



Intercropping organic broccoli with *Rhododendron tomentosum* and *Fagopyrum esculentum*: a test of bottom-up and top-down strategies for reducing herbivory

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Abstract

Brassicaceous plants are attacked by a wealth of specialist herbivores that include the Diamondback moth (DBM) *Plutella xylostella* L. (Lepidoptera: Plutellidae), control of which requires novel biocontrol strategies. DBM is a cosmopolitan pest causing damage that varies yearly in Finland depending on the timing and extent of their migration. Intercropping with companion plants can hamper host location by herbivores or attract their natural enemies. We tested two sustainable companion plant-based protection strategies on field-grown broccoli (*Brassica oleracea* var. *italica*), which comprised 1) aromatic and repellent-releasing *Rhododendron tomentosum* (RT) (bottom-up strategy), and 2) nectar-producing buckwheat *Fagopyrum esculentum* (FE) (top-down strategy) combined with an early-season floating row cover (mechanical control) (MC + FE). In addition, a control (no companion plant or cover) and mechanical control (MC) without FE were included. DBM adults on yellow sticky traps and larvae on plants were counted, and feeding damage on leaves was quantified. Volatile organic compounds emitted by broccoli plants in control and RT plots, and emitted by boundary RT plants in RT plots, were identified and quantified. There was a mass outbreak of DBM in early summer with a population peak in mid-July when the second adult generation emerged. DBM adult densities were significantly lower in RT and MC + FE than in control plots. Broccoli in RT plots had a lower larval density and lower damage intensity than in control plots in the early-season. Larval densities and damage intensities were the highest in the latter half of July. Control plots had the highest number of larvae followed by RT, MC, and MC + FE plots. Damage intensities in control plots were significantly higher than in all other treatments throughout the season. Damage intensity was lower in MC and MC + FE plots than in RT plots at the end-of-July. *R. tomentosum* emitted two characteristic sesquiterpene alcohols, palustrol and ledol, but no evidence of adsorption and re-release of these compounds from *Brassica* plants grown in RT plots was found. We conclude that incorporating RT as a boundary plant and using a mechanical row cover reduces DBM damage on broccoli, but further multi-year trials under varying degrees of pest pressure are needed.

Keywords *Plutella xylostella* · Integrated pest management · Floating row cover · Plant volatiles · Sesquiterpenes · Insect-plant interactions

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Introduction

Achieving food security is a global priority, which needs to be accomplished in the midst of a generally growing population in much of the developing world (Fróna et al. 2019). Many insect pests can destroy crops and there are estimations that over 45% of annual global food production is lost to pests (Abhilash and Singh 2009). The predominant insect pest management methods are based on synthetic pesticides. However, the development of novel, non-toxic insect pest control methods, e.g. the use of intercropping and companion plants or the use of natural chemicals as biopesticides that have pest repellent or crop plant defence-inducing properties, is critical for more sustainable production of pest-prone field crops and vegetables.

Intercropping vegetables with pest-regulating companion plants (CPs), i.e. having pest-sensitive vegetables accompanied by non-sensitive, non-host plants (Ninkovic et al. 2021; Parolin et al. 2012; Stenberg et al. 2015) could be a potential solution for insect pest control and overcome the drawbacks of chemical pesticides. Some CP strategies are being used as promising alternative pest control methods, notably against aphid pests (Hemiptera: Aphididae) (Ben-Issa et al. 2017; Baudry et al. 2021). Intercropping with CPs diversifies the cropping system and consequently alters resource availability for pests and their natural enemies. In many cases, CPs influence insect herbivores by both bottom-up (i.e. reinforcing host plant defences against pest insects) (Han et al. 2022; Stenberg et al. 2021) and top-down (i.e. enhancing biocontrol by attracting natural enemies) strategies (Ben-Issa et al. 2017; Baudry et al. 2021). Moreover, CPs with specific properties, such as the nectar-providing flowering CP buckwheat, (*Fagopyrum esculentum* Möench; Polygonales: Polygonaceae), may confer additional protection to early-season mechanical control by row covers (MC) by attracting natural enemies (top-down approach) (Sarkar et al. 2018). Row covers are typical early-season mechanical pest control measures for growing organic products, therefore, MC serves as a reference pest control method (Dhokal and Nandwani 2020).

Volatile organic compounds (VOCs) are produced by plants and are emitted mostly by flowers and foliage (Sarkar et al., 2018; Hammerbacher et al. 2019). These compounds are sensed by many animals including insects and have important roles in ecosystem function. VOCs attract pollinators, can protect plants directly against both herbivores and microbes (Hammerbacher et al. 2019) and can act in plant communication with herbivores and their natural enemies (Coco et al. 2022). Moreover, earlier results from laboratory (Mofikoya et al. 2018b) and field (Baudry et al. 2021) studies have supported the use of non-host plants with specific VOC characteristics in

CP strategies to reduce herbivore pressure on crop plants. In a natural environment, *Rhododendron tomentosum* Harmaja (Ericaceae) (RT), a perennial shrub, is a strong VOC emitter with leaves covered by easily rupturing glandular trichomes that store VOCs. In an earlier study, it was detected that RT-released semi-volatile organic compounds (RT SVOCs) were on neighbouring birch trees (Himanen et al. 2010). Higher emission rates in the morning than the afternoon indicated a loss of these compounds during foliage warming. Dampc and Luczkiewicz (2013) also suggested that RT compounds can be used to manage agricultural insect pests as a potential environmentally friendly alternative to synthetic insecticides. In the laboratory, *R. tomentosum* had a high emission rate of volatile terpenoids such as mono- and sesquiterpenes (Butkienė et al. 2008), which are a potential determinant of reduced oviposition and larval feeding by Diamondback moth (DBM) *Plutella xylostella* L. (Lepidoptera: Plutellidae) (Himanen et al. 2015) and *Pieris brassicae* (Lepidoptera: Pieridae) (Bui et al. 2021) on RT-exposed broccoli. This observation indicated that a beneficial environmentally acquired chemical camouflage was obtained through the adsorption of RT volatiles to broccoli leaves, which, importantly, did not disturb host selection and orientation of larval parasitoids of the herbivores (Bui et al. 2021). Extracts of RT leaves have been found to repel and inhibit feeding by bark beetles (Coleoptera: Scolytidae) feeding the large pine weevil (*Hylobius abietis* L., Coleoptera: Curculionidae), leaf beetles (Coleoptera: Chrysomelidae) (Egigu et al. 2011), and grain beetles *Tenebrio molitor* (Coleoptera: Tenebrionidae) (Kuusik et al. 1995), but did not repel widely distributed aphid pests (Dampc and Luczkiewicz 2013). Associational resistance based on adsorbed VOCs of neighbouring plants (Himanen et al. 2010; Mofikoya et al. 2018b) can be considered to represent a resource-dependent bottom-up mechanism for protecting crop plants from herbivory due to these VOCs being released from the host plant together with host plant VOCs in a temperature-dependent way (Schaub et al. 2010; Vidal and Murphy 2018).

Top-down strategies for regulating herbivores are based on natural enemies reducing herbivore numbers via predation or parasitism (Coco et al. 2022). Companion plants can produce floral nectar and pollen that supports beneficial insects, e.g. predatory aphidophagous hoverflies and parasitic wasps, and may attract insect pests, thus reducing pest pressure on food providing plants (Marques Arce et al. 2021). Reduced herbivory and substantial increases in predator and parasitoid species have been found in diversified agricultural habitats (Andow 1991; Lindgren et al. 2018; Marques Arce et al. 2021; de Groot et al., 2021). Moreover, buckwheat is an example of a CP that when flowering can release VOCs, e.g. phenylacetaldehyde and salicylaldehyde

that attracts natural enemies of *Brassica*-feeding herbivores (Marques Arce et al. 2021). *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae) is a parasitoid of DBM, which is a major insect pest of brassicaceous crops globally (Furlong et al. 2013). Lavandero et al. (2005) reported an increased parasitism rate of DBM by *D. semiclausum* in broccoli plots with buckwheat as a cover crop. Stenberg et al. (2021) documented the use of buckwheat as a potential CP for aiding the biocontrol of various agricultural pests, including various herbivorous Hemiptera. The nectar of buckwheat can attract insect pests that may serve as food for beneficial insects. However, *P. brassicae* L. parasitism was not affected by buckwheat strips in collard fields (Philips et al. 2014).

Evidence shows that VOCs contribute to plant defence indirectly by attracting natural enemies, and/or directly by repelling pest insects (Marques Arce et al. 2021; Baudry et al. 2021; Ninkovic et al. 2021). We had particular interest in SVOCs of RT plants because after emission into the atmosphere during warm daytime weather SVOCs can be condensed at lower night-time temperatures onto different surfaces, such as the leaves of neighbouring plants (Himanen et al. 2010), and can act on crop plant foliage as herbivore repellents (Mofikoya et al. 2018b).

In the present study, we tested the bottom-up strategy based of naturally well-defended RT plants with strong aromatic VOC emissions as a CP in comparison to no pest control or use of an early-season floating row cover as a reference pest control method on a one hand; the top-down strategy based on buckwheat as a CP to support mid- and late-season emerging natural enemies in order to provide additional protection to the early-season DBM reference control method on the other hand. The objectives of both the bottom-up and top-down strategies were to reduce 1) the density of adult DBM in traps, 2) the density of DBM larvae on plants and 3) and the amount of damage on broccoli. In addition, we also wanted to know whether RT VOCs are adsorbed to broccoli foliage and edible flower heads and if they are detectable in the morning and afternoon conferring potential VOC-mediated associational resistance.

Materials and methods

Field site

A field experiment was established in 2013 in an organically managed field plot located at the Karila research station (Mikkeli, Finland) maintained at the time by MTT Agrifood Research Finland (coordinates DD 61.68, 27.22). The soil type was fine sand with a pH of approximately 6. The experimental plots were fertilized manually using organic NPK fertilizer at 4000 kg ha⁻¹ (Arvo 4–1–2 NPK, Novarbo Ltd,

Eura, FI), micronutrient fertilizer at 400 kg ha⁻¹ (Micronutrient mixture, Yara Finland Ltd, Espoo, FI), calcium fertilizer at 400 kg ha⁻¹ (Kalsiumravinne Ca 21%, Yara Finland Ltd, Espoo, FI), and potassium fertilizer at 200 kg ha⁻¹ (Patentkali 25%, Honkajoki Ltd, Honkajoki, FI). Before planting, the area was ploughed and harrowed to remove weeds. Plots were prepared for planting with a rotary tiller and the area between the plots and surrounding the experiment were sown with timothy grass and mowed regularly. Manual weeding was done when the weed height was about 7–10 cm.

According to data from the Finnish Meteorological Institute, in the summer of 2013, the mean temperature in Mikkeli was 17.6°C in June (3.1°C above 30-year (1991–2020) average), 16.4°C in July (0.7°C below average), and 15.7°C in August (0.6°C above average). The precipitation sums were 58.7 mm in June (96 % of 30-year average), 53.3 mm in July (72 % average), and 81.6 mm in August (122 % average) 2013.

Experimental setup

The experiment was set up in a Latin Square design (4 × 4 = 16) with four blocks to control for variation in field characteristics as well as the surrounding area (Fig. S1). The total area of the experimental field was 32 m × 34 m = 1088 m² with four treatments and four replications (experimental plots measured 3.5 m × 5.5 m = 19.25 m²). In the middle of each experimental plot, there was a 1.5 m × 3 m observation plot including 15 broccoli plants. The observation plots were surrounded from two sides by strips of 1 m × 3.5 m of the used intercrop co-species or broccoli in Control treatments (Fig. S1).

The four treatments tested included: (1) Control: broccoli without insect pest management, surrounded by broccoli, (2) *R. tomentosum* (RT): repellent or odour masking treatment, broccoli surrounded by *R. tomentosum* plants (repellent SVOC-emitting CPs), (3) Mechanical cover (MC): early-season mechanical pest control with a floating row cover (commonly used method in open-field organic broccoli production). (4) Mechanical cover and *Fagopyrum esculentum* (MC + FE) (natural enemy attraction): broccoli surrounded by floral nectar providing buckwheat, *F. esculentum* plants combined with early-season mechanical pest control. *R. tomentosum* was hypothesized to confer early-season repellence or camouflage to broccoli and therefore could potentially serve as a replacement method for mechanical cover due to expected timing of the main effect coinciding with the typical time of use of row cover in Finnish vegetable farms. The main purpose of RT or MC as a pest management strategy is to prevent early-season herbivore arrival, whereas the uses of FE combined with MC are to associate a direct early-season effects on herbivores with FE for indirect

pest control by a hypothesized attraction and the support of natural enemies such as parasitic wasps when in bloom in mid and late season.

Plant material Four-week-old seedlings of Broccoli cultivar (cv.) ‘Monaco’ (seeds from Syngenta Ltd., Illinois, US, approximate days to maturity 98) were purchased from a local organic cabbage producer (Kalliolan Luomu, Mikkelin, FI) who had grown the seedlings under greenhouse conditions for approximately 30 days in 32 cm³ seed trays. Seedlings were planted in the field on June 4th, 2013. The distance between broccoli plants in a row and between rows was 50 cm. *R. tomentosum* seedlings for the experiments were produced at the Research Garden of the University of Eastern Finland Kuopio campus and were sown in 500 ml plastic pots in a peat: sand (1:1) mixture at the end of November 2012. *R. tomentosum* plants were grown for 6 months in greenhouse conditions until they were transferred to the experimental field and planted on June 4th, 2013. Buckwheat (organic seed, Hyötykasviyhdistys, Helsinki, FI) was manually seeded into the two boundary strips (1 m × 5.5 m) with inter-row spacing of 12.5 cm and intra-row spacing of 5 cm to achieve plant densities of 160 plants/m² and with a sowing depth of 3 cm. Between June 4th and July 1st, MC and MC + FE were covered with a protective floating non-woven row cover (17 g m⁻²) made of polypropylene microfiber to prevent herbivorous insect arrival but letting moisture and light pass.

Monitoring of Diamondback moth adults and larvae and broccoli damage assessment

One yellow sticky trap (10 cm × 25 cm, model Horiver[®], Koppert biological systems, Berkel en Rodenrijs, Netherlands) was set at the seedling top level next to experimental plants in the middle of the longer plot side of each experimental plot. The traps were positioned outside of the cover in covered plots. These traps were used to monitor DBM adult flight activity starting when the experiment was established on June 4 and ending on July 29 (Fig. 1). Traps were changed at 6- or 8-day intervals and DBM adults were counted under a binocular stereomicroscope (Nikon model SMZ800, Nikon healthcare, Tokyo, Japan).

Observations of DBM larvae were conducted over the growing season by visual inspection of leaves, with larvae counts made at 6 to 8-day intervals. At the first observation point, 10 plants were randomly selected for each plot, and latter observations were made from these same plants. Other foliage-feeding insects and predators were occasionally observed, but only DBM larvae were consistently monitored. From June 17th to July 1st, no monitoring of DBM larvae was done for the MC and MC + FE treatments due to the plots being covered. On July 1st, row covers were removed from the MC and MC + FE plots and DBM larvae were recorded from July 16th to 29th as in the C and RT plots. The recorded damage intensities on all 15 broccoli plants per plot for all treatments were assessed visually using scale

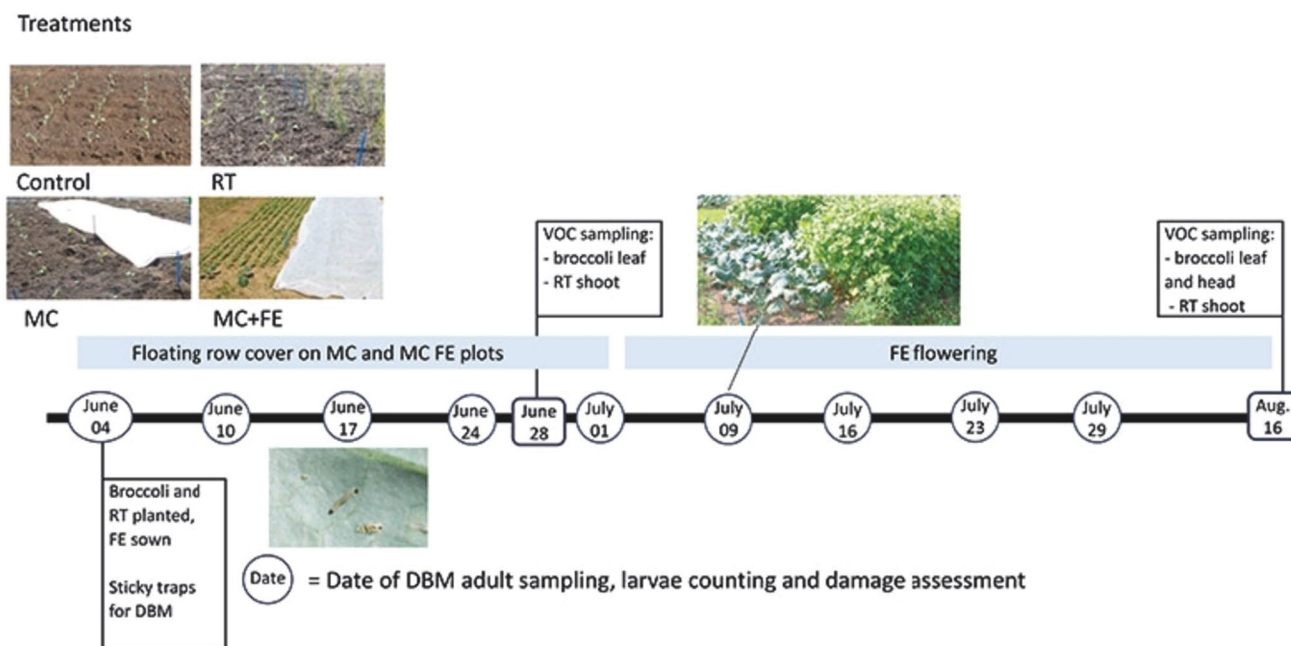


Fig. 1 Timeline showing the Diamondback moth (DBM) *Plutella xylostella* monitoring, VOC sampling dates and the time periods for floating row cover use and flowering buckwheat (*Fagopyrum esculen-*

tum (FE) Mönch) border for maintenance of natural enemies. Photos illustrate the experimental plots in early-season, the flowering of *F. esculentum*, and DBM larvae on a broccoli leaf

evaluations of 0–5 (0 = no damage, 5 = severe damage, with approximate percentages of damaged leaf areas as follows, 0 = 0%; 1 = 0.1–10.0%; 2 = 10.1–25.0%; 3 = 25.1–50.0%; 4 = 50.1–75%; 5 > 75%).

VOC sampling

VOC samples were collected using a portable volatile collection system (Mäntylä et al. 2008) on two occasions: June 28 and August 16th, 2013. In the first collection round, the whole above-ground part of the young broccoli or RT plants was enclosed in a sampling bag. One randomly selected broccoli plant per Control and RT plot was sampled twice; the first sampling was from 09:00 to 12:00 and the second sampling from 13:00 to 15:00. One plant from a control plot and one plant from an RT plot were sampled with a two-channel sampling system at the same time. The aim was to determine whether morning samples had an indication of RT volatiles on the broccoli foliage and if these were still detectable in the afternoon. In addition, whole shoot VOC sampling of one boundary RT plant per plot was carried out once in the afternoon after 13:00 on the same day to have the highest emission rate of RT VOCs for detection. Control blank samples were collected from empty bags to test the efficiency of input air filtering. On the second VOC sampling date, single collections were made from a leaf and a head of one broccoli plant per plot for Control and RT treatments. A shoot of one boundary RT plant per plot was also sampled. Plant samples were enclosed in disposable pre-cleaned (heated at 120°C for 1 h) polyethylene terephthalate (PET) cooking bags (35 × 43 cm, Look Iso-pussi, Euracoon Oy, Finland) that were secured around the plant with thin garden wire. The air temperature inside the PET bags was recorded with wireless loggers (Hygrochron DS1923-f5 iButton, Maxim Integrated Products, San Jose, CA, USA), while air temperature outside the collection bag at the canopy level and photosynthetically active radiation (PAR) inside an empty bag were also recorded during VOC collections (S-LIA-M003 for PAR and S-THA-M006 for temperature; Hobo Micro Station, Onset Computer Corporation, Bourne, MA, USA).

After enclosing the plant, a hole was cut in an upper corner of the bag and a Teflon® air inlet tube was inserted into each bag and secured with thin garden wire. Air was passed at a flow rate of 600 ml/min through a charcoal-filter and an MnO₂ scrubber (to remove ozone) and into the PET bags for 10 min to flush out residual contaminants. Stainless steel tubes filled with 150-mg of Tenax TA adsorbent (Supelco, Bellefonte, PA, USA) were inserted at a second corner of the bag and fastened with another garden wire. A silicone sampling line was attached to the adsorbent-filled tube. The inflow of air into the bags was reduced to a rate 300 ml/min and VOC samples were pulled through the adsorbent-filled

tubes at a rate of 200 ml/min with a vacuum pump (Thomas 5002 12 V DC, Gardner Denver, Inc. Milwaukee, WI, USA). The volatile sampling time for blank sample and RT plants was 15 min, while for broccoli plants it was 30 min. Adsorbent-filled tubes were sealed with Teflon-coated brass caps immediately after collection. During transportation to the lab, they were kept in cold boxes at +4 °C and stored in a refrigerator until analysis. Lastly, sampled plants were harvested, and oven dried at 60 °C for 72 h to provide plant biomasses for expression of the emission rates.

VOC analyses

All VOC samples were analysed by thermal desorption gas chromatography-mass spectrometry (GC–MS) (GC type 6890, MSD 5973; Hewlett Packard; Wilmington, DE, USA) as described by (Blande et al. 2009). Trapped compounds were thermally desorbed using an automatic thermal desorber (ATD400, Perkin Elmer, USA), at 250 °C for 10 min, and cryofocused at – 30 °C in a liquid nitrogen cooled cryotrap and injected onto an HP-5 capillary column (the type of column: 50 m × 250 µm × 0.25 µm, Hewlett Packard). The carrier gas used was helium. The temperature program sequence was as follows: 50 °C for 1 min, increases of 5 °C min⁻¹ to 210 °C and by 20 °C min⁻¹ to 250 °C with a final hold time of 1.5 min. Emitted compounds were identified and quantified using synthetic standards (Himanen et al. 2009) and verified with the Wiley mass spectral library. However, ledene and palustrol standards were not available, so a ledol standard (ChemDiv Inc., Del Mar, CA, USA) was used to calculate their emissions. Emissions are expressed in ng g⁻¹ leaf DW h⁻¹. VOCs detected in blank samples were subtracted from the totals present in the samples to determine the actual emissions from plants.

Statistical analysis

Linear Mixed Model analyses were carried out for three response variables, DBM adult density (number of adults per sticky trap), DBM larval density (number of larvae per broccoli plant), and damage intensity, using the GLIMMIX procedure of SAS 9.4 software (SAS Institute Inc., Cary, NC, USA). In all models, treatment (control, *R. tomentosum*, MC and MC + FE), time and their interaction were used as fixed effects. As the set-up followed a Latin square design, the row and column were included as random effects. For DBM adult density, one model including all eight time periods was used. For DBM larval density and damage intensity, two separate models were used. The first model included the first four time periods and control and RT as treatments. The second model included the three last periods and all four treatments: control, RT, MC, and MC + FE. The normal distribution assumption seemed sufficient for all response

variables, but the correlation and variance of observations were defined separately for each response variable. Differences in treatment means and periods were compared using the Bonferroni method with a 0.05 significance level. In the case of a significant treatment \times time interaction, the treatments were compared separately for each time point. All models were fitted using the restricted maximum likelihood estimation method. The degrees of freedom were calculated using the Kenward-Roger method.

Statistical analyses of VOC data were conducted with the statistical package IBM SPSS statistics 25.0 for Windows (IBM Corp., Armonk, NY, USA). Two-way Anova (Treatment, Time, Treatment*Time) was used to test for differences in the broccoli VOC emission rates (ng g^{-1} day wt h^{-1}) from control and RT plots in the morning and afternoon in June. Differences between control and RT treatment VOC emission rates from broccoli leaves and head in August were tested with independent samples t-tests. Differences in RT VOC emission rates between RT treatments in June and August were analysed using the Mann–Whitney U test because data could not be normalized.

Results

DBM adult monitoring

The density of DBM adults peaked in control plots in the week ending June 24th (14.5 moths/trap) and July 16th (16.5 moths/trap) (Fig. 2). There were significant main effects of treatment ($F_{3,26} = 9.31$, $P = 0.0002$) and time ($F_{7,32} = 23.31$, $P < 0.0001$). The number of DBM adults per yellow trap was higher in the control plots than in the RT and MC+FE plots ($t_{25,8} = 4.78$, $P = 0.0004$ and $t_{25,8} = 4.21$, $P = 0.0016$, respectively). The density of DBM adults was significantly lower in the week ending on July 23rd than in all other weeks (Jun 10th: $t_{16,5} = 4.12$, $P = 0.007$; Jun 17th $t_{16,8} = 6.1$, $P < 0.0001$; Jun 24th: $t_{20,0} = 7.71$, $P < 0.0001$; July 01st: $t_{23,4} = 4.92$, $P = 0.0007$; July 9th: $t_{19,6} = 9.69$, $P < 0.0001$; July 16th: $t_{12,7} = 7.27$, $P < 0.0001$; July 29th: $t_{20,9} = -6.90$, $P < 0.0001$). In addition, DBM density was significantly lower in the week ending on July 1st than in weeks ending on June 17th ($t_{17,5} = 3.69$, $P = 0.0229$), June 24th ($t_{17,5} = 4.64$, $P = 0.0016$), July 9th ($t_{21,6} = -5.68$, $P < 0.0001$), and July 16th ($t_{15,7} = -4.09$, $P = 0.0075$). DBM density was significantly higher in the week ending on July 9th as well as the peak week ending on July 16th than in the week ending on July 29th ($t_{22,0} = 3.99$, $P = 0.0101$ and $t_{15,7} = 3.54$, $P = 0.0352$, respectively).

DBM larval density on broccoli

In observations of herbivore densities on broccoli plants, DBM larvae were the main leaf-feeding herbivore species

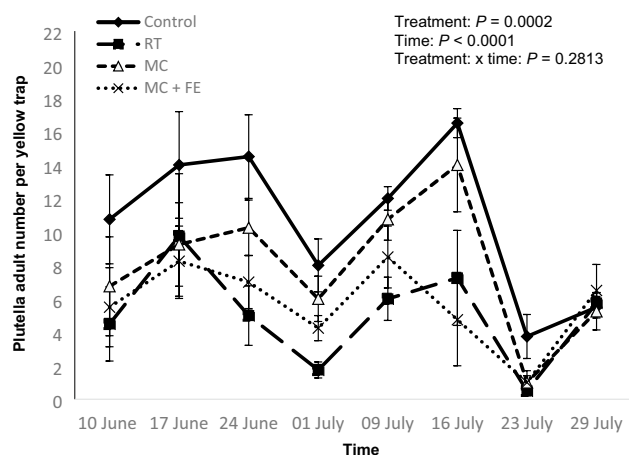


Fig. 2 Mean *P. xylostella* (DBM) adult density (\pm SE) on yellow sticky traps with P -values representing the main effects of treatment, time, and their interaction (linear mixed model analysis, $n = 4$ per treatment-time combination). Four treatments: Control = broccoli, *Rhododendron tomentosum* (RT) = broccoli with *R. tomentosum* plants (repellent/odour masking plant) border, Mechanical control (MC) = broccoli with mechanical control, and MC+FE = broccoli with mechanical control plus buckwheat (*Fagopyrum esculentum* (FE) Mönch) border for maintenance of natural enemies

detected. There were significant main effects of treatment ($F_{1,5} = 9.75$, $P = 0.0241$) and time ($F_{3,6} = 15.6$, $P = 0.0027$) on DBM larval density during the first 4 weeks of the season when only control and RT plots were assessed (Fig. 3). DBM larval densities on broccoli plants were higher in the Control than RT plots during this period ($t_{5,3} = 3.12$, $P = 0.0241$). In the first week, ending on June 17th, there were fewer larvae on plants than in the following 3 weeks (Jun 24th: $t_{7,3} = -6.67$, $P = 0.0028$; Jul 01st: $t_{6,2} = -4.28$, $P = 0.0289$; Jul 09th: $t_{4,9} = -4.83$, $P = 0.0159$, respectively).

In July, during the weeks ending July 16th, 23rd, and 29th, all four treatments were assessed. There were significant main effects by treatment ($F_{3,15} = 86.8$, $P < 0.0001$) and time ($F_{2,16} = 22.8$, $P < 0.0001$) as well as a significant interaction effect between treatment and time ($F_{6,17} = 3.84$, $P = 0.0128$, Fig. 3). In this period, higher larval density was found in control than in all other treatments for the weeks ending on July 16th and July 23rd (July 16th: C vs MC $t_{9,2} = 9.55$, $P < 0.0001$, C vs RT $t_{15,4} = 4.95$, $P = 0.0007$, C vs MC+FE $t_{9,5} = 9.95$, $P < 0.0001$; July 23rd: C vs MC $t_{9,2} = 10.1$, $P < 0.0001$, C vs RT $t_{15,4} = 5.73$, $P = 0.0001$, c vs MC+FE $t_{9,5} = 10.37$, $P < 0.0001$). In the last week of July, control plots had a significantly higher DBM density than MC and MC+FE plots ($t_{9,2} = 4.58$, $P = 0.0015$ and $t_{9,5} = 5.23$, $P = 0.0004$), while there was only a marginally significant difference between C and RT plots ($t_{15,4} = 2.66$, $P = 0.0976$). RT plots had a higher larval density than MC and MC+FE plots in the weeks ending July 16th (RT vs MC $t_{9,3} = -5.6$, $P = 0.0002$; RT vs MC+FE $t_{10,0} = 6.22$, $P <$

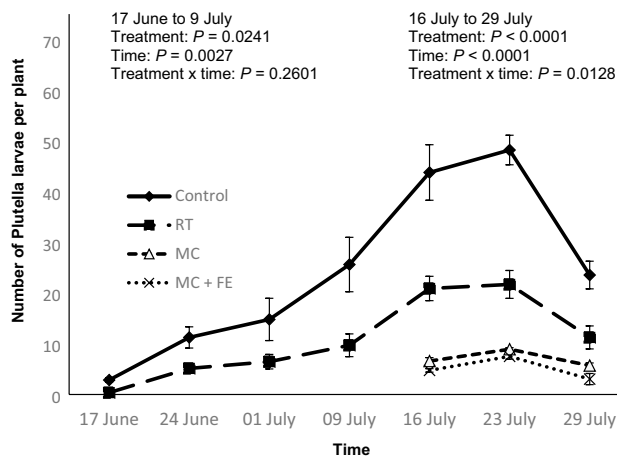


Fig. 3 Mean density (\pm SE) of *P. xylostella* (DBM) larvae per broccoli plant with *P* values representing the main effects of treatment, time, and their interaction (linear mixed model analysis, $n=4$ per treatment–time combination). The data obtained were analysed to test differences from June 17 to July 09 (between two treatments of Control and *R. tomentosum*); and between July 16–29 (between four treatments). Four treatments: Control=broccoli, *R. tomentosum* (RT)=broccoli with *R. tomentosum* (repellent/odour masking plant) border, MC=broccoli with mechanical control, and MC+FE=broccoli with mechanical control plus buckwheat (*F. esculentum* Mönch) border for maintenance of natural enemies

0.0001) and July 23rd (RT vs MC $t_{9,3} = -5.0$, $P = 0.0006$; RT vs MC+FE $t_{10,0} = 5.46$, $P = 0.0002$). In the last week of July, RT plots differed significantly only from the MC+FE plots, which had the lowest larval density ($t_{10,0} = 3.16$, $P = 0.0338$). Larval densities in the MC plots were also higher than densities in the MC+FE plots in that week ($t_{13,3} = 3.55$, $P = 0.0145$).

Herbivore damage intensity

In the first 4 weeks of the season, broccoli plants in the control plots had a higher mean herbivore damage intensity than those in the RT plots (Fig. 4, $F_{1,3} = 33.8$, $P = 0.0161$). There was also a significant main effect of time ($F_{3,15} = 18.8$, $P < 0.0001$). Damage intensity was higher in the weeks ending on July 1st and 9th than in the first week ($t_{20,1} = -3.96$, $P = 0.0073$; $t_{17,2} = -7.2$, $P < 0.0001$) and further increased in the week ending July 9th compared to the two previous weeks (Jun 24th vs July 9th $t_{20,1} = -6.1$, $P = 0.0001$; July 1st vs July 9th $t_{15,8} = -5.62$, $P = 0.0003$).

During the 4 weeks of July when damage intensity in all four treatments was assessed, there were significant main effects of treatment ($F_{3,6} = 30.8$, $P = 0.0006$) and time ($F_{2,23} = 6.0$, $P = 0.0079$) plus a significant interaction between treatment and time ($F_{6,23} = 12.1$, $P < 0.0001$, Fig. 4). Damage intensity was higher in control than in all other treatments during this period (C vs MC $t_{5,8} = 7.0$, $P = 0.003$; C

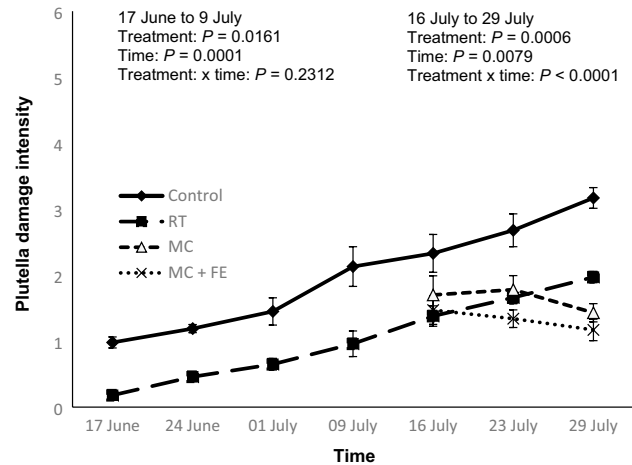


Fig. 4 Mean *P. xylostella* (DBM) damage intensity (\pm SE) per broccoli plant with *P* values representing the main effects of treatment, time, and their interaction (linear mixed model analysis, $n=4$ per treatment–time combination). The data obtained were analysed to test differences from June 17 to July 09 (between two treatments of Control and *R. tomentosum*); and between July 16–29 (between four treatments). Four treatments: Control=broccoli, *R. tomentosum* (RT)=broccoli with *R. tomentosum* (repellent/odour masking plant) border, MC=broccoli with mechanical control, and MC+FE=broccoli with mechanical control plus buckwheat (*F. esculentum* Mönch) border for maintenance of natural enemies

vs MC+FE $t_{5,8} = 9.0$, $P = 0.0008$; C vs RT $t_{5,8} = 6.78$, $P = 0.0035$). In the last week of July, the RT plots had a significantly higher damage intensity than MC and MC+FE plots ($t_{9,5} = -3.04$, $P = 0.0353$ and $t_{9,5} = 4.48$, $P = 0.001$), while there was no difference between MC and MC+FE plots.

VOC emission from *R. tomentosum* plants

The total VOC emission rate of *R. tomentosum* plants (Table 1) grown in the RT plot boundaries was more than three times higher on June 28th than on August 16th. The specific *R. tomentosum* SVOCs ledol and palustrol were detected on both sampling dates. In the June 28th sampling, the dominating compounds in the VOC emissions were bornyl acetate, palustrol, γ -terpinene, α -terpinene, and sabinene, whereas in the August 16th sampling, the dominating compounds were β -myrcene, palustrol, β -ocimene, limonene, and γ -terpinene. Significant reductions in emission rates of α -terpineol, linalool, and (*E*)-DMNT were found in the August samples while trans- β -farnesene was detected only in the June samples.

VOC emissions from broccoli plants

On June 28th (Table 2), the total VOC emission rate of Control plants in the morning was more than 1.6 times higher than in the afternoon sampling. The dominating compounds

Table 1 *Rhododendron tomentosum* emissions rates (ng g⁻¹ day wt h⁻¹, mean ± SE, n=4) on June 28 and August 16 from boundary plants of *R. tomentosum* plots

	Compound	Chemical group	<i>R. tomentosum</i> VOCs		P value
			Jun 28	Aug 16	
	Monoterpenes	C10			
1	α-Thujone	Ketone, monoterpene (MT)	153.70 ± 94.71	50.97 ± 41.59	0.29
2	α-Pinene	MT	760.09 ± 506.13	259.34 ± 229.57	0.294
3	Camphene	MT	609.46 ± 421.19	136.69 ± 113.62	0.345
4	Sabinene	MT	788.49 ± 532.38	221.04 ± 203.03	0.654
5	β-Pinene	MT	626.62 ± 409.16	208.47 ± 200.30	0.501
6	β-Myrcene	MT	84.48 ± 51.56	949.73 ± 908.10	0.829
7	3-Carene	MT	13.36 ± 5.34	5.05 ± 5.05	0.074
8	Limonene	MT	ND	382.14 ± 379.16	0.144
9	1,8-Cineole	MT	ND	3.96 ± 2.77	0.144
10	Allo Ocimene	MT	262.6 ± 168.69	227.76 ± 135.18	0.594
11	α-Phellandrene	MT	685.18 ± 466.1	180.82 ± 175.10	0.355
12	γ-Terpinene	MT	1804.01 ± 1204.02	349.77 ± 333.20	0.832
13	α-Terpineol	MT alcohol	34.55 ± 17.8	ND	0.027*
14	α-Terpinene	MT	1530.40 ± 1000.66	ND	0.29
15	β-Ocimene	MT	715.8 ± 481.56	477.51 ± 304.26	0.594
16	Terpinolene	MT	255.13 ± 162.13	51.65 ± 43.90	0.501
17	Linalool	MT alcohol	48.85 ± 27.24	ND	0.027*
18	Borneol	MT alcohol	465.58 ± 344.5	14.86 ± 11.61	0.228
19	Terpinen-4-ol	MT alcohol	109.13 ± 70.87	21.31 ± 17.86	0.228
20	Bornyl Acetate	Borneol derivative (C12)	2553.02 ± 1664.92	114.97 ± 94.41	1
21	E DMNT	Homoterpene (C11)	37.67 ± 21.59	ND	0.027*
	Sesquiterpenoids	C15			
22	α-Humulene	Sesquiterpene (SQT)	8.74 ± 5.72	ND	0.144
23	Aromadendrene	SQT	364.68 ± 261.42	74.25 ± 24.75	0.642
24	γ-Elemene	SQT	227.08 ± 161.68	ND	0.027*
25	Trans-β-Farnesene	SQT	ND	87.12 ± 49.50	<0.001***
26	Palustrol	SQT alcohol	2333.55 ± 1716.82	516.28 ± 391.63	0.829
27	Ledol	SQT alcohol	587.4 ± 442.91	97.53 ± 67.31	1
	GLVs				
28	Z-3-hexenyl acetate	Acetate (GLV)	0 ± 0	5.17 ± 3.39	0.144
29	Nonanal	Aldehyde	13.16 ± 10.21	ND	0.144
	Total VOCs		14 236.13	4 177.05	–

ND not detected

Statistically significant differences are indicated by asterisks (Mann Whitney U test, "*" at $P < 0.05$; "***" at $P < 0.001$)

emitted in the morning and afternoon were (Z)-3-hexenyl acetate, sabinene, limonene, β-myrcene, and 1, 8 cineole. The only compound for which emission rate was significantly affected by both sampling time ($P < 0.001$; $P = 0.001$) and RT treatment ($P < 0.001$; $P = 0.008$) was 1-tridecene, which was emitted at lower rates from RT plots. None of the compounds showed an interactive effect of treatment × sampling time. Emission rates of β-ocimene, terpinolene, and α-terpinen were higher in Control plants than in RT plots ($P < 0.05$; $P = 0.036$; $P = 0.024$; $P = 0.020$, respectively). Sampling time on the day affected the emission rates of α-terpinene, (E)-DMNT, methyl salicylate,

and terpinen-4-ol ($P < 0.05$; $P = 0.037$; $P = 0.034$; $P = 0.041$, respectively). Herbivore-induced (E)-DMNT and methyl salicylate were emitted at higher rates in the morning. Emissions of typical herbivore-induced "green leaf volatiles" (GLVs) (Z)-3-hexenyl acetate and (Z)-3-hexen-1-ol were not significantly affected by sampling time or RT plot, but (Z)-3-hexenyl acetate was emitted at very high rates from some of the control plants in the morning sampling.

On August 16th (Table 3), in an analysis of broccoli VOC emission rates of individual compounds from both leaves and heads, there was no significant difference between treatments, except that the β-myrcene emission rate from broccoli heads

Table 2 Broccoli VOCs emissions ($\text{ng g}^{-1} \text{ day wt h}^{-1}$, mean \pm SE, $n=4$) VOC emission rates ($\text{ng g}^{-1} \text{ day wt h}^{-1}$) in the morning (from 10.30 am to mid-noon), and afternoon sampling (between 1.45 and 4 pm) from the whole broccoli plant in Control and *R. tomentosum* plots on June 28

Treatment	Compounds	Control		RT		P values		
		Morning	Afternoon	Morning	Afternoon	Time	Tr	Time*Tr
1	α -Thujone	75.74 \pm 37.77	117.1 \pm 39.47	58.63 \pm 17.81	71.65 \pm 23.58	0.389	0.323	0.652
2	α -Pinene	37.73 \pm 15	56.78 \pm 15.69	35.29 \pm 7.65	38.08 \pm 9.44	0.388	0.403	0.519
3	Camphene	7.26 \pm 3.26	19.33 \pm 11.08	7.34 \pm 3.24	4.83 \pm 2.96	0.446	0.253	0.248
4	Sabinene	362.46 \pm 198.2	569.61 \pm 217.45	246.22 \pm 95.75	339.31 \pm 134.57	0.381	0.313	0.738
5	β -Pinene	24.45 \pm 8.12	36.45 \pm 6.9	23.01 \pm 2.43	25.99 \pm 3.83	0.206	0.313	0.442
6	β -Myrcene	112.63 \pm 58.39	203.77 \pm 73.94	80.61 \pm 26.12	114.73 \pm 39.43	0.098	0.055	0.393
7	α -Phellandrene	10.15 \pm 3.31	13.62 \pm 2.57	12.15 \pm 3.12	12.43 \pm 3.03	0.541	0.894	0.601
8	Δ -3-Carene	5.67 \pm 3.27	ND	11.16 \pm 3.56	5.48 \pm 3.31	0.063	0.072	0.999
9	α -Terpinene	10.09 \pm 7.57	25.72 \pm 2.9	13.8 \pm 3.59	20.31 \pm 1.82	0.021*	0.853	0.322
10	Cymene	6.91 \pm 1.74	19.29 \pm 4.51	7.99 \pm 2.54	9.24 \pm 1.4	0.094	0.165	0.051
11	Limonene	196.37 \pm 104.79	259.75 \pm 120.28	145.2 \pm 50.88	222.89 \pm 78.96	0.213	0.452	0.677
12	1, 8 Cineole	76.51 \pm 36.16	132.63 \pm 43.1	65.21 \pm 19.68	93.41 \pm 28.85	0.1	0.098	0.383
13	β -Ocimene	16.24 \pm 3.6	21.38 \pm 1.48	14.96 \pm 2.61	17.16 \pm 1.99	0.086	0.036*	0.569
14	γ -Terpinene	22.98 \pm 9.03	29.63 \pm 3.45	21.43 \pm 2.3	22.56 \pm 2.63	0.456	0.408	0.596
15	Terpinolene	14.87 \pm 4.26	23.03 \pm 1.86	16.15 \pm 2.83	17.12 \pm 2.64	0.142	0.024*	0.193
16	Nonanal	16.69 \pm 3.93	21.46 \pm 1.05	18.84 \pm 1.86	18.89 \pm 1.99	0.333	0.082	0.343
17	α -Terpineol	8.67 \pm 4.01	13.93 \pm 4.17	3.7 \pm 3.34	8.26 \pm 4.19	0.076	0.020*	0.433
18	1-Tridecene	21.61 \pm 4.38	41.58 \pm 4.46	9.26 \pm 2.06	17.80 \pm 2.18	0.008**	0.001***	0.168
19	α -Farnesene	22.17 \pm 5.45	29.98 \pm 3.34	24.7 \pm 4.29	28.39 \pm 3.79	0.19	0.913	0.634
20	(Z)-3-hexenyl acetate	2235.05 \pm 2081.11	298.92 \pm 201.29	105.46 \pm 40.72	507.9 \pm 442.92	0.479	0.377	0.283
21	(Z)-3- hexenyl-1-ol	ND	38.47 \pm 28.69	2.2 \pm 2.2	47.39 \pm 43.29	0.119	0.832	0.898
22	E-DMNT	12.99 \pm 3.78	11.02 \pm 3.92	15.21 \pm 3.36	10.39 \pm 4.06	0.037*	0.126	0.616
23	(Z)-3- hexenyl-butyrate	0.29 \pm 0.29	1.01 \pm 0.78	0.17 \pm 0.17	1.76 \pm 1.30	0.207	0.685	0.613
24	(Z)-3- hexenyl-isovalerate	1.03 \pm 0.60	2.69 \pm 1.51	0.50 \pm 0.31	1.48 \pm 0.86	0.175	0.42	0.706
25	Methyl salicylate	0.2 \pm 0.1	0.2 \pm 0.4	0.2 \pm 0.6	ND	0.034*	0.155	0.19
26	Allo Ocimene	ND	6.48 \pm 3.96	ND	ND	0.056	0.113	0.113
27	Camphor	3.43 \pm 3.18	4.98 \pm 3.44	ND	ND	0.744	0.083	0.335
28	Bornyl acetate	ND	5.05 \pm 3.79	ND	ND	0.194	0.194	0.194
29	Terpinen-4ol	ND	7.73 \pm 4.18	ND	3.65 \pm 3.3	0.041*	0.449	0.449
	Total VOCs	3302.19	2011.59	939.39	1661.1			

ND not detected

Statistically significant differences are indicated by asterisks (two-factor Anova, “*” at $P < 0.05$; “**” at $P < 0.01$; “***” at $P < 0.001$)

was higher from the RT treatment than from control plants ($P = 0.049$). The dominating volatile compounds in broccoli leaf and head emissions were β -myrcene, sabinene, limonene, *cis*-3-hexenyl acetate, and 1,8-cineole.

Detection of possible *R. tomentosum* volatiles from broccoli: The typical RT-specific semi-volatile sesquiterpene alcohols ledol and palustrol were not detected in broccoli plant emissions in the RT plots in any of the VOC samplings.

Discussion

Herbivore abundance and damage to broccoli intercropped with *R. tomentosum*

This field experiment was conducted in central-eastern Finland and showed reductions in DBM adult catch

Table 3 Average (\pm SE) VOC emission rates (ng g^{-1} day wt h^{-1}) from broccoli leaves and heads from control and *R. tomentosum* plots on August 16th

		Leaf		<i>P</i> value	Head		<i>P</i> value
		Control	RT		Control	RT	
1	α -Thujone	31.73 \pm 6.59	37.29 \pm 8.84	0.622	13.09 \pm 1.62	13.71 \pm 1.86	0.804
2	α -Pinene	25.50 \pm 3.69	38.88 \pm 14.64	0.402	12.25 \pm 1.99	12.53 \pm 1.96	0.922
3	Camphene	ND	13.16 \pm 10.82	0.263	ND	ND	–
4	Sabinene	120.37 \pm 42.22	138.25 \pm 49.26	0.787	25.31 \pm 3.42	24.75 \pm 4.60	0.924
5	β -Pinene	17.62 \pm 1.22	24.84 \pm 9.29	0.466	ND	1 \pm 0	–
6	β -Myrcene	44.90 \pm 11.15	58.52 \pm 17.13	0.518	15.48 \pm 1.58	20.84 \pm 1.91	0.049*
7	Z-3-hexenyl acetate	19.83 \pm 2.41	106.51 \pm 64.35	0.220	28.69 \pm 6.74	36.36 \pm 11.01	0.564
8	α -Phellandrene	8.35 \pm 3.41	27.61 \pm 18.71	0.343	ND	ND	–
9	3-Carene	2.68 \pm 2.50	ND	0.320	5.36 \pm 3.24	8.06 \pm 3.55	0.583
10	Limonene	77.71 \pm 23.13	152.47 \pm 86.83	0.430	14.65 \pm 2.75	14.02 \pm 2.92	0.876
11	1, 8-Cineole	41.07 \pm 8.32	42.58 \pm 9.48	0.906	14.08 \pm 2.66	13.56 \pm 2.89	0.896
12	β -Ocimene	6.76 \pm 3.29	28.35 \pm 25.44	0.427	ND	ND	–
13	γ -Terpinene	16.30 \pm 2.51	36.24 \pm 19.98	0.354	2.90 \pm 2.71	5.96 \pm 3.48	0.500
14	Terpinolene	13.73 \pm 3.53	15.99 \pm 6.01	0.752	ND	ND	–
15	Linalool	14.63 \pm 3.23	6.84 \pm 3.61	0.131	ND	ND	–
16	α -Terpineol	7.42 \pm 4.20	ND	0.121	ND	ND	–
17	Allo Ocimene	ND	13.54 \pm 10.52	0.239	ND	ND	–
18	Borneol	ND	4.92 \pm 3.43	0.194	ND	ND	–
19	1-Tridecene	23.42 \pm 3.36	29.25 \pm 4.39	0.311	13.61 \pm 4.72	19.26 \pm 3.91	0.351
20	Bornyl Acetate	ND	11.35 \pm 8.00	0.199	ND	ND	–
21	a-Farnesene	ND	5.00 \pm 4.25	0.278	ND	ND	–
	Total VOCs	472.02	791.59		145.42	170.05	

ND not detected

Statistically significant differences are indicated by asterisks (independent samples *T* test, “*” at $P < 0.05$, $P = 0.049$)

numbers, larval density, and foliar feeding damage in broccoli plots surrounded by RT plants compared to controls. This result supports earlier observations showing repellent properties of RT-VOCs to herbivorous insects (Himanen et al. 2010, 2015; Holopainen 2011; Mofikoya et al. 2019; Bui et al. 2021). Reduction in feeding damage intensity in RT treatments was comparable to that in covered plots where DBM attack was blocked mechanically with row covers. Larval densities and damage intensities on MC and MC + FE treatments were lower than on Controls at all observation times, but DBM adult density per trap did not differ between MC and Control treatments.

In the study year, 2013, there was a DBM outbreak with early arrival in Finland. The first individuals recorded on oilseed rape in southwestern Finland were detected on May 22nd and the highest number of DBM recorded on yellow sticky traps was on June 6th (Huusela-Veistola 2013). At the experimental site, the DBM population peaked approximately a week later and continued until June 24th. The intensity of the outbreak resulted in a high damage index on Control plants without any pest control measures. This suggests that when DBM appears at outbreak densities the use of row covers (to prevent access of moths to crop

plants) and repellent plants (such as *R. tomentosum*) can result in significantly reduced herbivore pressure.

An average reduction of DBM adults of over 50% and reduced feeding damage to broccoli plants in RT plots compared to Controls, suggests that strongly aromatic CP species such as RT could be important components of pesticide-free insect pest control (Stenberg et al. 2021). Our results were in line with earlier work done using coriander CP and cabbage (Adati et al. 2011) showing that DBM larval densities in a cabbage monoculture were higher than in a cabbage crop with CPs. DBM larval densities in all four treatments rose gradually and reached the highest value on July 23rd, which probably included larvae from both the first and second generations. By July 29th, DBM larval densities had dropped dramatically, which was likely due to an increasing pupation rate, and older broccoli leaves becoming too hard for DBM larvae to eat (Moreira et al. 2016). Another factor that could affect the larval population decrease is the presence of natural enemies in the later stages of the growing season. Earlier laboratory experiments by Himanen et al. (2015) noted that RT VOC-exposure of DBM-damaged broccoli plants does not hamper the attractiveness of the damaged broccoli to *Cotesia*

vestalis (Haliday) (Hymenoptera: Braconidae) parasitoids compared with unexposed broccoli plants.

VOC emissions of *Brassica*

When *Brassica* plants (e.g. broccoli) are damaged by DBM, they release higher rates of several monoterpenes, the homoterpene (*E*)-DMNT, and the sesquiterpene α -farnesene (Li and Blande 2015). These damage-induced volatiles can attract certain herbivores and their natural enemies (Dicke et al. 2009; Basu et al. 2018) and may be repellent to other herbivorous species. In June, higher damage indices were found in Control than in RT-exposed plants, but only α -terpineol, β -ocimene (in the morning and afternoon) and terpinolene (in the afternoon) had higher emission rates. However, the only compound in the June VOC sampling that significantly responded to the RT treatment was 1-tridecene, which also had higher emission rates in the afternoon than the morning. Earlier, this compound was not associated with herbivory, but it was reported to be formed and released during the photolysis of *Brassica* leaf waxes under high UV-B radiation (Bruhn et al. 2014). In our results, higher emission rates of 1-tridecene in the afternoon than in the morning support the role of solar UV-B radiation in the formation of this compound. In August, the compound was also detected in broccoli leaf and head emissions, however, 1-tridecene was not detected in RT plant emissions, which therefore cannot be the source. Why RT-exposed broccoli plants had a higher 1-tridecene emission rate than control plants remain uncertain, although a higher DBM leaf damage index in control plants might have reduced the wax-containing leaf area.

When herbivore-induced VOCs are released, plants tend to become more attractive to the natural enemies of the herbivores causing the damage (Himanen et al. 2015; Bui et al. 2021; Borghi et al. 2017), but the same VOCs also act as cues representing danger to neighbouring plants (Hu 2021; Rosenkranz et al. 2021), which can respond by activating their chemical defences (Loreto and D'Auria 2021; Rosenkranz et al. 2021). In the morning sampling in June, we found that Control plants had a high peak of (*Z*)-3-hexenyl acetate, a typical herbivore-induced VOC, which could be indicative of herbivore damage within a few minutes from the start of larval feeding (Maja et al. 2014), but there was no *R. tomentosum* treatment effect on (*Z*)-3-hexenyl acetate emissions.

Why *R. tomentosum* semivolatiles were not detected on *Brassica* plants?

There was no evidence of environmentally acquired chemical camouflage (Kessler and Kalske 2018) through the adsorption and re-emission of specific RT SVOCs or VOCs by broccoli plants in the RT treatment. This result is against our original hypothesis. Earlier lab results (Himanen et al.

2015; Bui et al. 2021) showed that exposure of *Brassica* plants to RT VOCs results in the adsorption of SVOCs to *Brassica* foliage. Similarly, several lab studies that were summarized by Tamiru and Khan (2017) showed the potential to improve crop plant resistance against insect pest attacks by manipulating the plant-derived volatile semiochemical emissions from crop plants or CPs. Nonetheless, the functional applications against important economic crop pests under real field conditions are still limited.

VOC sampling was conducted in the mornings and afternoons, and we cannot rule out the possibility that traces of those compounds were condensed on foliage during colder night periods and were present on broccoli foliage earlier in the morning as shown by Himanen et al (2010). To determine the full diurnal pattern of VOC emissions from broccoli and the possibility of night-time chemical camouflage, VOC, emission monitoring should be conducted in field conditions throughout the night. It is possible that some common VOCs that were emitted by both broccoli and *R. tomentosum* could also be adsorbed to broccoli, which is generally a lower terpene emitter than RT. Examples of compounds that may be adsorbed include dominating RT VOCs β -myrcene, alloocimene, borneol, and bornyl acetate. On August 16th there was a significantly increased β -myrcene emission rate from the heads of broccoli plants grown in RT plots. However, β -myrcene can be emitted from numerous sources including flowering weeds (Alasalvar et al. 1999; Tomczykowa et al. 2005; Bufalo et al. 2015; Ghanbarian et al. 2015)) and is not specifically indicative of RT VOCs. Moreover, Helmig et al. (2004) and Schaub et al. (2010) earlier documented the adsorption of less volatile VOCs to the surface of sampling cuvettes while compounds with higher volatility, e.g. monoterpenes and GLVs, did not have a similar adsorption. On plant leaf surfaces, external exposure to VOCs results in the adsorbed compounds being localized to the plant leaf wax layer and gradually being re-released into the atmosphere (Camacho-Coronel et al. 2020; Li and Blande 2015). The higher night temperatures of mid-summer might weaken the adsorption process and may have influenced the detection of environmental camouflage in this field study.

Crop plants that grow together with a CP that releases strong repellent aromatic VOCs may benefit through “associational resistance” against major herbivores (Karban 2010; Himanen et al. 2010). This type of resistance against DBM can be divided into two separate components. First, direct repellence of aromatic RT emissions may reduce the arrival/presence of flying moths on the crop plant (Reddy et al. 2016). Secondly, odour masking (including blocking of insect perception of attractive volatiles emitted by the host plant) or environmentally acquired chemical camouflage (Kessler and Kalske 2018) where adsorbed CP VOCs on the leaf surface and leaf waxes may prevent the DBM females

laying eggs on crop plants and reduce larval feeding (Bui et al. 2021). Both types of "associational resistance" will result in reduced feeding damage and decreased crop losses. The missing evidence of accumulation of RT VOCs on broccoli foliage in this field study suggests that direct repellency against flying DBM by RT VOCs in the atmosphere could have been the main mechanism that reduced feeding damage and crop losses in RT plots. This was supported by the fact that in June, average RT emissions were relatively high when DBM was actively ovipositing, particularly in the morning (Uematsu and Yoshikawa 2002).

***Rhododendron tomentosum* and MC + FE as boundary/CPs**

Rhododendron tomentosum is a strongly aromatic plant that produces VOCs that are repellent to many insect species. *R. tomentosum* stores VOCs in glandular trichomes on its leaf surfaces and has a notably higher total VOC emission rate than broccoli plants. Foliar VOC emission rates are typically dependent on the glandular trichome density on the leaf surface (Guan et al. 2022; Mofikoya et al. 2018a). When used as a CP, *R. tomentosum* emissions represent the 'push component' of an integrated pest management (IPM) strategy (Alkema et al. 2019; Balaso et al. 2019; Kopper and Ruelle 2021; Diabate et al. 2021) pushing the crop plant specialists away from the target crop.

In the *R. tomentosum* and MC+FE plots, our results showed that the number of DBM adults on yellow sticky traps did not significantly differ, although they were significantly lower in both treatments than in the Control plots. The use of row covers in the MC+FE plots made the direct comparison of the efficiency of *R. tomentosum* and FE as CPs very difficult.

Fagopyrum esculentum has been shown to be suitable for intercropping and IPM practices as it provides food resources for the maintenance of adult stages of predatory and parasitic insect populations (Géneau et al. 2012; Alcalá Herrera et al. 2021; Holm et al. 2021). Combinations of both bottom-up repelling plants and top-down natural enemy supporting companion crops are also a possibility for increasing efficiency of pest control. The use of pest-suppressive CPs with a good market demand in intercropping systems can potentiate a lower need for pesticides while facilitating a higher income from multi-crop yields (Géneau et al. 2012; Alcalá Herrera et al. 2021; Holm et al. 2021). *R. tomentosum* oils are used by the biomedical industry due to the discovery of promising anti-inflammatory, antioxidant, antidiabetic, and anticancer properties (Dampc and Luczkiewicz 2013) and buckwheat has market interest due to its modest agricultural input need along with being gluten-free. As exposure of

broccoli to RT does not repel DBM parasitoids in field conditions (Amoabeng et al. 2019; Mofikoya et al. 2019) and the scent can even attract them (Egigu et al. 2010), odour masking does not interfere with natural indirect defence and the system could have potential to be tested further. Larger scale field experiments are needed to compare the efficiency of CP-based strategies to control DBM populations of *Brassica* plants in the boreal zone.

The efficiency of floating row covers in DBM control

Row covers have been shown to reduce insect damage on vegetable crops and are an option for sustainable organic vegetable production (Dhakal and Nandwani 2020) (e.g. on white cabbage (Übelhör et al. 2014), on tomatoes (Mutisya et al. 2016, Al-Shihi et al. 2016) and on Pak-choi (Okimura and Hanada 1993) first and MC + FE plots were covered, and DBM density and damage analysis showed that the cover was the most efficient method for preventing damage by the first waves of DBM adults. In the comparison of MC versus MC + FE, the presence of flowering buckwheat seemed to lead to a slight reduction in DBM larval density and damage at the end of July, indicating its potential to support relevant natural enemies of DBM. However, the late flowering may have obscured a potentially larger effect, and the use of row-covers was warranted for protection of the plants before flowering.

An important finding was that MC + FE did not attract DBM adults more than the control plots even during their flowering period. This is particularly relevant as it has been found that DBM might benefit from the availability of buckwheat nectar (Chen et al. 2020). The small plot size in this experiment may hamper the adequate assessment of DBM attraction, which was focused on assessing the smaller-scale plant-plant interaction mechanisms mediated by VOCs. The timing of buckwheat flowering and DBM peaks can also influence the outcome. In Finland, the scattered pressure exerted by DBM populations depends on the warm weather and prevailing wind direction during late May and early June, when the first generation of DBM adults are taken by air currents from northern Central Europe (Leskinen et al. 2011). Comparing the differences between row cover treatments and RT after cover removal on July 16th and July 23rd, showed that larvae numbers in both covered plot treatments were still significantly lower than in control and RT plots. In the last week of July, MC and MC + FE had a lower larval density than all other treatments, making it the most effective treatment to reduce larval density, even compared to RT. The damage index was also lower in the last week of July in both covered plot treatments than in RT and control plots.

Conclusion

In this study, the use of RT plants as a boundary to broccoli plots was effective in reducing DBM damage to broccoli compared to the control treatment. This field study did not give unambiguous evidence of environmentally acquired chemical camouflage, i.e. adsorption of RT volatiles on broccoli surfaces as shown earlier in lab conditions, but rather suggested direct repellent effects of RT volatiles against oviposition by DBM females. It is notable that the use of a row cover was the most efficient treatment for reducing DBM larval density on organic broccoli. Flowering buckwheat only reduced DBM larval density on broccoli compared to the early-season mechanical control at the end of July, but there was no reduction in damage intensity. The use of a row-cover alongside buckwheat is needed due to the late flowering preventing the earlier attraction of natural enemies. Both RT as a repellent-releasing boundary plant and the use of a mechanical row cover was demonstrated to help reduce DBM damage on broccoli. However, multi-year trials under varying degrees of pest pressure are needed to verify this. We conclude that RT volatiles could be a potential source of repellent compounds to utilize in IPM for control of DBM as a potential alternative to the use of chemical pesticides.

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Author contributions AM analysed VOC data. TNTB conducted the fieldwork, participated in the statistical analyses of the field and analysed VOC data, and wrote the first draft of the manuscript. All authors participated in the design and data interpretation of the experiments and reviewed the manuscript.

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Data availability Intercropping organic broccoli with *Rhododendron tomentosum* and *Fagopyrum esculentum*: a test of bottom-up and top-down strategies for reducing herbivory” by Thuy Nga Bui Thi et al. for eventual publication in Arthropod-Plant Interactions. This is an original manuscript and any part of it has not been published elsewhere. All authors have read and commented manuscript and accepted the final version. We declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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