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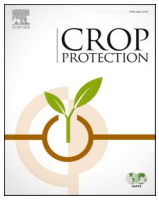
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Peppermint interplanting and nitrogen fertilisation for green peach aphid management in peach orchards: Field evidence of VOC-mediated effects

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ABSTRACT

A potential strategy for reducing pesticide applications within a cropping system is the use of agroecological practices to alter pest behaviour. Among these practices are the use of companion plant and the management of nitrogen fertilisation. Companion plants (CPs) emit volatile organic compounds (VOCs) that can influence aphid behaviour. Nitrogen fertilisation may affect aphid feeding and, consequently, aphid population growth, as it alters plant composition and development. The objective of this study was to determine whether the combination of nitrogen fertilisation and *Mentha* × *piperita* ground cover could modify the incidence of *Myzus persicae* in a peach orchard. We conducted a factorial experiment quantifying *M. persicae* incidence, VOC emissions, *Prunus persica* growth, and agronomic performance under contrasting nitrogen levels, with or without *Mentha* × *piperita* cover. This study provides field evidence of peppermint VOC production. We identified specific volatile compounds around peach trees associated with peppermint, including menthone, menthyl acetate, and eucalyptol. A high nitrogen level increased peppermint VOC emissions, reduced *M. persicae* incidence, and enhanced peach tree growth. The peppermint cover appeared to slightly improve the visual appearance of fruits at harvest. Fruits quality remained within commercial standards in terms of sugar content and overall yield, and fruit size was not significantly reduced despite potential resource competition with peppermint. Further research is needed to better understand the specific factors influencing VOC emissions and their effects on aphids at a finer temporal scale.

1. Introduction

In orchards, standard fruit production aims to produce large fruit with no visible damage, thereby ensuring both profitability and quality. This strategy of high fruit productivity is typically achieved through intensive cultivation practices involving numerous pesticide applications. These aim to produce large fruit with no visible damage, thereby ensuring both profitability and quality. In France, an average of 21 treatments are applied in peach orchards, of which 20 %–40 % are insecticides (Agreste, 2021). This high number of treatments is related to the number and diversity of pests and diseases such as aphids (*Myzus* spp. and *Hyalopterus pruni*), oriental fruit moth (*Grapholita molesta*), powdery mildew (*Podosphaera pannosa*), peach leaf curl (*Taphrina deformans*), and brown rot (*Monilinia* spp.) (Plénet et al., 2023).

Intensive use of pesticides has led to harmful effects on human health (Elbaz et al., 2009; Carvalho, 2017) and the environment (Beers et al., 2016), as well as the evolution of widespread resistance to pesticides in many orders and families of insects (Mottet et al., 2024). The green peach aphid *Myzus persicae* (Sulzer) has developed numerous resistances to insecticides, allowing this species to tolerate a wide range of chemical treatments (Bass et al., 2014; Mottet et al., 2024). Controlling *M. persicae* is an important issue, as it is considered the major pest in Mediterranean and temperate orchards, causing significant damage and yield losses (Ali et al., 2023). *M. persicae* can cause direct damage by puncturing and removing carbohydrates and nitrogen, preferentially on growing shoot apices and flowers, leading to leaf and fruit deformation and drop, as well as reducing plant vigour in the case of multiannual attacks (Capinera, 1969; Blackman et al., 1976). Green peach aphids can also cause indirect damage through the production of honeydew that serves as a breeding medium for pathogens (Ali et al., 2023) and the transmission of pathogenic viruses (Rimbaud et al., 2015). Introducing polygenic resistance to aphids in commercial cultivars can help reduce aphid pressure in orchards in the long term (Rousselin et al., 2017). Nonetheless, despite numerous breeding efforts to develop resistant

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peach cultivars (Sauge et al., 2006; Zhang et al., 2024), aphid control in orchards still relies heavily on pesticide use.

A solution for regulating pests is to seek agroecological alternatives to pesticides in orchards, to limit pest attacks and damage (Simon et al., 2010; Penvern et al., 2016). These approaches make use of ecological resources through top-down and bottom-up processes throughout the aphid's life cycle (Goggin, 2007; Rousselin et al., 2017). Top-down processes involve biological control by natural enemies (predators and parasitoids, entomopathogenic fungi and nematodes). Implementing agroecological infrastructures (hedgerows, flowering strips) can maintain predators and parasitoids in the field. Bottom-up processes involve modifying environmental and growing conditions to alter host plant suitability. Interplanting with companion plants (CPs) or modulating nitrogen fertilisation are promising strategies to limit aphid infestations.

Some CPs produce volatile organic compounds (VOCs) that can be used to control pest populations in crops (Ben-Issa et al., 2017; Yang et al., 2025). Firstly, these VOCs can act directly on aphid performance by disturbing feeding behaviour and reducing fecundity (Dardouri et al., 2021; Ameline et al., 2023), altering host plant selection, and/or masking the attractant host plant odour (Dardouri et al., 2019; Dieudonné et al., 2022). Secondly, CPs with flowers can attract natural enemies (Rizzi et al., 2025; Song et al., 2012) by increasing floral resource provisioning (Laffon et al., 2024). Peppermint (*Mentha* × *piperita*) could be a promising CP in orchards due to its potential negative effects on aphids, its perennial nature (four to five years under growing conditions), and its preference for partially shaded environments. The effects of peppermint on *M. persicae* populations have been shown under controlled conditions with essential oils and plant extract. Essential oils have shown both toxic (Ebadollahi et al., 2017; Hori, 1999; Kalemba and Synowiec, 2019; Kimbaris et al., 2010) and repellent effects (Cantó-Tejero et al., 2022), whereas peppermint extract has exhibited mitigated repellent effects (Ikeura et al., 2012). Although peppermint essential oils have shown notable negative effects on *M. persicae*, they were effective only for very short durations, typically lasting less than 2 h (Koul et al., 2008). Consequently, the need for frequent reapplication of essential oils in outdoor settings has been identified as a major constraint. Introducing peppermint as a CP could provide a continuous source of VOCs. Nevertheless, in the field, CPs are exposed to multiple stresses simultaneously, which can affect VOC emission and consequently their effects on aphids. For instance, some studies have shown that agricultural practices and environmental conditions can modulate the bouquet of aromatic compounds produced (Zheljazkov et al., 2010). Nutrient deficits may either increase or decrease the emission of specific VOCs (Dicke and Loreto, 2010; Holopainen and Gershenzon, 2010). Therefore, introducing CPs in orchards may lead to competition for nutrients and water (Gao et al., 2013; Luo et al., 2023), potentially affecting VOC emission, but may also affect tree growth (Novara et al., 2021).

Tree vegetative growth and nitrogen fertilisation can affect *M. persicae* populations. Notably, fertilisation affects tree growth, modifies the nutrient balance in plants, enhances plant tissue nutritional status, and influences the synthesis of defence compounds (Zaffaroni et al., 2020). How aphids might be affected by plant nutrient status is supported by two opposite hypotheses. On the one hand, the plant stress hypothesis (White, 1984) argues that pests perform better on stressed plants that would not have resources to deploy defences and/or whose nutritional quality might be enhanced. Sauge et al. (2010) showed that *M. persicae* populations increased as peach nitrogen status decreased below a nitrogen threshold and decreased thereafter, showing no correlation with vegetative growth. Nitrogen fertilisation modulated the concentrations of plant defence-related metabolites in the peach shoots, but the authors could not directly explain the reduced aphid performance by the induction of plant defence compounds at the highest nitrogen level. On the other hand, the plant vigour hypothesis (Price, 1991) proposes that pest populations should increase most rapidly on fast-growing shoots and organs since they provide more resources. Some authors have shown that *M. persicae* feeding behaviour depends on the vegetative growth of peach trees (Jordan et al., 2019) and that a large proportion of fast-growing shoots on peach trees, associated with a high nitrogen supply, can foster the development of aphid colonies (Grechi et al., 2008; Rousselin et al., 2016b). Regarding fruit production, reducing fertilisation may lead to a decrease in yield, both in quantity and quality. Nitrogen fertilisation must therefore be combined with other practices to achieve an optimal balance between pest control and production, considering both fruit yield and quality (Rousselin et al., 2016a).

While previous studies have examined the individual effects of CPs and nitrogen fertilisation on aphid performance, their combined impact on *M. persicae* populations under peach orchard conditions has not yet been evaluated. To our knowledge, the combined use of CPs and nitrogen fertilisation has been explored only in cereal and legume systems (Ahmed et al., 2019; Veromann et al., 2013; Yan et al., 2024). Here, we present an original study investigating the potential of combining peppermint and nitrogen supply in a peach orchard to reduce *M. persicae* incidence and maintain acceptable fruit production, both in quantity and quality. Our approach aims to contribute to a better understanding of the factors that may influence VOC emissions, plant growth, and aphid control, and to predict the effectiveness of combining CP interplanting and nitrogen modulation on *M. persicae* populations in peach orchards. We assumed that (1) peppermint interplanting could provide a continuous source of VOCs and that nitrogen fertilisation could influence VOC emissions; (2) both peppermint interplanting and nitrogen fertilisation could affect *M. persicae* incidence through VOC emissions and changes in peach tree vigour; and (3) these factors could affect the agronomic performance of the peach orchard. Our study also provides experimental feedback that may be helpful for designing new targeted experiments combining companion plants and nitrogen fertilisation to rethink the control of *M. persicae*–peach orchard systems.

2. Material and methods

2.1. Experimental site and orchard management systems

The study was carried out from 2021 to 2023 at the INRAE experimental station in southern France, in Avignon (43°60′N, 4°49′E, 24 masl), under a Mediterranean climate. The mean annual temperature was 14.5 °C, with cumulative annual rainfall of 673 mm and potential evapotranspiration of 1082 mm. The surface soil horizon (0–30 cm) consisted of 33.7 % clay, 54.0 % silt, and 13.0 % sand, corresponding to a silty clay loam texture. The soil was rich in calcium carbonate (36.7 %) and had a pH of 8.1. Soil analyses performed the year prior to the experiment confirmed plot homogeneity in terms of texture, humidity, and nitrate content (less than 5 % variability between samples taken in each row).

The orchard was planted in February 2013 with *Prunus persica* (L.) Batsch var. *nucipersica*, cultivar 'Nectarlove' grafted onto rootstock *P. persica* × *P. amygdalus* 'INRA® GF677' rootstock. 'Nectarlove' cultivar is a white-fleshed, mid-season nectarine cultivar with high potential for producing large fruit.

For irrigation, tree water requirements were estimated through the crop coefficient (Kc) and reference evapotranspiration (ET_0), corresponding to maximum evapotranspiration, and amounted to 868 ± 21 mm. Rainfall during the irrigation period (April to the end of September) was 245 ± 22 mm. The orchard was irrigated using a micro-sprinkler system. The inter-rows were grass-covered, predominantly with tall fescue.

Fruits were manually thinned during the first 15 days of May to leave 480 fruits per tree and to homogenise fruit load across the experiment. Fruit load was determined based on tree vigour, the quality of one-year-old fruit-bearing shoots, flower bud density, fruit set rate, and the target yield according to tree age.

For weed management, mechanical tillage on the row was performed

in May 2020 before the implementation of the experiment.

For pest protection, the objective was to drastically reduce chemical pesticide use in accordance with the French National Plan Ecophyto (Lamichhane et al., 2019). Alternative techniques were used, including biocontrol products, physical barriers, intensified conservation for biological control, sanitation practices, and increased thresholds for pest and disease symptom monitoring. For disease management, six treatments with copper or lime mixtures (one treatment per week from mid-February) were applied against leaf curl, and three sulphur treatments were applied against powdery mildew (every ten days from mid-April). Three treatments with yeasts were applied against monilia (once a week from mid-June). For oriental fruit moth management, mating disruption was used from March, complemented by two treatments with granulovirus in June and July. Against thrips, one application of talcum powder was performed in March. For green peach aphids, the decision rule was to apply only two treatments with a biocontrol product (white oil) at the wintering stage, to maximise the potential "peppermint and nitrogen effect" and to promote biological control by natural enemies. Overall, aphid pressure was high in 2021 and 2023, with more than 20 % of shoots infested. To avoid compromising tree development, additional applications of a biocontrol product containing potassium salts were applied to every tree in the orchard, two 2021 (12 March and 23 April) and one in 2023 (14 April). These biocontrol sprays were aimed at reducing aphid populations in 2021 and 2023 and influenced the developmental dynamics of aphid colonies.

2.2. Experimental design

The assay consisted of six rows, each containing 15 to 16 trees, planted at a density of 909 trees/ha (5 m × 2.2 m) with trained in a simple oblique Y shape (two main branches). To minimise border row effects, the system was divided into 24 plots (four plots per row), with each experimental treatment replicated in three plots across the assay (Fig. 1). Each individual plot comprised four trees, but measurements and observations were carried out only on the two central trees, resulting in a total of 48 trees monitored.

The experiment involved a combination of two factors: a nitrogen factor (N) and a companion plant factor (CP).

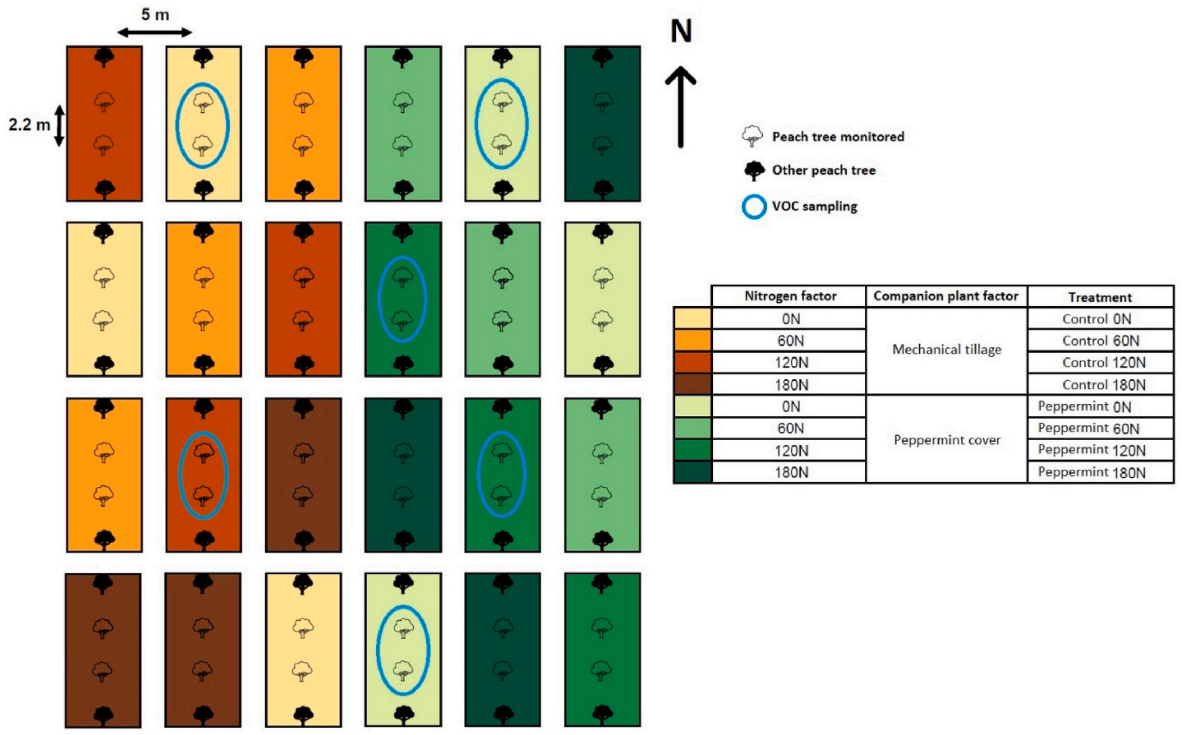
The N factor included four treatments: 0N, 60N, 120N (reference dose) and 180N (in kg N/ha/year), which were randomly distributed across the field. Calcium nitrate was applied four times at equivalent doses, once per month from March and June, to induce a rapid and marked differentiation in the nitrogen status of the trees.

The CP factor included two treatments: a control (mechanical tillage on the row) and peppermint interplanting on the row (*Mentha* × *piperita*). Mechanical tillage on the row for the control treatment was performed twice a year, in March and June, between 2021 and 2023. There was no weed management in the peppermint interplanting treatments. The CP factor was not randomly distributed but arranged in two subblocks, each comprising three adjacent rows. This non-randomised spatial arrangement of CPs promotes a more homogeneous olfactory landscape, but it represents a design limitation, as any differences attributed to CPs may reflect unmeasured gradients despite soil homogeneity within the orchard. The north-south orientation of the rows minimised variability due to light interception or the influence of prevailing northerly and southerly winds.

Young peppermint plants, grown in a nursery (Duplan de Provence, Carpentras, France), were transplanted onto the tree rows in May 2020 at a density of 7 plants/m^2. To promote peppermint establishment along the rows, plants were cut to 10 cm above ground level several times during the experiment. In 2021, peppermint was allowed to root naturally, with only one cut performed in July. In 2022, three cuts were carried out (April, May, and June). By 2023, the peppermint was well established, and only one cut was made (July).

2.3. Sampling and characterisation of VOC emissions

VOCs were sampled once a month between mid-April and early July,



Nitrogen factor	Companion plant factor	Treatment
0N	Mechanical tillage	Control 0N
60N		Control 60N
120N		Control 120N
180N		Control 180N
0N	Peppermint cover	Peppermint 0N
60N		Peppermint 60N
120N		Peppermint 120N
180N		Peppermint 180N

Fig. 1. The experimental design consisting of 24 plots combining the nitrogen (N) factor and the companion plant (CP) factor. The N factor included four treatments (0N, 60N, 120N, and 180N), and the CP factor included two treatments (control with mechanical tillage on the row and peppermint interplanting). There were three replicates for each treatment.

on three dates in 2022 and four dates in 2021 and 2023, only for the following treatments: Control 0N, Control 120N, Peppermint 0N, and Peppermint 120N (Fig. 1). Due to limited air sampling equipment, it was necessary to restrict the number of samples to carry out measurements under similar weather conditions and avoid bias between the first and last samples.

When peppermint was cut, VOCs were sampled 24 h after the cut. In each plot, open-air samples were collected simultaneously from both central trees at two heights: sampling tubes were placed on a support bracket at heights of 30 cm and 100 cm. To characterise the VOCs emitted by the CPs, an additional air sample was taken by enclosing peppermint with a cylindrical, odourless enclosure (80 cm × 39 cm) consisting of a metallic frame covered with polytetrafluoroethylene film. This enclosure covered the ground and the entire height of the peppermint plants. The enclosure was placed between the two central trees, and the sampling tubes were fixed to its structure at a height of 60 cm.

Regardless of the sampling method used, air containing VOCs was drawn using micro-pumps (PAS-500, Supelco) at a regulated flow rate of 0.2 L/min for 20 min through a sampling tube (PerkinElmer ref. N9307005) filled with Tenax TA®. All VOCs were collected in the early afternoon, when VOCs production generally at its highest due to high temperatures (Holopainen and Gershenzon, 2010; Mofikoya et al., 2019).

The sampling tubes were stored at 4 °C until analysis. VOCs were thermally desorbed for 10 min at 280 °C using a PerkinElmer Turbomatrix 650 ATD (PerkinElmer, Inc., Waltham, USA) coupled to a gas chromatograph–mass spectrometer system (Trace GC Ultra-ISQ; Thermo Scientific, Austin, Texas, USA). Helium was used as the carrier gas at a flow rate of 0.8 mL/min. Chromatographic separation was performed using a DB5-MS column (30 m length × 0.25 mm ID × 0.50 μm film thickness). Mass spectra were acquired in electron ionization mode at 70 eV over a range of 35–450 m/z. Compounds were identified and semi-quantified by AMDIS 32 deconvolution software (v.2.73, 2017 NIST) by comparing the mass spectra with those from the NIST 17 library (National Institute of Standards and Technology, Gaithersburg, MD, USA). Retention indices for most identified compounds were calculated using commercial standards (Sigma Aldrich®). The relative abundance of peak areas was used to estimate emission rates for each VOC of interest.

2.4. Monitoring aphid development

The dynamics of aphid infestation were monitored from bud burst. Ten shoot buds were randomly selected and tagged on each of the two central trees per plot. The ten shoot buds were selected from all around the tree, across the bottom half of the canopy. They were re-tagged annually. Green peach aphid incidence on tree shoots was assessed weekly from mid-April to mid-June, resulting in 14–16 observation dates per year. After mid-June, no aphids were observed on the trees. For each date and plot, the percentage of infested shoots, defined as shoots hosting at least one green peach aphid, was calculated by averaging the values from all monitored shoots on the two central trees.

2.5. Monitoring plant growth dynamics and peach nitrogen status

Peppermint growth dynamics were monitored between mid-April and early July. The percentage of soil surface covered by peppermint was visually estimated using eight quadrats of 0.25 m^2 each, distributed along the east and west sides of the row. Measurements were taken on three to four dates during this period.

To characterise peach growth dynamics and nitrogen status, trunk circumference was measured in July, 5 cm above the graft union, on the two central trees of each plot, allowing estimation of trunk cross-sectional area. Annual trunk growth was calculated as the increase in cross-sectional area between two consecutive years. Additionally, four young, vigorous shoots were selected and labelled on each of the two central trees per plot. Shoot length was measured every 14 days from mid-April to the end of June, resulting in five sampling dates per year. The daily vegetative growth rate (DVG) was calculated as the difference in shoot length between two consecutive sampling dates, divided by the number of days between samplings. On the same dates, but using different shoots, five mature leaves per tree were randomly collected from the middle part of shoots located at the eastern side of the central trees. The ten leaves per plot were pooled. Fresh weight was recorded, followed by dry weight after oven drying at 80 °C for 48 h. Leaf area was measured using a planimeter (total surface area of the ten sampled leaves). Specific leaf area (SLA) was calculated as the ratio of leaf area to dry weight. The dried leaf samples were ground into a fine powder. Total nitrogen content was then determined using the Dumas dry combustion method (Dumas, 1831), and leaf surface nitrogen content was calculated as the ratio of total nitrogen to leaf surface area.

2.6. Assessment of peach agronomic performance

At harvest (three pickings), the fresh weight of fruit per tree was measured on the two central trees per plot. Fruits were graded according to European marketing standards based on visual imperfections and size. Two yield metrics were calculated: gross yield, which included all fruits harvested from the trees as well as fallen fruits, and marketable yield, which included only fruits meeting commercial quality standards.

Visual imperfections on fruits by aphid pricking were recorded, and the percentage of pricked fruits was calculated by averaging the observations from all harvested fruits of the two central trees in each plot (three replicates per treatment).

The percentage of fruit meeting the marketing standard size was calculated by averaging the number of marketable fruits over the total number of harvested fruits from the two central trees of each plot (three replicates per treatment).

A sample of 36 marketable fruits was randomly selected from each central tree. Fruit quality was assessed by measuring their refractometric index (RI, °Brix), the main quality indicator used in the fruit industry. RI was measured on fruit pieces sampled from three longitudinally equidistant locations on each fruit. The average of the three measurements was used to determine the RI for each fruit.

2.7. Statistical analyses

All statistical analyses were performed using R software.

The diversity of all VOCs collected each year was shown on a principal component analysis (PCA), with the projection of the barycentres of individuals corresponding to treatments with or without peppermint. To test the correlation between peppermint coverage rate and VOC peak areas, a Spearman correlation test was performed, or a Kendall correlation test when the data did not follow from a normal distribution.

To analyse the VOC peak areas, a one-way ANOVA (analysis of variance) was first conducted to check homogeneity between replicates at each date. Then, a two-way ANOVA was performed to assess the possible effects of the interaction between N and CP treatments on VOC peak areas at each date. When significant differences were found, a Tukey multiple comparison test with a 95 % family-wise confidence level was used to separate means. Non-parametric Kruskal–Wallis tests were used when data did not meet ANOVA assumptions. In such cases, significant differences were further explored using pairwise Wilcox tests.

To model aphid incidence, peppermint growth dynamics, peach growth and nitrogen status dynamics, and peach agronomic performance over time in response to N and CP treatments, we employed a generalised linear mixed-effects model. Given the repeated measurements on the same trees in replicates over time, we used nested linear models.

For aphid incidence, a binomial distribution and a logit link were used. For peppermint coverage rate, the percentage of fruits meeting the market standard size, and the percentage of pricked fruits, a beta

distribution [after rescaling to (0,1)] was used. For other variables, we evaluated data normality using quantile–quantile (QQ) plots and the Shapiro–Wilk test. In cases where data deviated from normality, log transformation was applied to annual trunk growth, specific leaf area, leaf surface nitrogen content, gross and marketable yields, and soluble sugar content. A gamma distribution was used for daily vegetative growth, as all data were strictly positive.

The models included year, N and CP treatments (as fixed effects) and all interactions between factors. Random intercepts were included for dates and trees nested within replicates. We did not include CP treatments as a fixed effect to analyse peppermint coverage rate, nor date as a random effect to analyse annual trunk growth and peach agronomic performance. All models were fitted using the glmmTMB package in R. Model residuals were checked for normality and homogeneity of variance to validate model assumptions. Post hoc tests were performed using estimated marginal means with Tukey adjustment.

3. Results

3.1. Peppermint VOCs production in orchards in relation to nitrogen fertilisation

A total of 22 VOCs were identified in the air samples collected over the three years of the experiment. The PCA explained more than 80.2 %, 62.6 %, and 65.8 % of the total variability in the data in 2021, 2022, and 2023, respectively (Fig. 2). The two principal components allowed discrimination between the control and peppermint treatments. The 12 VOCs contributing most to the PCA axes are listed in Table A in Appendix.

The composition and relative abundance of VOCs varied across years and sampling dates. For both CP treatments, VOC levels were higher in May 2022 and consistently elevated in June and July across all years (Fig. 3).

Nine VOCs were consistently detected across all three years, while the remaining compounds were observed only in 2022 and 2023 (Table A in the Appendix). Menthone, menthyl acetate, and eucalyptol were specific to peppermint and were significantly more abundant for peppermint treatments every year, although statistical tests indicated substantial variability among replicates in 2022 (Table B in Appendix, $p < 0.01$). Menthone and menthyl acetate were particularly abundant in May 2022 and in June 2022 and 2023. Additional VOCs were also significantly more abundant in peppermint treatments, including γ-terpinene and limonene in 2022, and pulegone, β-myrcene, γ-terpinene, thujanol, α-terpinene, α-thujene, cymene, piperitone, and sabinene in 2023 (Table B in Appendix, $p < 0.01$). Statistical tests also indicated substantial variability among replicates for β-myrcene, γ-terpinene, α-terpinene, and piperitone in 2023.

Peppermint-specific VOCs (menthone, menthyl acetate, and eucalyptol) were more abundant in peppermint treatments under high nitrogen levels (120N) compared to low nitrogen levels (0N) (Fig. 4). The CP × N interaction factor significantly influenced their emission each year (Table B in Appendix, $p < 0.05$). Five additional VOCs, not specific to peppermint, were also significantly affected by the CP × N interaction: thujanol, sabinene, and limonene in 2022, and thujanol, sabinene, β-myrcene, and cymene in 2023. These compounds were more abundant in the 120N peppermint treatments.

The difference of VOC abundances between nitrogen levels may be related to peppermint cuttings and/or peppermint biomass. Peppermint coverage decreased after cuts in July 2021 and in July 2023 for both nitrogen levels (0N and 120N), and specifically for the 120N treatments (Fig. 4). In 2022, however, peppermint regrowth following cutting did not affect coverage rate. Peppermint coverage remained equivalent between 0N and 120N treatments for both years ($p > 0.05$), although it tended to be lower in the 120N treatments in 2022 because of weed development competing with peppermint.

Kendall's rank correlation tests highlighted positive correlations

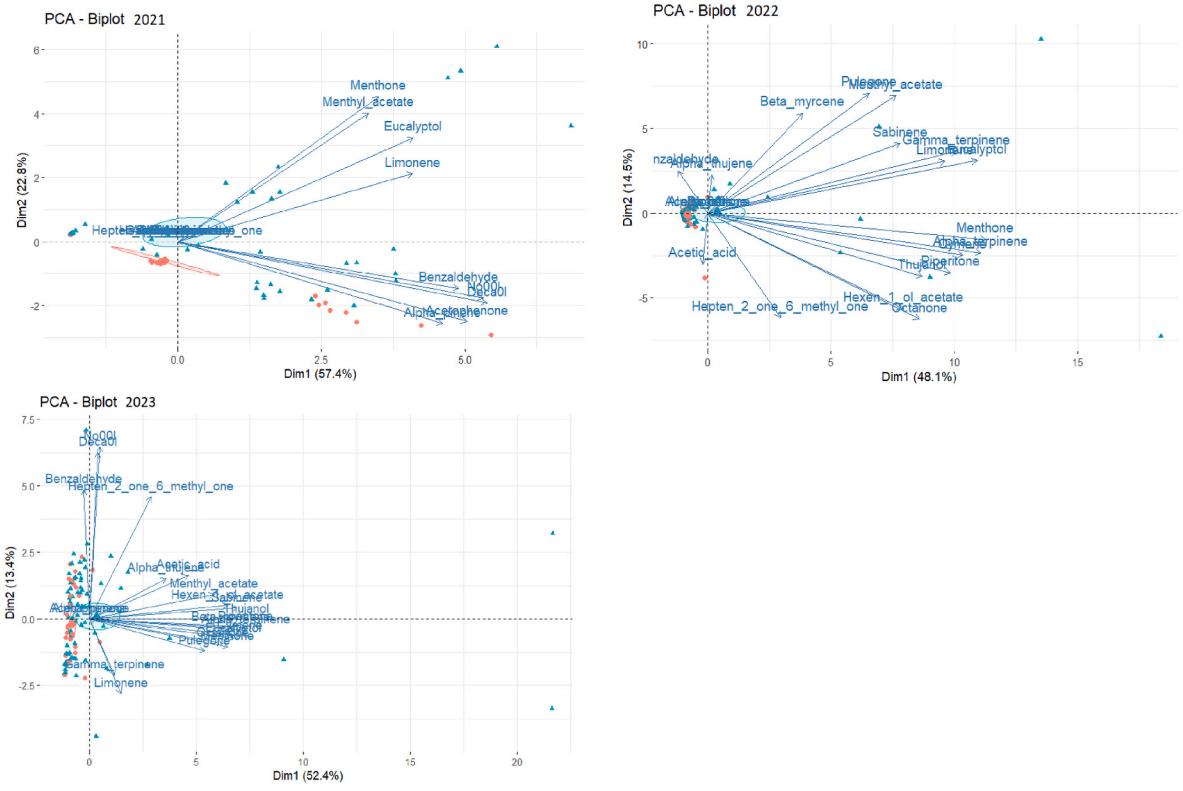


Fig. 2. Distribution of VOCs on the PCA axes for each year. The ellipses surrounding each group of individuals in the Peppermint treatment (blue symbols) and Control treatment (pink symbols) represent the 95 % confidence interval. VOC data correspond to two to four sampling dates per year, collected between March and July. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

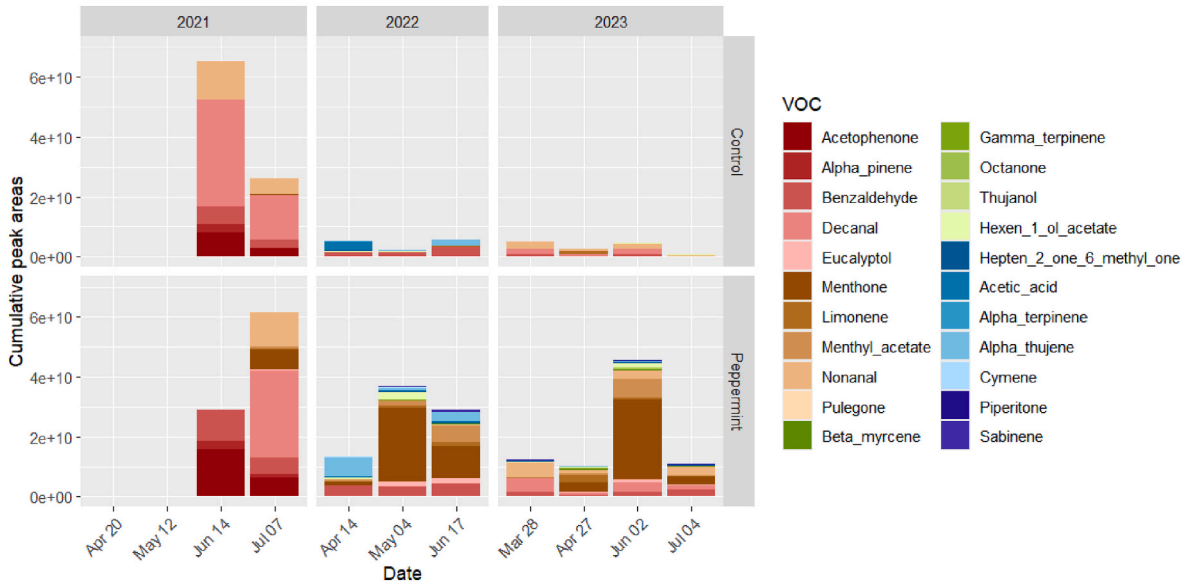


Fig. 3. Evolution of cumulative VOC peak areas in the CP treatments (control and peppermint interplanting) over the three years of experimentation, for the 0N and 120N nitrogen treatments.

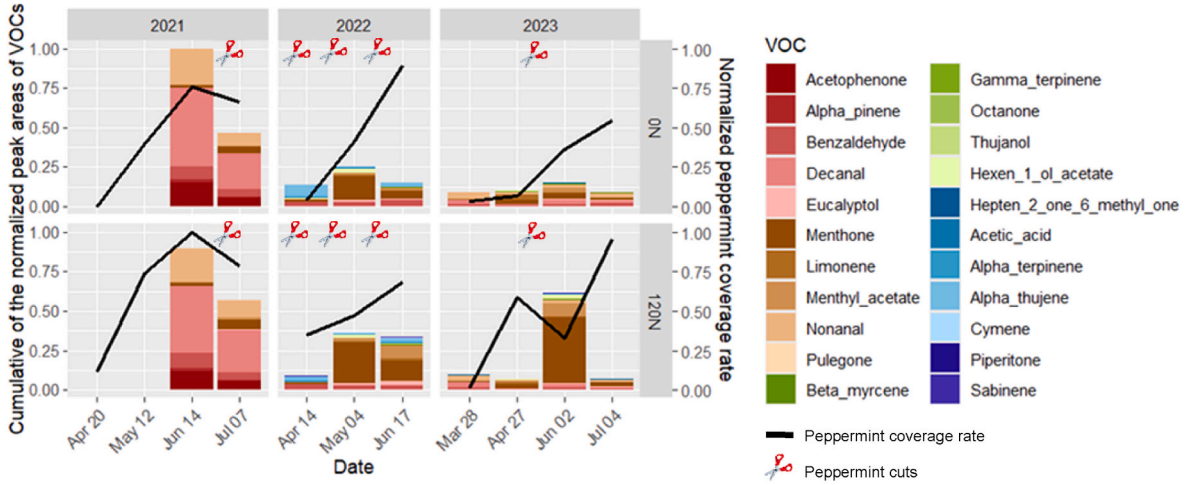


Fig. 4. Evolution of the nine VOC peak areas and peppermint coverage rate for the two nitrogen doses (0N and 120N) over the three years of the experiment. Data were normalised using the formula: [X – min(X)]/[max(X) – min(X)], where X is the variable to normalise (VOC peak area or peppermint coverage rate).

between the peak areas of 13 VOCs and peppermint coverage rate, depending on the year (Table C1 in Appendix). These correlations could not be directly related to nitrogen level, as the CP × N interaction did not significantly affect all 13 VOCs.

Temperature and relative humidity conditions varied between the VOC sampling dates (Table C2 in Appendix). Correlation tests showed positive correlations between the peak areas of 11 VOCs and the mean temperature on each sampling date, but the strength of the correlation varied by year.

3.2. *Effect of nitrogen fertilisation and companion plants on M. persicae incidence*

Infestation dynamics were similar in 2022 and 2023, with an aphid infestation period occurring between late March and mid-May (Fig. 5). Maximum incidence reached 18 % of infested shoots on June 1, 2021 and 27 % on April 22, 2022. Maximum incidence was lower in 2023, with a peak of 16 % of infested shoots between 17 and 25 April. This percentage remained stable for one week before decreasing over one, two, or three weeks in 2021, 2023, and 2022, respectively, showing that the infestation period was shorter and occurred later in 2021.

Infestation was significantly affected by the interaction between the N factor and year ($p < 0.05$). The risk of aphid infestation was lower for the 120N and 180N treatments in 2022 and 2023 compared to the 0N treatment (respectively, 6.2 and 45.6 times lower for the 180N treatments compared to the 0N treatment in 2022 and 2023, and 6.9 times lower for the 120N treatments compared to the 0N treatment in 2023). In contrast, the 60N treatment showed a 1.6-fold higher risk of aphid infestation in 2022 and 2023 compared to the 0N treatment. No differences between nitrogen treatments were observed in 2021. Peppermint treatments did not show a significant effect on aphid incidence compared to the control treatments ($p > 0.5$; GLM, binomial distribution; post hoc estimated marginal means with Tukey adjustment). The interactions between year, nitrogen doses, and CP treatments were not significant ($p > 0.5$). Random factor variances indicated substantial variability among trees nested within replicates, reflecting heterogeneity in aphid incidence across trees and replicates.

The N factor had a significant overall effect on all four indicators of

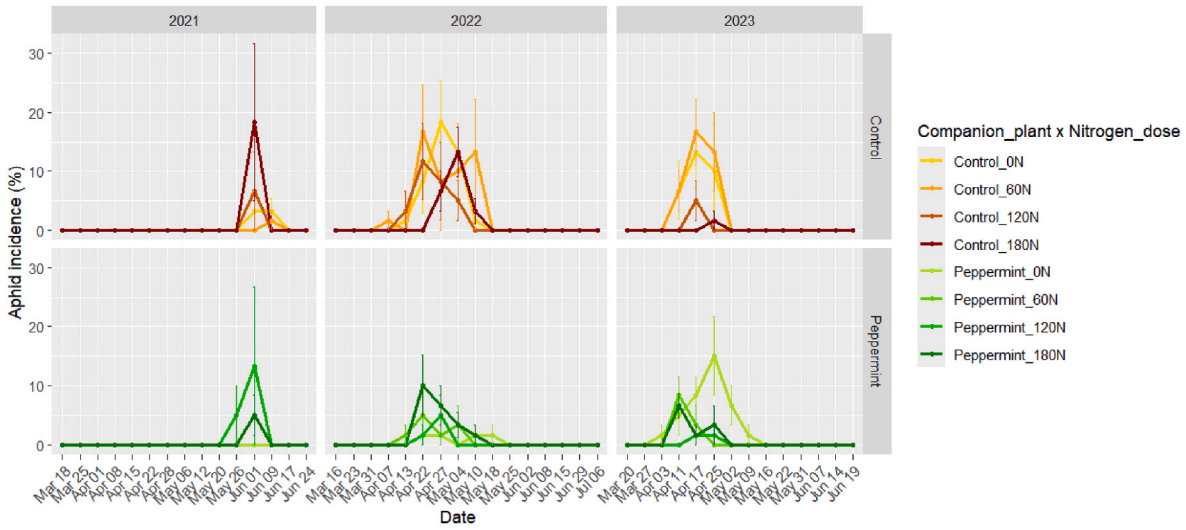


Fig. 5. Proportion of infested shoots (number of infested shoots/10 shoots × 100, mean ± standard error) for each treatment and year. Peppermint treatments and control treatments are shown in green and brown respectively. Darker shades indicate higher levels of nitrogen fertiliser application. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

peach growth and nitrogen status. Annual trunk growth, DVG, SLA, and leaf surface nitrogen content were negatively affected in the absence of nitrogen application, whereas the CP factor did not affect peach growth or nitrogen status ($p < 0.05$; Tables D1 and D2 in Appendix). Interactions between N, CP, and year factors were observed for DVG, SLA, and leaf surface nitrogen content. DVG appeared to increase over time for 120N and 60N peppermint treatments compared to 0N control treatments, between 2021 and 2022 and between 2021 and 2023, respectively ($p < 0.05$; Tables D1 and D2 in Appendix). SLA and leaf surface nitrogen content appeared to decrease between 2021 and 2023 for 120N and 180N peppermint treatments compared to 0N control treatments. Random factor variances showed low variability among trees nested within replicates, reflecting homogeneity in tree growth and leaf surface nitrogen content across trees and replicates.

Table 1
Annual averages of agronomic indicators across all treatments (mean ± standard error) and summary of statistical tests evaluating the effect of companion plant and nitrogen factors on these indicators.

Indicators	Year	Peppermint 0N	Peppermint 60N	Peppermint 120N	Peppermint 180N	Control 0N	Control 60N	Control 120N	Control 180N	Effect and p-value[a] (p-value comparison)
Gross yield (t/ha)	2021	/	/	/	/	/	/	/	/	/
	2022	27.5 ± 0.9	61.0 ± 2.2	73.3 ± 2.5	62.0 ± 1.5	47.1 ± 0.9	68.9 ± 1.7	81.3 ± 2.2	73.7 ± 1.2	**N factor** $p < 0.05$ (for 120N–0N and 180N–0N)
	2023	61.2 ± 2.1	105.1 ± 4.9	162.2 ± 7.7	146.0 ± 7.0	62.9 ± 1.3	119.9 ± 7.2	133.3 ± 7.5	170.0 ± 10.4	**Year factor** $p = 0.001$ (for 2023–2021)
Marketable yield (t/ha)	2021	/	/	/	/	/	/	/	/	/
	2022	17.3 ± 0.5	37.0 ± 1.3	41.8 ± 1.4	31.0 ± 0.7	26.6 ± 0.7	36.3 ± 1.3	42.0 ± 1.1	31.8 ± 0.6	**N factor** $p = 0.037$ (for 120N–0N)
	2023	32.2 ± 0.6	59.0 ± 2.9	89.9 ± 3.7	79.7 ± 3.4	33.9 ± 1.0	55.0 ± 2.7	70.5 ± 3.8	69.9 ± 3.8	**Year factor** $p = 0.005$ (for 2023–2021)
Fruits meeting the marketing standard size (%)	2021	/	/	/	/	/	/	/	/	/
	2022	67.0 ± 10.8	47.5 ± 10.8	73.5 ± 9.0	67.3 ± 10.6	60.4 ± 7.1	71.0 ± 7.1	77.3 ± 9.0	63.0 ± 11.0	**N factor** $p = 0.018$ (for 120N–0N)
	2023	61.7 ± 9.8	68.3 ± 7.8	60.1 ± 10.6	60.5 ± 10.5	68.9 ± 6.7	62.3 ± 9.2	64.4 ± 8.7	56.0 ± 8.0	
Picked fruits (%)	2021	/	/	/	/	/	/	/	/	/
	2022	15.6 ± 5.7	15.4 ± 3.0	14.3 ± 3.3	21.5 ± 2.7	22.0 ± 3.7	25.9 ± 3.8	20.6 ± 5.1	23.0 ± 3.1	**N factor** $p = 0.009$ (for 180N–0N)
	2023	17.3 ± 3.9	17.0 ± 3.0	22.3 ± 3.5	18.6 ± 4.1	21.5 ± 4.9	15.7 ± 4.8	13.8 ± 3.0	20.3 ± 4.6	**CP factor** $p = 0.011$ (for control – peppermint)
Soluble sugar content (°Brix)	2021	/	/	/	/	/	/	/	/	/
	2022	15.3 ± 0.7	16.2 ± 0.6	16.2 ± 0.4	17.5 ± 0.6	14.9 ± 0.6	16.8 ± 0.8	17.2 ± 0.5	17.4 ± 0.3	$p < 0.05$ (for 60N–0N, 120N–0N and 180N–0N)
	2023	17.1 ± 0.4	16.9 ± 0.7	16.7 ± 0.6	16.1 ± 0.7	17.6 ± 0.4	17.4 ± 0.4	16.6 ± 0.4	17.2 ± 0.3	**Year factor** $p = 0.004$ (for 2023–2021)

[a] For statistical models, GLMMs with log-normal distributions were used for yields and soluble sugar content, and GLMMs with beta distributions were used for fruits meeting the market standard size and pricked fruits. Only significant p-values are shown. Green font indicates a positive difference between treatments.

3.3. Effects of nitrogen fertilisation and companion plant on peach tree agronomic performances

A spring frost in April 2021 led to complete fruit drop by May, resulting in no harvest that year. Gross and marketable yields were highly variable among trees, replicates, treatments, and years (Table 1). The significant lower yields in 2022 were attributed to an intense heatwave and drought in June and July, which stopped fruit development and ripening. Gross and marketable yields were significantly affected by the N factor in 2022 and 2023 ($p < 0.05$; Table 1). On average, the 0N treatments showed 2.3-fold lower gross yields than the 120N and 180N treatments, and two-fold lower marketable yields than the 120N treatments. The 60N treatments showed intermediate yields, with no significant differences compared to the other nitrogen treatments. Peppermint treatments tended to produce lower gross and marketable yields compared to the control treatments in 2022 and 2023, although statistical analysis did not show any significant effect.

The percentage of commercially sized fruits (≥ grade A) was also significantly affected by the N factor ($p < 0.05$; Table 1). The 0N treatments showed a 2.6-fold lower proportion of commercially sized fruits than the 120N treatments.

The percentage of fruits showing visual defects caused by aphids ("pricked fruits") was significantly affected by the N factor and the CP factor ($p < 0.05$; Table 1). The 0N treatments and the control treatments showed a 2.46-fold higher proportion of pricked fruits than the 180N treatments and all the peppermint treatments.

Fruit quality, assessed by soluble sugar content, was significantly reduced in the 0N treatments compared to the other treatments (Table 1), with a refractometric index decrease ranging from 0.3 to 0.6 °Brix. Nevertheless, all treatments remained within the commercial standard (>12 °Brix). Random factor variances indicated substantial variability among trees nested within replicates, reflecting heterogeneity in agronomic performance across trees and replicates.

4. Discussion

The present work corroborates findings that the introduction of peppermint as a companion plant increases the presence of VOCs around trees in orchard environments. Very few studies have successfully sampled and analysed VOCs emitted by CPs in open-field. For instance, some authors measured VOC emissions in open-air environments using a closed system that included only the CPs (Rizzi et al., 2025) or collected VOCs at companion plant height, providing no information on the VOCs present at tree level. The VOCs identified in our experiment are consistent with the existing literature on the characterisation of peppermint under controlled conditions. In particular, menthone, menthyl acetate, and eucalyptol have been reported in *Mentha* spp. oils (Kimbaris et al., 2010; Behi et al., 2017; Ikbal and Pavela, 2019; Lacotte et al., 2023).

Peppermint VOC emissions were higher in the 120N treatments than in the 0N treatments. Previous studies have already showed the positive effect of nitrogen application on CP growth and essential oil yield (Jeliazkova et al., 1997; Zheljazkov et al., 2010). In the context of mints intercropped with fruit trees, Paulus et al. (2019) reported increased essential oil yields associated with higher leaf area and biomass. We did not observe a consistent correlation between VOC peak areas and peppermint ground cover. Cultural practices and abiotic factors could also modify the volatile blend released (Holopainen and Gershenzon, 2010). Weed development may have influenced VOC emissions through radiation and water competition (Ormeño et al., 2007), or temperature variation throughout the growing season. Although no strong correlations were found between VOC peak areas and mean temperature, emissions typically peaked in June or July, depending on the year, consistent with studies indicating that high temperatures can enhance VOC production (Holopainen and Gershenzon, 2010; Mofikoya et al., 2019).

Notably, we did not observe an effect of peppermint cover on aphid incidence, in contrast with experiments conducted under controlled conditions. Peppermint essential oils have been shown to be effective against *M. persicae* and the pea aphid *Acyrthosiphon pisum* in controlled conditions, through both repellency and toxicity effects (Behi et al., 2017; Ikbal and Pavela, 2019; Kimbaris et al., 2010; Lacotte et al., 2023). Other VOCs foundin peppermint treatment samples (α-terpinene, pulegone, piperitone, β-myrcene, and sabinene) have been shown to repel *M. persicae* under controlled conditions (Petrakis et al., 2014; Dardouri et al., 2019; Ikbal and Pavela, 2019; Lacotte et al., 2023). Rizzi et al. (2025) also did not observe a significant reduction in aphid incidence with peppermint plants in apple orchards. This contrast between efficacy under controlled conditions and these field results can be attributed to the complexity of environmental conditions that can dilute or affect VOCs, such as relative humidity, temperature, and light (Davis et al., 2006). Moreover, as suggested by Song et al. (2013) and supported by Rizzi et al. (2025) in apple orchards, aphid regulation is likely mediated by the cumulative effects of aphid repellency and the attraction of natural enemies. The diversity and abundance of natural enemies are important factors in regulating aphid populations (Soares et al., 2020), and they may have had a significant effect in our experiment.

Nevertheless, aphid incidence was affected by the interaction between the nitrogen factor and year.

The high-nitrogen treatments (120N and 180N) showed lower infestation risks, whereas the intermediate treatment (60N) showed the highest infestation risk only in 2022 and 2023. Our results contrasted with the plant vigour hypothesis (Price, 1991), which states that pest populations should increase most rapidly on vigorously growing plants that provide more resources. The model reproduced by Zaffaroni et al. (2020) indicates that the effect of fertilisation on aphid populations cannot simply be reduced to a positive or negative effect; it depends on the levels of fertilisation considered and on the timing of observations during the growing season. Experimental evidence suggests that intermediate levels of fertilisation can be associated with large green peach aphid infestations, whereas either lower or higher nitrogen supply tends to result in smaller aphid populations (Sauge et al., 2010; Rousselin et al., 2016a). Increasing nitrogen availability may have enhanced the flush of new leaves on trees under high-N treatments, leading to a potential dilution effect on aphid incidence. Indeed, peach tree growth responded positively to nitrogen fertilisation, with SLA, DVG, and annual trunk growth all increasing in the high-nitrogen treatments. These results align with previous studies showing positive effects of nitrogen treatments on vegetative growth (Rousselin et al., 2016b). Another explanation would be in accordance with the plant stress hypothesis (White, 1984), which argues that pests perform better on stressed plants that lack the resources to deploy defences and/or whose nutritional quality might be enhanced. Sauge et al. (2010) showed that *M. persicae* abundance was negatively correlated with peach nitrogen status above intermediate nitrogen levels. In fact, leaf nitrogen content in the 0N treatments fell below the normal range (3.5–4 % of foliar dry weight; Gomez et al., 2020).

The nitrogen factor also affected agronomic performance in our experiment. The 0N treatments showed the lowest yields. In particular, in 2022, the marketable yields measured were below the ranges observed for mid-season (27.7 t ha^{-1} of marketable yield) in the same peach–nectarine cultivars during the 2013–2019 period (Plénet et al., 2023). Based on the same study, the percentages of fruits meeting the market standard size were all below the reported ranges (79.9 % of fruits with grade ≥ A). The percentage of fruits meeting the market standard size, visual appearance, and soluble sugar content decreased in the 0N treatments. These results are consistent with previous studies showing the positive effect of fertiliser application on peach yield and quality (Rousselin et al., 2017; Cai et al., 2023). Fruit quality, measured by soluble sugar content, was significantly lower in low-nitrogen treatments, but it remained within the commercial standard for all treatments, with a minimum of 8 °Brix, which is acceptable for the peach

market.

Interestingly, fruits in peppermint treatments appeared to show fewer visual defects caused by aphids ("pricked fruits"), without positively affecting marketable yield. This result cannot be attributed to aphid dynamics during the growing season, in contrast with a study showing a correlation between the maximum percentage of shoots with *Dysaphis plantaginea* colonies and the damage observed in different apple cultivars in the field (Miñarro and Dapena, 2007). Other agronomic performance measures were not affected by the presence of peppermint, although weed competition, which can be associated with a CP, tends to reduce the number and weight of fruits per tree (Glenn and Newell, 2008; Tworkoski and Glenn, 2010), as well as the sucrose content of peach fruits (Morandi et al., 2008). However, it appeared that the presence of peppermint in combination with the nitrogen factor affected some peach growth indicators over time. SLA and leaf nitrogen content decreased in the 120N and 180N peppermint treatments in 2022 and 2023 compared to the 0N treatments in 2021, suggesting competition for nutrients and water between intercropping and trees (Gao et al., 2013; Luo et al., 2023), which could limit tree growth (Novara et al., 2021).

Our analyses could not confirm that peppermint VOC emissions respond positively to increases in nitrogen fertilisation or temperature. The experiment was limited by the narrow range of nitrogen levels tested, due to the absence of sampling in the 60N and 180N peppermint treatments. For a more comprehensive understanding of the mechanisms involved, future studies should increase VOC sampling capacity to better characterise emission dynamics across the full nitrogen gradient. Peppermint VOC emissions also did not respond to peppermint coverage rate. A more precise characterisation of peppermint biomass, considering other plant traits such as height, nutritional status, and phenological stage, would also be valuable in future experiments (Holopainen and Gershenzon, 2010; Zheljazkov et al., 2010; Dardouri et al., 2021). Other parameters may also have interfered with VOC emission, including agricultural practices and environmental conditions. The present work shows the importance of limiting practices, such as plant protection, to assess the impact of CPs and homogenise weed and peppermint management. Biocontrol products were applied during years of high aphid pressure, diluting the potential effect of CPs in untreated plots. Future experiments must avoid applying biocontrol products, strictly control weed development across all treatments, and remove or cut CPs more regularly each year. Secondly, environmental factors such as relative humidity, temperature, and light interception (Davis et al., 2006), as well as conditions during the previous winter, which can partly influence aphid pressure, should be recorded to include these variables as covariates in future experimental analyses.

We noted a contrast between the efficacy of peppermint under controlled conditions and the present field data. Given the high variability of VOC composition over time, it will be necessary to conduct VOC assays under controlled conditions to identify how aphids respond to specific compounds or VOC blends. Moreover, as natural enemies may also influence aphid regulation, future experiments should include observations of natural enemies, since there may be correlations among their abundance, plant volatile emissions, and nitrogen content in peach trees.

Regarding the mechanisms involved in modulating nitrogen fertilisation and competition, we confirmed its potential role in aphid regulation but also underlined the difficulty of implementing it during a multi-year experiment. Additional surveys could help to determine how to modulate it more efficiently. It would also be useful to integrate the total count of peach shoots per tree to characterise overall tree growth and to analyse, for example, the potential dilution effect on aphid incidence. The severity of aphid colonies should likewise be recorded to better characterise aphid population dynamics. Moreover, the analysis of plant defence-related metabolites in peach shoots could help to explain the reduced aphid performance observed under the highest nitrogen level. Thus, better characterisation of tree shoots and aphid dynamics, as suggested previously, together with long-term experiments, would be valuable to study the impact of CP intercropping on agronomic performance over the lifetime of an orchard.

5. Conclusion

The objective of this study was to determine whether the combination of nitrogen fertilisation and peppermint ground cover could modify the incidence of *M. persicae* in a peach orchard. In the present study, we identified specific volatile compounds around peach trees associated with peppermint. Peppermint VOC emissions were higher in the 120N treatments compared to the 0N treatments, but we could not relate this increase in VOCs to peppermint coverage rate. Peach tree growth, nitrogen status indicators, and agronomic performance responded positively to nitrogen fertilisation. Increased peach vigour may have led to a reduction in aphid infestation, but this effect depended on the year. It appeared that *M. persicae* incidence was not affected by the presence of peppermint, although peppermint cover appeared to improve the visual appearance of harvested fruits in relation to aphid damage, in some years, without affecting yields or fruit quality.

The experimental data acquired in this study provided valuable insights into the practical limitations of the experiment and suggested areas for improving future experiments. This system-specific knowledge on pest dynamics under the influence of nitrogen and peppermint interplanting may form part of the implementation of IPM strategies, in line with national and European policies for the transition to sustainable agriculture. However, this strategy raises issues of experimentation and evaluation, which need to be addressed to ensure widespread adoption. The challenge for our future work is to gain a deeper understanding of the ecological mechanisms driving pest regulation and to demonstrate how farmers can apply this knowledge as practical agricultural alternatives to chemical pesticides, without technical complexity or economic losses.

CRediT authorship contribution statement

Julie Borg: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Conceptualization. **Guy Costagliola:** Writing – review & editing, Investigation, Formal analysis. **Claude Castella:** Writing – review & editing, Investigation, Formal analysis. **Gilles Vercambre:** Writing – review & editing. **Hélène Gautier:** Writing – review & editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2025.107434.

Data availability

Data will be made available on request.

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