "vegan" R package), after verification of the application conditions. Principal Component Analyses (PCA) were performed on the same data (R package "FactoMineR", “factoextra”) to obtain a graphical representation. For each compound of interest, univariate analyses (ANOVA when the application conditions were met, Kruskal-Wallis test if not) were carried out to compare the emitted amounts between the three varieties, at a given development stage.

The number of replicates in each experiment is provided in Table 2 (Supplementary data).

## RESULTS

**Feeding activity** - Injuries caused by wireworms were measured by the sizes of galleries in potato tubers (Figure 1), which were significantly different between varieties ($F_{2,65} = 8.51$, $P < 0.001$). Wireworms created significantly longer galleries in Monalisa tubers than in the two other varieties (Tukey’s HSD test, “Monalisa vs Charlotte”: $P < 0.001$; “Monalisa vs Spunta”: $P = 0.007$; Figure 1). Over the 15-day bioassay, most potato tubers gained weight, ranging from

0.02 to 3.20 grams (Figure 2). Some tubers from Monalisa (n = 6) and Spunta (n = 4) varieties lost weight. The median weight gain of the controls and tubers exposed to wireworms did not differ significantly for the Charlotte variety (W = 67, P = 0.362). Tubers exposed to wireworms gained significantly less weight than those without wireworms for Spunta (W = 91, P = 0.048) and Monalisa (W = 106, p = 0.002) varieties (Figure 2).

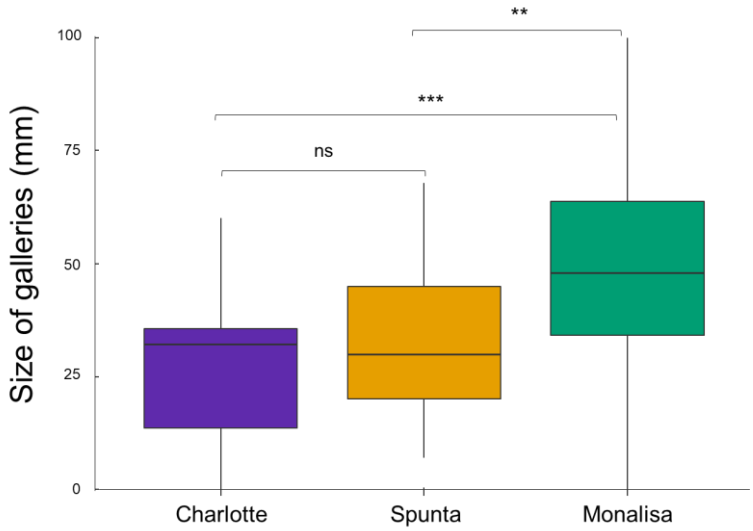


**Fig. 1.** Total size sum of the galleries in each of the potato varieties after no-choice test (n=23). Differences are designated by asterisks (*** = p<0.001; ** = p<0.01; * = p<0.05; ns= not significative differences) and were determined by Tukey's HSD

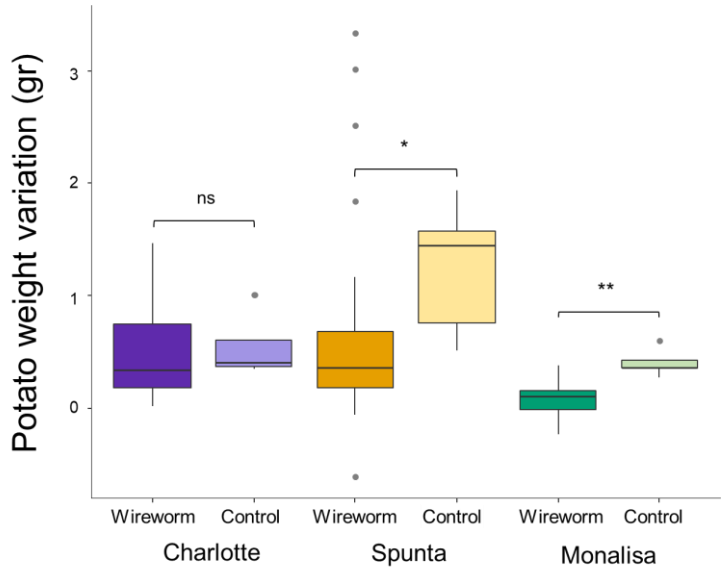


**Fig. 2.** Variation in the weight of potato for each variety after no-choice test (Charlotte n=21, Spunta and Monalisa n=23, Control n=5). Out layers are represented by dots. Differences are designated by asterisks (** = p<0.01; * = p<0.05; ns= not significative

**Life history traits -** All wireworms gained weight and grew during the bioassay (Figure 3A and B). As time passed, the variety on which wireworms fed induced significant differences in weight ($P < 0.001$, Figure 3A) and size ($P < 0.001$, Table 1, Figure 3B). Wireworms that fed on Monalisa gained significantly more weight ($P = 0.038$) and size ($P = 0.009$) than those that fed on Charlotte. Wireworms that fed on Spunta variety did not exhibit significant differences in weight and growth over time when compared to those exposed to Monalisa (weight: $P = 0.901$; size: $P = 0.290$) and Charlotte (weight: $P = 0.081$; size: $P = 0.226$).

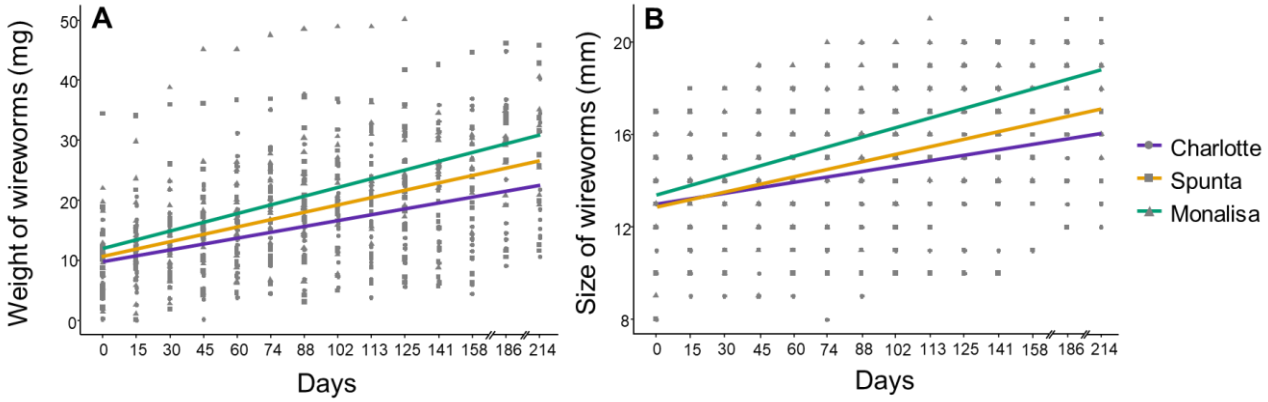


**Fig. 3.** Weight **(A)** and size **(B)** variations of wireworm feeding on three potato varieties: Charlotte, Spunta and Monalisa.

**Table 1.** Summary statistics from the lmer model run on weight and size of wireworms during the life history traits bioassays.

| | Weight (mg) | | Size (mm) | |
|---|---|---|---|---|
| *Predictors* | *Est.* | *CI* | *Est.* | *CI* |
| Intercept | 0.01 | 0.01 - 0.01 | 13.01 | 12.34 - 13.69 |
| Variety [Charlotte] * Time | 0.00 | 0.00 - 0.00 | 0.25 | 0.17 - 0.33 |
| Variety [Monalisa] * Time | 0.00 | 0.00 - 0.00 | 0.43 | 0.34 - 0.52 |
| Variety [Spunta] * Time | 0.00 | 0.00 - 0.00 | 0.34 | 0.26 - 0.42 |
| Marginal $R^2$ /Conditional $R^2$ | 0.408 / 0.904 | | 0.331 / 0.886 | |
| | *df* | *χ2* | *P* | *df* | *χ2* | *P* |
| Variety:Time | 2 | 7.729 | **< 0.001** | 2 | 6.137 | **< 0.001** |

**Dual-choice bioassays –** Over sixty percent of the tested wireworms had made a choice during the behavioural assays. The results were statistically similar for both technical replicates ("Spunta *vs* Charlotte", Z-ratio = 0.324, P = 0.746; "Charlotte *vs* Monalisa", Z-ratio = 0.443, P = 0.658), except for the dual choice test "Spunta *vs* Monalisa" (Z-ratio = 4.229, P = 2.34e-05). These data are thus presented separately in Figure 4. Wireworms were significantly more attracted towards Spunta tubers compared to Charlotte and Monalisa varieties ("Spunta *vs* Charlotte": $\chi 2 = 4$, df = 1, P = 0.045; "Spunta *vs* Monalisa": first technical replicate $\chi 2 = 4.545$, df = 1, P = 0.033; second technical replicate $\chi 2 = 18$, df = 1, P < 0.001; Figure 4). Monalisa and Charlotte tubers were equally attractive for wireworms ($\chi 2 = 0.320$, df = 1, P = 0.572; Figure 4).

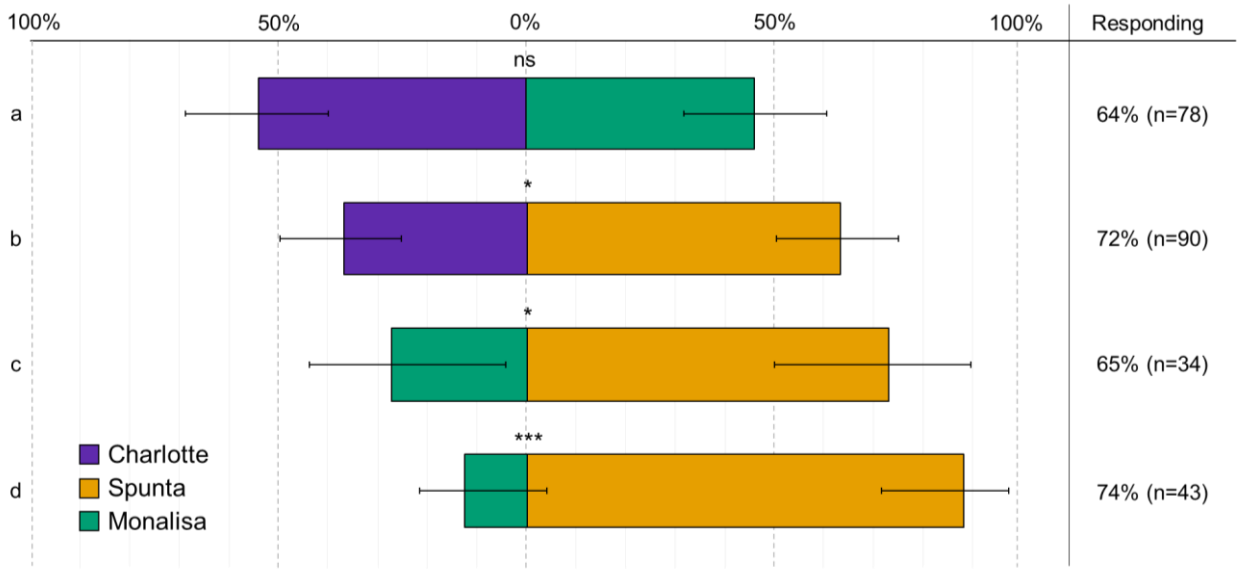


**Fig. 4.** Percentage of wireworms reaching one side of the olfactometer connected to the couple of varieties "Charlotte vs Monalisa" **(a)** and "Charlotte vs Spunta" **(b)** for all technical replicates, "Monalisa vs Spunta" for the first **(c)** and the second **(d)** technical replicate. Differences are designated by asterisks (*** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significative differences) and were determined by chi-square test. The confidence intervals were estimated following a binomial calculation.

**Volatiles organic compounds produced by potato tubers -** Analysis of potato tuber volatile emissions revealed a complex blend of 63 VOCs (Table 3, Supplementary data). The PermManova analysis showed that the developmental stage of the tuber influenced the volatile profiles ($F_{1,22}$ = 13.93; P < 0.001), while the variety did not have any significant effect ($F_{2,22}$ = 1.02; P = 0.406) (Figure 5). Physiological stage 1 of potato tubers (1.06 ± 0.04 g of dry peel per tuber) emitted less diversified VOC profile (45 identified compounds) than physiological stage 2 (1.97 ± 0.07 g of dry peel per tuber) which was characterised by 63 identified compounds. No qualitative differences were observed among the three varieties (all VOCs were emitted by all varieties). As stage 2 tubers are more susceptible to wireworms' attacks, further analysis was conducted only on this stage. A PermManova performed on this subsample did not identify a significant difference between varietal odour profiles but showed higher differentiation than when the dataset gathers the two developmental stages ($F_{2,15}$ = 1.601; P = 0.105). Focusing on the most emitted compounds (peaks with relative areas above 1% of the total emissions), we observe that the quantities of VOCs emitted by the varieties differed: Charlotte tubers emitted lower amounts of 2-undecanone (0.58 ± 0.17 gr of dry peel) and benzaldehyde (2.73 ± 0.07 ng/gr of dry peel) compared to Monalisa tubers (7.71 ± 3.16 ng/gr of dry peel; 7.78 ± 1.46 ng/gr of dry peel; respectively) (Kruskal-Wallis, 2-undecanone: $\chi2$ = 9.131, df = 2, P = 0.01; benzaldehyde: $\chi2$ = 11.11, df = 2, P = 0.003). Monalisa tubers emitted higher amounts of 6-methyl-5-hepten-2-one and 2-butoxyethanol (5.35 ± 1.74 ng/gr of dry peel; 5.12 ± 1.41 ng/gr of dry peel; respectively) compared to the other two varieties (Kruskal-Wallis, 6-methyl-5-hepten-2-one: $\chi2$ = 8.024, df = 2, P = 0.018; 2-butoxyethanol : $\chi2$ = 9.309, df = 2, P = 0.009). Finally, Charlotte tubers emitted higher amounts of Nonadecane (2.06 ± 0.24 ng/gr of dry peel; $F_{2,13}$ = 7.84; P < 0.01) compared to the two other varieties (Tukey's HSD test, "Monalisa vs Charlotte": P < 0.01; "Spunta vs Charlotte": P = 0.02).

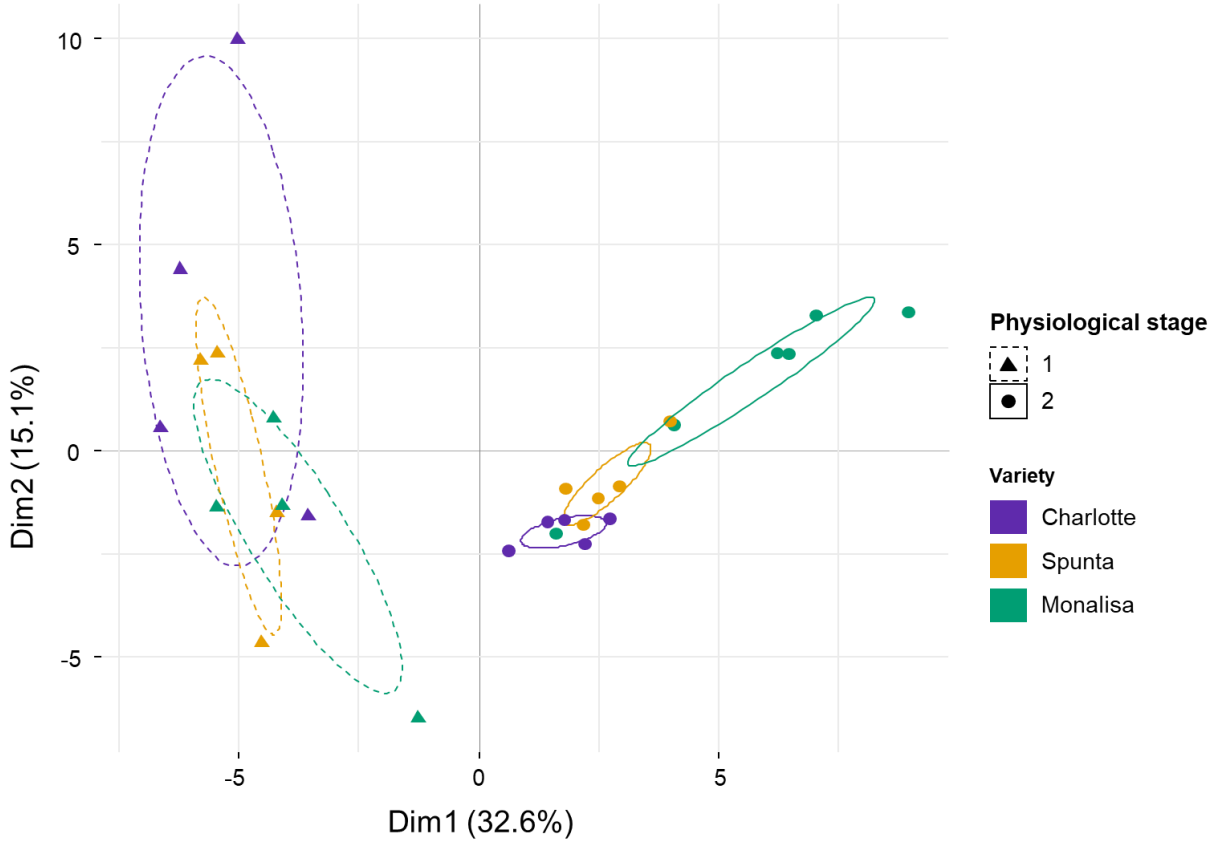


**Fig. 5.** Principal component analysis (PCA) performed on the VOC profiles of tubers of the three potato varieties at two stages of development.

## DISCUSSION

In this laboratory study, we have raised two hypotheses, one of which being confirmed, the other one disconfirmed. Based on the results of our bioassays, we confirm previous field observation that wireworms feeding activity is higher on Monalisa tuber. Wireworms produced longer galleries on the tuber of this variety compared to Spunta and Charlotte varieties. Monalisa and Spunta tubers also gained less weight in presence than in absence of wireworms. This behavioural observation can easily be linked with the wireworms' life history traits recorded after one year of feeding activity on the three varieties: on Monalisa, wireworms gained more weight and size than those that fed on the Charlotte variety. On the other hand, we must disconfirm the hypothesis that wireworms are more attracted by the odours of Monalisa tubers than the odours of the other varieties. Based on our behavioural assays, we found that

wireworms exhibit greater attraction towards Spunta tubers as opposed to those of Monalisa and Charlotte. The volatile collection analyses could not highlight significant difference in the odour profile of the three varieties (except for some compounds).

According to the optimal foraging theory, insects adopt foraging strategies that maximize their fitness, providing them with the most energy benefit for the lowest cost, maximizing the net energy gained. Wireworms were found to dig larger galleries on Monalisa compared to the other two varieties. Wireworm development was significantly better on that variety, with larvae feeding on Monalisa being heavier and developing faster. These results confirm the field observation suggesting Monalisa being more susceptible to wireworms' damage. Wireworms can distinguish odours and tastes via peg organs, located on the galeae, labial and maxillary palps which lead to orientation toward the host and biting (Crombie & Darrah, 1947). Phagostimulant molecules perceived during a bite could somehow give them information about the nutritional qualities of the vegetal consumed. Belowground phytophagous insects' growth is constantly challenged by the high energy requirements needed to move in the matrix, low nutritional values of roots or defensive secondary metabolites (Altesor et al. 2014, Erb et al. 2013). The host plant quality is then assessed by their contents in primary metabolites (fatty acids, amino acids, and carbohydrates; Erb et al. 2013, Friend 1958). Sugars (poly- and monosaccharides) are known to be main phagostimulants for a large variety of phytophagous insects (Erb et al. 2013). Previous studies have shown that simple sugars are involved in the mechanisms inducing the biting behaviour of wireworms (Crombie & Darrah, 1947). Quantification of these monosaccharides carried out in various studies on Charlotte, Spunta and Monalisa varieties showed differences in values (Amrein et al., 2003; Vivanti et al., 2006; Yang et al., 2016; work in progress at inov3PT/FN3PT in the framework of the TAUPIC project). Despite differences in protocol, year of sampling and tuber origins, these studies revealed a varietal pattern in monosaccharide contents. Monalisa being the variety that would present the

highest levels of glucose, fructose and sucrose followed by Spunta variety. Charlotte tubers always containing the lower amounts of these sugars. The developmental difference could reflect either higher consumption of Monalisa tubers, better nutritional contents in Monalisa tubers, or a combination of both. Our results associated with the literature support the idea of the ability of wireworms to choose between various food sources, considering their taste in association with nutritional values. Indeed, phytophagous insects need monosaccharides for their larval development (Friend 1958). Thus, varieties with higher monosaccharide contents would be more susceptible to wireworm attacks, which would be in line with laboratory studies showing wireworms' preference for sucrose over other substances (Thorpe et al. 1947).

The concentration of plant secondary metabolites may explain wireworms feeding preference for some potato varieties. Glycoalkaloids and polyphenols are known to be effective in protecting a plant from insect feeding (Altesor et al. 2014; Erb et al. 2013). In addition, the analysis of the content of thirteen polyphenols considered beneficial to human health (Deußer et al. 2012; Scalbert et al. 2005) showed that of the seventeen varieties studied, Charlotte had the lowest polyphenols peel content, twice lower than Monalisa and Spunta. Deußer et al. (2012) found larger amounts of α-solanine and α-chaconine in Charlotte and Spunta than in Monalisa, data that were later confirmed in France on the same varieties (Ngala et al. 2023; GEVES organism, unpublished data). However, polyphenols appear to be more concentrated in Monalisa and Spunta than in Charlotte (Deußer et al., 2012; Scalbert et al., 2005). Glycoalkaloids and/or polyphenols contents in potato tubers could be part of the interpretation of the wireworm responses observed in our feeding bioassays. As future directions, we suggest quantifying other macro- and micronutriments necessary for insect development (like fatty acids and amino acids) in susceptible and tolerant varieties.

Efficiently locating food sources is essential for maximizing energy intake in the optimal foraging theory. If the implication of VOCs in host plant selection by wireworms has been

demonstrated before (Johnson et al. 2012, Barsics et al. 2014), only a few molecules released by plant roots have been demonstrated for their role in wireworms' orientation behaviour. They include 2-pentylfuran (Barsics et al. 2012; La Forgia et al. 2023) and a blend of four aldehydes, namely hexanal, (*E*)-hex-2-enal, (*E*)-non-2-enal and (*E*,*Z*)-nona-2,6-dienal (Gfeller et al. 2013, Barsics et al. 2017; La Forgia et al. (2020). Varieties of the same plant species may differ in their root volatile emissions, as confirmed by La Forgia et al. (2020) in maize. The volatile profile was found to differ both in quality and quantity of VOCs. While we found potato tubers to release a complex blend of volatiles, we could not demonstrate varietal differences in terms of volatile emissions, regarding the total blend. Yet, a few major chemical compounds were released in different quantities according to the variety. One volatile (nonadecane) emitted in higher amount by the less susceptible variety, could be associated with a plant defence mechanism. Other compounds, emitted in higher amounts by the more damaged variety, could inform about the presence of a suitable host (2-butoxyethanol, benzaldehyde, 6-methyl-5-hepten-2-one and 2-undecanone). Further investigations should be led to evaluate the attractiveness/repellence potential of these compounds for wireworms. Finally, we were unable to identify any specific compounds emitted by the most attractive variety (Spunta). For the time being, we must reject our initial hypothesis according to which field differences in potato varietal susceptibility to wireworms' attacks can be explained by different blends of VOCs.

The difference in susceptibility to wireworms' attacks is probably not the result of VOCs emissions but could be associated with other volatile emissions, like $CO_2$. Carbon dioxide is known to be one of the most bioattractive compounds for soil dwelling insects. We hypothesize that potato varieties release contrasted concentrations of carbon dioxide, participating to the differences in susceptibility (Erb et al. 2013, Brandl et al. 2017; Barsics et al. 2017).

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**SUPPLEMENTARY MATERIAL**

Potato cultivar susceptibility to wireworms: feeding behaviour, fitness and semiochemical-based host selection

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Short title: Potato cultivar susceptibility to wireworms

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**Table S1.** Number of replicates performed in each experiment.

| Experiment | Total of replicates | Replicates per variety | |
|---|---|---|---|
| Feeding bioassay | 69 | 23 | |
| Dual-choice bioassays | 272 | 96 | charlotte-monalisa |
| | | 99 | charlotte-spunta |
| | | 77 | monalisa-spunta |
| Chemical analyses | 27 | 4 | development stage 1 |
| | | 5 | development stage 2 |
| Life history traits | 51 | 17 | |

**Table S2.** Compounds identified from gas chromatography-mass spectrometry (GC-MS) analyses of 2 physiological stages for three potato varieties. a Retention indices without an asterisk correspond to the publication Babushok et al., 2011. Those with an asterisk refer to the FFNSC 3 database, those with two asterisks to the NIST17 database.

| Compounds | Retention time | Retention index | | Quantity emitted (ng/g of dry peel) (Mean ± S.E.) | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | First physiological stage | | | Second physiological stage | | |
| | (min) | Calculated | Literature | Charlotte | Spunta | Monalisa | Charlotte | Spunta | Monalisa |
| **Aldehydes** | | | | | | | | | |
| 3-Methylbutanal | 3.635 | 668 | 652 | 2.0 ± 0.55 | 1.3 ± 0.21 | 1.3 ± 0.17 | 3.8 ± 0.46 | 4.8 ± 1.04 | 6.2 ± 1.11 |
| Heptanal | 10.89 | 902 | 902 | 5.8 ± 5.2 | 2.6 ± 1.99 | 0.4 ± 0.26 | 1.4 ± 0.22 | 2.0 ± 0.29 | 1.8 ± 0.17 |
| (*E*)-2-Heptenal | 12.802 | 957 | 956 * | -- | -- -- | -- -- -- | 0.2 ± 0.04 | 0.2 ± 0.03 | 0.5 ± 0.13 |
| Benzaldehyde | 12.974 | 962 | 962 | 4.2 ± 1.4 | 1.9 ± 0.33 | 1.7 ± 0.15 | 2.7 ± 0.07 | 4.3 ± 0.56 | 7.8 ± 1.46 |
| Octanal | 13.19 | 968 | -- | -- | -- -- | -- -- -- | 0.1 ± 0.03 | 0.1 ± 0.03 | 0.4 ± 0.09 |
| Benzeneacetaldehyde | 15.821 | 1046 | 1046 | 1.1 ± 0.24 | 0.7 ± 0.29 | 0.7 ± 0.26 | 3.2 ± 0.67 | 3.1 ± 0.37 | 3.9 ± 0.56 |
| (*E*)-2-Octenal | 16.249 | 1059 | 1060 | -- | -- -- | -- -- -- | 0.7 ± 0.14 | 0.7 ± 0.14 | 1.9 ± 0.43 |
| (E)-4-Nonenal | 17.407 | 1094 | -- | -- | -- -- | -- -- -- | 0.3 ± 0.08 | 0.4 ± 0.11 | 0.9 ± 0.21 |
| Nonanal | 17.75 | 1105 | 1103 | -- | -- -- | -- -- -- | 11.2 ± 1.55 | 13.8 ± 4.20 | 20.7 ± 3.84 |
| (*E*)-2-Nonenal | 19.503 | 1161 | 1162 | 3.0 ± 2.52 | -- -- | -- -- -- | 1.9 ± 0.44 | 2.3 ± 0.23 | 3.1 ± 1.14 |
| (*E,E*)-2,4-Nonadienal | 21.171 | 1216 | 1215 | -- | -- -- | -- -- -- | 0.2 ± 0.06 | 0.2 ± 0.06 | 0.2 ± 0.08 |
| (*E*)-2-Decenal | 22.566 | 1264 | 1263 | -- | -- -- | -- -- -- | 0.2 ± 0.04 | 0.3 ± 0.04 | 0.4 ± 0.09 |
| **Alcohols** | | | | | | | | | |
| 3-Methyl-1-butanol | 5.465 | 732 | 737 | 0.1 ± 0.14 | 0.1 ± 0.08 | 0.1 ± 0.07 | 0.7 ± 0.19 | 0.8 ± 0.14 | 1.0 ± 0.34 |
| Propylene glycol | 5.52 | 734 | 734 * | 1.5 ± 0.49 | 1.3 ± 0.62 | 1.1 ± 0.67 | 3.9 ± 0.73 | 4.6 ± 0.74 | 4.6 ± 0.77 |
| 2,3-Butanediol | 6.761 | 776 | 786 * | -- | -- -- | -- -- -- | 0.2 ± 0.08 | 0.2 ± 0.13 | 0.3 ± 0.14 |
| 1-Hexanol | 9.753 | 868 | 870 | 0.2 ± 0.14 | 0.2 ± 0.09 | 0.2 ± 0.11 | 1.0 ± 0.20 | 1.3 ± 0.20 | 2.1 ± 0.64 |
| 2-Butoxyethanol | 11.03 | 906 | 936 ** | 5.2 ± 4.2 | -- -- | 0.3 ± 0.31 | 2.2 ± 0.35 | 2.3 ± 0.38 | 5.1 ± 1.41 |
| Hexylene glycol | 11.542 | 920 | 872 ** | 1.1 ± 0.25 | 1.2 ± 0.56 | 0.5 ± 0.33 | 0.6 ± 0.15 | 0.5 ± 0.03 | 0.7 ± 0.13 |
| 1-Heptanol | 13.244 | 970 | 968 | 0.1 ± 0.06 | 0.1 ± 0.05 | 0.1 ± 0.05 | 0.3 ± 0.06 | 0.5 ± 0.09 | 0.7 ± 0.14 |
| 1-Octen-3-ol | 13.583 | 979 | 980 | 0.7 ± 0.2 | 0.4 ± 0.15 | 0.1 ± 0.04 | 7.0 ± 2.01 | 5.4 ± 2.43 | 37.2 ± 20.78 |
| 2-Ethyl-1-hexanol | 15.246 | 1029 | 1030 | 4.0 ± 1.38 | 2.2 ± 0.79 | 1.4 ± 0.48 | 2.4 ± 0.20 | 2.5 ± 0.31 | 2.7 ± 0.22 |
| Benzyl alcohol | 15.443 | 1035 | 1036 | 1.3 ± 1.10 | 0.1 ± 0.10 | 0.3 ± 0.30 | 2.4 ± 1.76 | 0.7 ± 0.31 | 1.7 ± 0.73 |
| 1-Octanol | 16.61 | 1070 | 1071 | -- | -- | -- | 2.2 ± 0.25 | 2.8 ± 0.83 | 3.8 ± 0.75 |
| 2-Phenyl-2-propanol | 17.186 | 1088 | 1107 * | 0.5 ± 0.18 | 0.5 ± 0.47 | 0.7 ± 0.39 | 0.8 ± 0.11 | 0.7 ± 0.18 | 0.5 ± 0.17 |
| Phenylethyl alcohol | 18.084 | 1116 | 1115 | 0.4 ± 0.10 | 0.2 ± 0.06 | 0.2 ± 0.08 | 1.0 ± 0.27 | 1.5 ± 0.31 | 1.0 ± 0.32 |
| 1-Nonanol | 19.804 | 1171 | 1173 | 2.5 ± 0.62 | 1.3 ± 0.37 | 1.2 ± 0.39 | 2.2 ± 0.17 | 2.9 ± 0.68 | 3.3 ± 0.44 |
| 2-Propyl-1-heptanol | 21.11 | 1214 | 1194 ** | 1.1 ± 0.24 | 1.0 ± 0.38 | 0.6 ± 0.20 | 0.2 ± 0.01 | 0.2 ± 0.03 | 0.2 ± 0.02 |
| 2-Phenoxyethanol | 21.374 | 1223 | 1222 * | 10.4 ± 6.20 | 2.0 ± 1.97 | 1.5 ± 1.36 | 36.7 ± 20.21 | 19.5 ± 4.39 | 25.8 ± 10.36 |
| 1-Decanol | 22.81 | 1272 | 1272 | 0.8 ± 0.32 | 0.3 ± 0.12 | 0.4 ± 0.14 | 0.9 ± 0.11 | 1.0 ± 0.17 | 1.2 ± 0.24 |
| **Acids and carboxylic acids** | | | | | | | | | |
| Propanoic acid | 4.456 | 697 | 706 ** | 0.05 ± 0.05 | 0.7 ± 0.67 | 1.3 ± 1.29 | 0.4 ± 0.13 | 1.0 ± 0.41 | 0.2 ± 0.10 |
| 2-Methylpropanoic acid | 6.046 | 752 | 770 * | 2.0 ± 0.70 | 2.0 ± 0.89 | 2.1 ± 1.19 | 1.8 ± 0.52 | 3.0 ± 0.78 | 3.2 ± 0.99 |
| 3-Methylbutanoic acid | 8.786 | 840 | 860 | 2.1 ± 1.07 | 1.6 ± 0.90 | 1.5 ± 0.84 | 3.1 ± 0.58 | 4.4 ± 0.79 | 3.4 ± 0.76 |
| 2-Methylbutanoic acid | 9.108 | 849 | 881 * | 0.2 ± 0.21 | 0.4 ± 0.42 | 0.4 ± 0.40 | 1.3 ± 0.30 | 2.1 ± 0.51 | 2.1 ± 0.70 |
| Pentanoic acid | 10.13 | 879 | 911 * | 0.1 ± 0.12 | 0.4 ± 0.39 | 0.3 ± 0.28 | 0.6 ± 0.11 | 0.4 ± 0.07 | 0.9 ± 0.22 |
| **Ketones** | | | | | | | | | |
| Butyrolactone | 11.26 | 912 | 941 * | 0.4 ± 0.19 | 0.2 ± 0.16 | 0.1 ± 0.05 | 0.2 ± 0.03 | 0.3 ± 0.03 | 0.2 ± 0.02 |
| Pentalactone | 12.673 | 953 | 954 * | 0.2 ± 0.12 | 0.3 ± 0.11 | 0.2 ± 0.14 | 0.2 ± 0.04 | 0.2 ± 0.08 | 0.2 ± 0.02 |
| 6-Methyl-5-hepten-2-one | 13.855 | 987 | 986 | -- | -- | -- | 1.0 ± 0.25 | 1.0 ± 0.30 | 5.3 ± 1.74 |
| 2-Undecanone | 23.462 | 1295 | 1293 | 0.8 ± 0.41 | 0.5 ± 0.20 | 0.2 ± 0.08 | 0.6 ± 0.17 | 5.1 ± 2.34 | 7.7 ± 3.16 |
| (*E*)-Geranylacetone | 27.815 | 1456 | 1452 | 1.9 ± 1.09 | 3.8 ± 1.57 | 2.3 ± 1.40 | 3.7 ± 0.74 | 3.5 ± 0.64 | 4.8 ± 0.63 |
| **Alkanes and Alkenes** | | | | | | | | | |
| Heptadecane | 33.704 | 1700 | 1700 | 2.1 ± 0.57 | 1.8 ± 0.36 | 1.5 ± 0.57 | 1.1 ± 0.13 | 1.1 ± 0.14 | 1.4 ± 0.14 |
| Nonadecane | 37.093 | 1900 | 1900 | 7.0 ± 2.21 | 2.5 ± 0.78 | 2.2 ± 0.83 | 2.1 ± 0.24 | 1.2 ± 0.18 | 1.1 ± 0.11 |
| Heneicosane | 38.815 | 2100 | 2100 | 4.7 ± 1.35 | 2.2 ± 0.99 | 2.3 ± 0.81 | 1.2 ± 0.39 | 1.0 ± 0.33 | 1.0 ± 0.10 |
| **Sesquiterpenes** | | | | | | | | | |
| Unidentified Sesquiterpene | 29.139 | 1508 | -- | 0.02 ± 0.03 | -- | 0.04 ± 0.04 | 0.2 ± 0.14 | 0.1 ± 0.08 | 0.6 ± 0.27 |
| Unidentified Sesquiterpene | 29.405 | 1519 | -- | -- | -- | -- | -- | -- | 0.7 ± 0.36 |
| **Aromatics** | | | | | | | | | |
| Styrene | 10.56 | 892 | 890 | 1.1 ± 0.25 | 1.2 ± 0.56 | 0.6 ± 0.32 | 0.6 ± 0.15 | 0.5 ± 0.03 | 0.7 ± 0.13 |
| Benzothiazole | 21.63 | 1232 | 1226 * | 2.0 ± 0.86 | 0.6 ± 0.22 | 0.5 ± 0.21 | 1.1 ± 0.27 | 1.1 ± 0.11 | 1.1 ± 0.13 |
| Diisopropylnaphthalene 1 | 33.456 | 1689 | | 4.9 ± 1.45 | 4.6 ± 0.94 | 3.2 ± 1.48 | 1.9 ± 0.44 | 2.3 ± 0.55 | 2.6 ± 0.68 |
| Diisopropylnaphthalene 2 | 33.58 | 1695 | | 6.8 ± 1.64 | 6.4 ± 1.04 | 4.6 ± 1.97 | 2.8 ± 0.55 | 3.2 ± 0.63 | 3.7 ± 0.85 |
| Diisopropylnaphthalene 3 | 34.459 | 1736 | Unidentified | 13.7 ± 1.95 | 13.1 ± 1.70 | 9.5 ± 3.80 | 5.7 ± 1.16 | 6.2 ± 1.13 | 7.2 ± 1.54 |
| Diisopropylnaphthalene 4 | 34.54 | 1740 | isomers | 6.1 ± 1.24 | 5.6 ± 0.69 | 4.1 ± 1.74 | 2.5 ± 0.56 | 2.7 ± 0.57 | 3.2 ± 0.80 |
| Diisopropylnaphthalene 5 | 34.619 | 1744 | | 8.2 ± 1.02 | 7.0 ± 0.82 | 5.6 ± 2.24 | 3.4 ± 0.67 | 3.6 ± 0.64 | 4.3 ± 0.91 |
| Diisopropylnaphthalene 6 | 34.717 | 1749 | | 3.2 ± 0.31 | 3.3 ± 0.51 | 2.2 ± 0.82 | 1.4 ± 0.24 | 1.5 ± 0.23 | 1.8 ± 0.35 |
| **Amines and Amides** | | | | | | | | | |
| Pyridine | 5.704 | 740 | 740 * | 0.5 ± 0.17 | 0.3 ± 0.13 | 0.4 ± 0.18 | 0.4 ± 0.09 | 0.4 ± 0.01 | 0.3 ± 0.05 |
| N-Butylformamide | 17.365 | 1093 | 905 ** | -- | -- | -- | 0.1 ± 0.05 | 0.3 ± 0.09 | 0.6 ± 0.22 |
| Methenamine | 21.583 | 1230 | 1204 ** | 0.1 ± 0.07 | 4.8 ± 4.77 | 3.4 ± 3.44 | 1.2 ± 1.22 | -- | 3.8 ± 2.35 |
| **Arenes** | | | | | | | | | |
| Ethylbenzene | 9.545 | 862 | 857 * | 3.8 ± 2.96 | 1.8 ± 1.61 | 0.1 ± 0.09 | 0.7 ± 0.19 | 0.6 ± 0.22 | 0.6 ± 0.21 |
| **Furans** | | | | | | | | | |
| 2-Pentylfuran | 14.04 | 993 | 992 | 0.3 ± 0.11 | 0.2 ± 0.06 | 0.2 ± 0.04 | 0.6 ± 0.11 | 0.4 ± 0.05 | 0.8 ± 0.10 |
| **Unidentified** | | | | | | | | | |
| Unidentified 2 | 13.4 | 974 | -- | -- | -- | -- | 0.4 ± 0.17 | 0.5 ± 0.20 | 3.8 ± 2.15 |
| Unidentified 3 | 14.776 | 1015 | -- | -- | -- | -- | 1.1 ± 0.22 | 1.2 ± 0.19 | 1.0 ± 0.23 |
| Unidentified 5 | 18.709 | 1136 | -- | -- | -- | -- | 0.1 ± 0.06 | 0.2 ± 0.01 | 0.2 ± 0.06 |
| Unidentified 6 | 33.843 | 1707 | -- | 1.4 ± 0.24 | 1.3 ± 0.19 | 0.9 ± 0.32 | 0.7 ± 0.05 | 0.7 ± 0.09 | 0.9 ± 0.10 |
| Unidentified 7 | 38.32 | 2035 | -- | -- | -- | -- | 0.6 ± 0.19 | 0.5 ± 0.15 | 0.3 ± 0.11 |
| Unidentified 8 | 38.51 | 2060 | -- | -- | -- | -- | 0.8 ± 0.23 | 0.7 ± 0.19 | 0.4 ± 0.14 |