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Title: INFLUENCE OF THE SECONDARY METABOLITES OF *MENTHA PIPERITA* L. ON *TETRANYCHUS URTICAE* KOCH

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Abstract approved:
Ralph E. Berry

A laboratory experiment was conducted to determine the response of twospotted spider mites (*Tetranychus urticae* Koch) to varying amounts of monoterpenes and phenolic compounds found in peppermint (*Mentha piperita* L.) leaves of different age and growth form. The reproductive succes of twospotted spider mites was analyzed on four different aged leaves per plant by confining mites in sticky Tack-Trap cages, and measuring the number of eggs laid per leaf, the development time from larvae to adult, and the percentage of mites caught in the Tack-Trap cages. The number of mites caught in the Tack-Trap cages was used as a measure of leaf repellency (Rodriguez 1969). Secondary metabolite content of leaves was estimated by analyzing the opposite leaf pair of each infested leaf for phenolic content and monoterpene composition.

Another experiment was conducted to analyze the effects of individual monoterpene vapors on twospotted spider mites feeding on bean leaf disks.

Twospotted spider mite reproductive success was greatest on upper, mature mainstem leaves, and lowest on the expanding leaves of lower lateral branches. Lateral leaves had nearly twice the amount of total phenolic compounds (mg quercitin per leaf disk) and monoterpenes (μg/gm/Fr. wt.) as the mainstem leaves.

The monoterpene content of leaves did not significantly affect spider mite reproductive success, although pulegone vapor, and to a lesser extent, menthol vapor was toxic to mites on bean leaf disks. Twospotted spider mites feeding on peppermint leaves probably do not encounter significant amounts of monoterpenes, which are sequestered in glandular trichomes on the leaf surface. Phenolic content of leaves significantly affected spider mite reproductive success; as the phenolic content of leaves increased, the number of eggs laid on each leaf decreased, the time required to complete development increased, and the percentage of immature mites caught in the Tack-Trap enclosures increased. Phenolic compounds probably act as feeding deterrents.

INFLUENCE OF THE SECONDARY METABOLITES OF *MENTHA PIPERITA* L. ON *TETRANYCHUS URTICAE* KOCH

by

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I would like to dedicate this thesis to my parents for their encouragement and support.

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INTRODUCTION

Prior to World War II spider mites (Acari: Tetranychidae) were considered to be relatively minor agricultural pests, but since that time they have become serious pests on a variety of crop plants (Jeppson et al. 1975). The increased importance of spider mites as agricultural pests has been attributed largely to improvements in plant nutrition and to the increased use of pesticides (Van de Vries et al. 1972). The reproductive potential of spider mites is usually increased on well fertilized plants (Watson 1964), while frequent pesticide use can eliminate natural population control by predators and select for spider mite populations resistant to pesticides (Van de Vries et al. 1972). Spider mite population control might best be achieved by limiting pesticide use, and developing effective biological control and host plant resistance programs.

Plants produce a wide variety of secondary metabolites that function primarily as herbivore feeding deterrents or toxins, and thus play an important role in host plant resistance to pests. Plants which have some resistance to spider mites often have higher levels of secondary metabolites than their susceptible counterparts (Patterson et al. 1974, Gould 1978, Lane and Schuster 1981). Peppermint produces large quantites of two classes of secondary metabolites--essential oils and phenolic compounds (Loomis and Battaile 1966, Burbott and Loomis 1967). The goal of this research was to determine if these substances interfere with twospotted spider mite reproductive success.

Secondary metabolites are not uniformly distributed throughout all tissues of a plant. A plant's capacity for synthesis and storage of secondary metabolites is dependent on tissue type and age, environmental conditions, and genetic make-up (McKey 1979). The result is substantial variation in secondary metabolite composition of different parts of the same plant. My experiments were designed to evaluate the response of twospotted spider mites to different concentrations of monoterpenes and phenolic compounds found in peppermint leaves of different age and growth form.

LITERATURE REVIEW

PEPPERMINT

Peppermint is an economically important crop plant in the Pacific Northwest, with more than 22,250 hectares in cultivation (Berry 1977). Peppermint is harvested for its essential oil, which is a mixture of various monoterpenes, with less than 2% sesquiterpenes (Croteau et al. 1972).

Peppermint essential oil is synthesized and stored in glandular trichomes located on both upper and lower leaf surfaces (Howe and Steward 1962). Within the glandular trichomes, peppermint monoterpenes undergo a series of interconversions as the leaves age (Battaile and Loomis 1961), resulting in seasonal and within plant variation in the composition of essential oil. Young leaves contain predominantly menthone and pulegone (Battaile and Loomis 1961, Burbott and Loomis 1969). Menthone content of midstem leaves reaches a peak just before flowering, and then declines as flowering proceeds. As the menthone content declines, the relative concentration of menthol increases (Battaile and Loomis 1961, Burbott and Loomis 1969). Young leaves have higher concentrations of oil per gram of tissue than do mature leaves (Burbott and Loomis 1967).

Peppermint leaves also have high concentrations of phenolic compounds (Loomis and Battaile 1966). Condensed tannins composed of trimers of caffeic acid have been reported from peppermint (Herrmann and Kucera 1967). The flavones luteolin and apigenin, and the phenylpropane derivatives caffeic and p-coumaric acids also have been isolated from peppermint (Stanislaw et al. 1975).

TWOSPOTTED SPIDER MITE

Twospotted spider mites (Tetranychus urticae Koch) develop rapidly through five instars: egg, larva, protonymph, deutonymph, and adult. The first half of each immature stage is spent actively feeding; the second half is spent in a quiescent state that lasts until the next molt (Laing 1969). Development and oviposition rates are dependent on environmental conditions such as temperature and relative humidity, the plant host species and its phsyiological condition, and the genetic make-up of the spider mite population (Watson 1964, Laing 1969, Hazan et al. 1973, Shih et al. 1976, Ponti 1977, Gould 1979, Herbert 1981). Twospotted spider mite development and oviposition rates have been measured under a variety of different conditions, resulting in a wide range of values reported by different workers.

On strawberry leaf disks at a mean temperature of 20.3° C (daily range from 28.3°C to 15.0°C), twospotted spider mites required 16.9 days for female development from egg to adult, and 16.1 days for males. The egg stage for females lasted about 6.7 days, the larval stage 3.7 days, the protonymphal stage 3.0 days, and the deutonymphal stage 3.5 days (Laing 1969). Development times for males were slightly shorter than for females (Laing 1969). In contrast, another population of mites fed on lima beans at 27°C developed much faster, averaging only 7.6 days for female development and 5.6 days for males (Shih et al. 1976).

Male twospotted spider mites are attracted to a pheromone produced by quiescent female deutomymphs (Cone et al. 1971a, 1971b). Males defend the quiescent deutonymph from other males until the adult female emerges and mating takes place. There is a short (average 2.1 days) preovipositional period before eggs are laid (Laing 1969). During this period, the teneral females tend to migrate vertically up the plant. This migratory behavior is present regardless of the condition of the host plant (Hussey and Parr 1963).

The preoviposition period is followed by about 16 days of oviposition (Laing 1969, Shih et al. 1976). Values reported for the number of eggs laid during this period range from an average of 37.9 eggs per female on strawberry leaves (Laing 1969), to an average of 143.9 eggs per female on lima bean leaves (Shih et al. 1976).

Twospotted spider mites are arrhenotokous; unfertilized eggs develop into haploid males and fertilized eggs into diploid females (Boudreaux 1963). Unmated females produce only male offspring, while mated females produce both males and females.

Twospotted spider mites overwinter as the fertilized adult female. Short photoperiod and low temperatures act on early instars of the female to induce a diapause form in the adult. A period of chilling is required before diapause is terminated (Parr and Hussey 1966).

The feeding organ of twospotted spider mites consists of a pair of recurved stylets, a stylophore, and a rostrum. Stylets of adult female _T. urticae_ average 130 μm in length from the recurved portion to the tip. The base of the stylets are embedded in the stylophore; the distal portions slide in a V-shaped groove on the dorsal surface of the rostrum. The groove runs the length of the rostrum and keeps the stylets aligned during feeding (Baker and Connell 1963). Each stylet ends in a dull point, which serves to break plant cells (Hislop and Jeppson 1976). It is unclear how the cellular sap is transported to the leaf surface where it can be sucked up using the pharyngeal pump (Hislop and Jeppson 1976).

Tetranychus spp. feed mainly on mesophyll cells, with some damage to palisade layers (Baker and Connell 1963, Sances et al. 1979). On heavily damaged strawberry leaves, Sances et al. (1979) observed deeper stylet penetration and consequently greater damage to palisade layers.

HOST PLANT CHEMISTRY/SPIDER MITE RELATIONSHIPS

Initially, research on the host plant chemistry/spider mite relationship concentrated on the effects of plant nutrition on mite fecundity. Workers examined mite response to different combinations and concentrations of inorganic nutrients supplied to plants. In general, an increase in mite fecundity was observed with increased nutrient supply to the plant; however, contrary results were not uncommon. Increased nitrogen level resulted in increased fecundity of T. urticae on beans (Henneberry 1962a,b, 1963, Watson 1964), apple (Rodriquez 1958, Storms 1969), and strawberry (Rodriguez et al. 1970), but decreased fecundity on tomatoes (Rodriguez 1951). High phosphorus levels in lima beans were both negatively correlated (Henneberry 1963) and positively correlated (Watson 1964) with mite fecundity. Analyses of this type are complicated by interactions between ions and the relationship of inorganic ions to the organic constituents of the leaf (Van de Vries et al. 1972).

The effects of leaf age on spider mite reproductive success were measured on several different plants. Mite reproduction was favored on young leaves of beans (Henneberry 1962b, Watson 1964), citrus (Henderson and

Holloway 1942), and corn (Feese and Wilde 1977), whereas it was favored on older leaves of avocado (McMurtry 1970), strawberry (Poe 1971, 1974) and apple (Dabrowski 1976).

Recently, the influence of secondary metabolites on spider mite biology has been investigated. Patterson et al. (1974) found that three times as many spider mites developed on a low-alkaloid tobacco cultivar compared to plants with normal alkaloid content. Gould (1978) found that the concentration of cucurbitacin-C, a tetracyclic triterpenoid, in cucumber seedlings was positively correlated with toxicity to twospotted spider mites. Toxicity was measured in terms of immature survival and development rates. Lane and Schuster (1981) measured condensed tannin concentration in cotton leaves and found that those cultivars with highest tannin concentration were resistant to twospotted spider mites, while cultivars with low tannin concentration were susceptible.

Spider mite response to phenolic compounds and essential oils of strawberry have been tested using various in vitro methods. The addition of phenols to sucrose diet reduced the rate of feeding by twospotted spider mites, and resulted in increased numbers of mites trapped in the sticky barrier surrounding the feeding arena (Dabrowski and Rodriguez 1972). Some phenolics tested were toxic, resulting in the death of mites (Dabrowski and Rodriguez

1972). The odor of most strawberry essential oils repelled twospotted spider mites (Dabrowski and Rodriguez 1971). In a later study, however, strawberry essential oil was either attractive or repellent depending on the concentration of individual oil components, and the make-up of the essential oil mixture (Rodriguez et al. 1976).

MATERIALS AND METHODS

SPIDER MITE CULTURE

Researchers have commonly reared twospotted spider mites on beans, and then measured their reproductive success on other plant species. In this laboratory, reproductive success was greatly reduced when a population of mites reared on lima beans was transfered to peppermint (unpublished data). Jesitor (1980) has shown that the transfer of twospotted spider mites to a new host species invariably reduces success in the first few generations. To avoid any negative impact of changing host plants on mite reproduction, mites for this experiment were reared on peppermint plants only.

Approximately 750 adult female twospotted spider mites were collected from populations infesting three peppermint fields in the Willamette Valley of western Oregon. These females were used to infest beds of peppermint plants which were maintained in an environmental chamber under constant illumination and temperature (21° C). Quiescent female deutonymphs were obtained by inoculating a new bed of mint with heavily infested leaves from the culture maintained in the environmental chamber. In 15 days large numbers of quiescent deutonymphs developed on the new plants, and were removed with a small camel's hair brush.

For experiments on development rate, newly hatched larvae were reared from eggs laid during a 12 hour period on detached mint leaves. The petioles of these leaves were wrapped in cotton, and kept in water soaked vermiculite in petri dishes.

PEPPERMINT CULTURE

Field collected rhizomes of Black Mitcham Peppermint (Willamette Valley clone) were planted in beds of vermiculite. Beds were cut back after ca. three weeks to maintain vigorous growth (Crane and Steward 1962). Cuttings were made of a stem and tuft of youngest leaves at the apex, plus the next expanded leaf pair, and planted in silica sand in 2.5 cm diameter rooting tubes. Stock beds and cuttings were watered with a modified Hoagland-Arnon nutrient solution (Crane and Steward 1962).

Growing conditions were: 14L:10D photoperiod; 23-25°C day:20-22°C night temperature regime; 40-60% RH. Quantum flux at the level of the cutting was ca. 250 microEinsteins/m/sec., measured with a LiCor Quantum/Radiometer/Photometer, model 185A (LiCor Inc., Lincoln, Nebraska).

EXPERIMENTAL DESIGN

EXPERIMENT 1. Eight weeks after cuttings were made, 20 plants were selected for uniformity. Four leaves per plant, an upper lateral and lower lateral leaf and a top and bottom mainstem leaf, were infested with mites (Fig. 1). Lateral leaves were still expanding at the start of the experiment; mainstem leaves were fully mature at the start of the experiment.

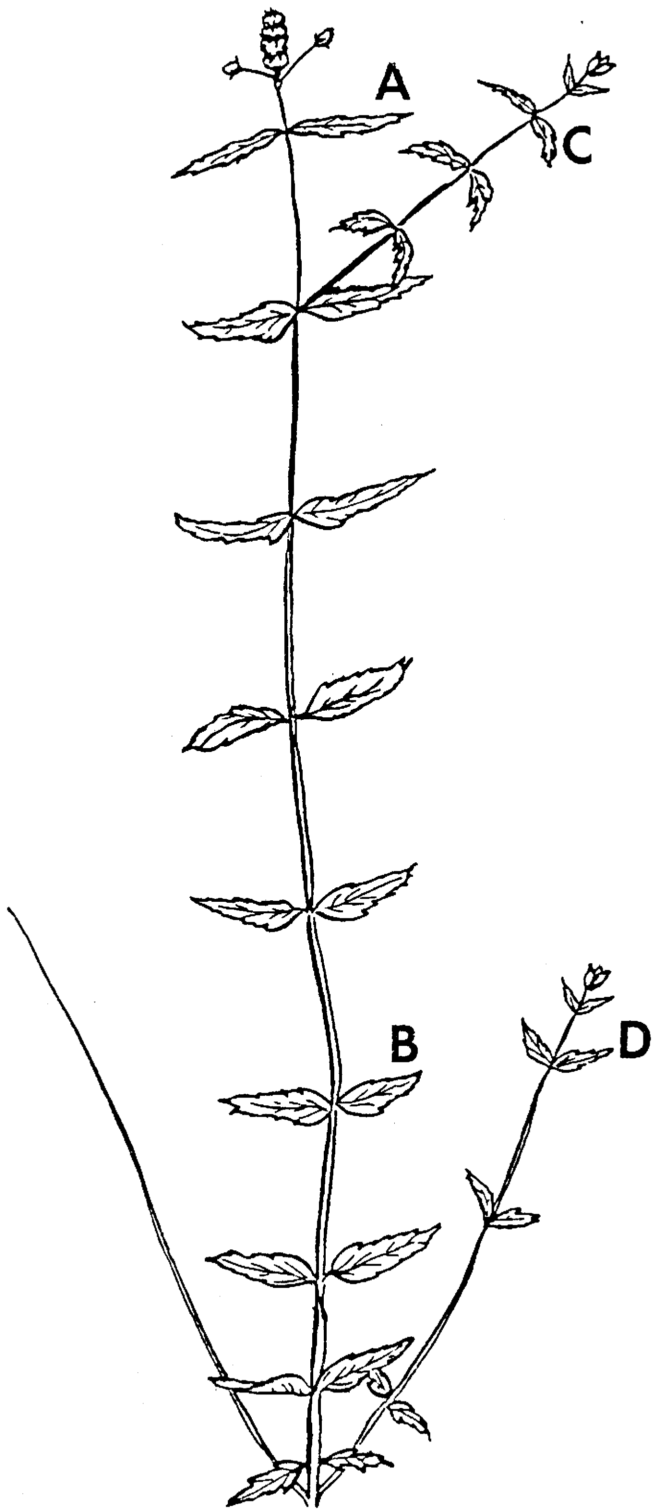
Mites were confined within 18 mm diameter enclosures of Tack-Trap (Animal Repellents Inc., Griffin, Georgia) on the lower surface of leaves. One enclosure for oviposition and one for immature development were put on each mainstem leaf. Because of the small size of lateral leaves, oviposition and immature development were measured on lateral leaf pairs, rather than on the same leaf.

The time required to develop from larva to adult was determined by placing 20 newly-hatched larvae on each of the four selected leaves per plant. Leaves were examined daily; adults were removed as they appeared, and the number of days elapsed since hatching was recorded. The number of mites caught in the Tack-Trap enclosures provided an index of the repellency of the leaf to mite feeding. Non-feeding mites are more active than feeding mites, and are thus more likely to be caught in a sticky enclosure (Rodriguez 1969).

Oviposition was estimated by placing five quiescent deutonymphs on each of the four selected leaves per plant. When adult females emerged the next day, all but two were removed. Eggs were counted and removed daily for 14 days,

Figure 1. Leaf arrangement of experimental plants. Leaves infested with spider mites are labeled as follows: A=top mainstem, B=bottom mainstem, C=upper lateral, D=lower lateral.

Figure 1



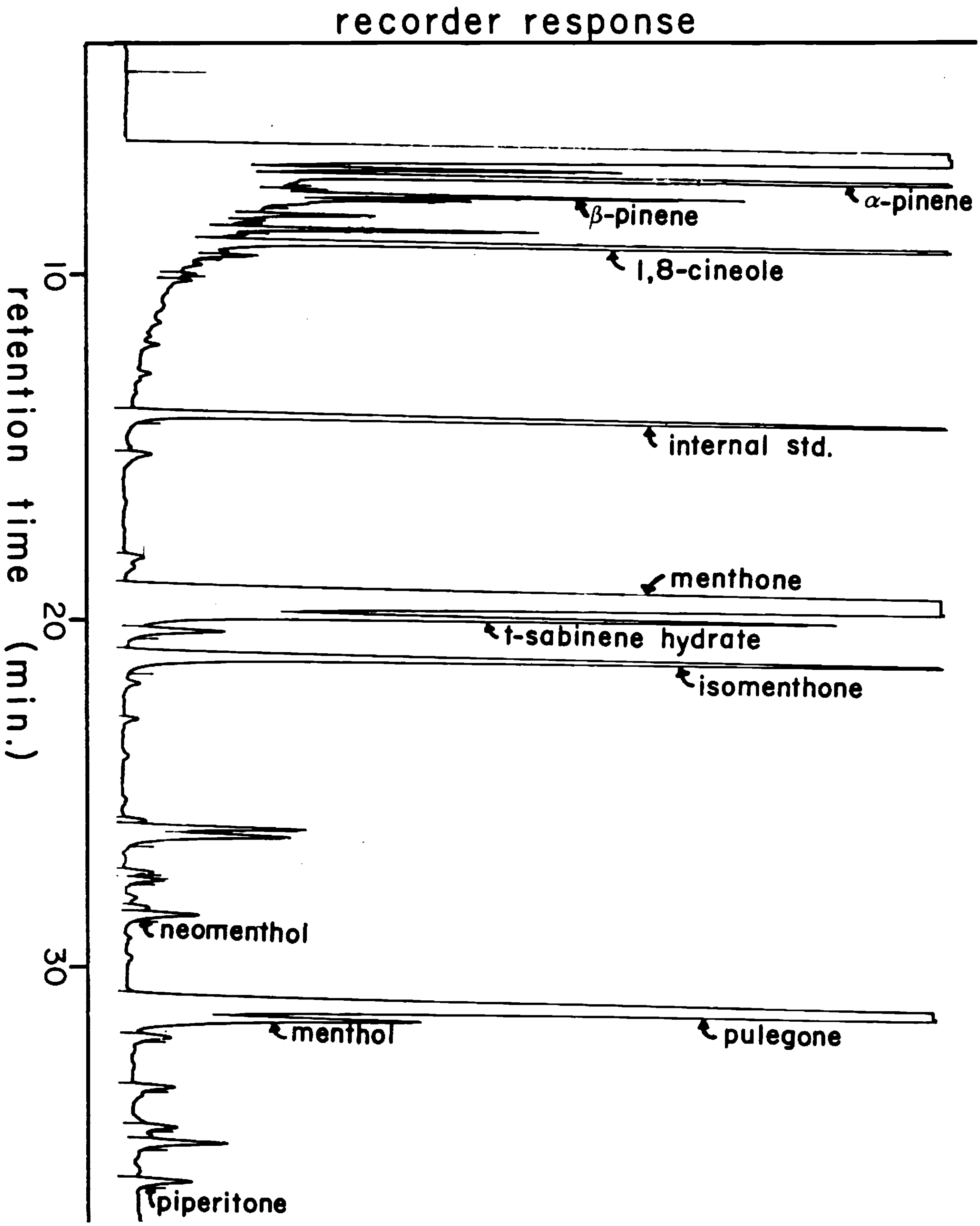
and the number of females caught in the Tack-Trap enclosure was recorded. The total number of eggs on each leaf after 14 days was used as an index of oviposition. Because some females were caught in the Tack-Trap enclosures, this measure of oviposition incorporated both the effects of leaf repellency and female fecundity. Estimates of female fecundity for mites ovipositing in Tack-Trap enclosures may not be valid, because the female mites are selectively removed from the egg laying population. Deutonymphs were used to maximize the impact of leaf chemistry on egg production. Female spider mites double in weight in the first four days after ecdysis, and since larger females produce more eggs (Mitchell 1973), any factors affecting the growth of the young female will presumably be reflected in the number of eggs laid.

To determine the effects of interplant variation of monoterpenes and phenolics on mite biology, a direct measure of leaf chemistry for each infested leaf was needed. Peppermint leaf pairs are highly correlated in terms of both monoterpene composition and concentration of total phenolic compounds (unpublished data), so the opposite pair of each infested leaf was sampled for plant chemistry. Four to seven days after leaves were infested with mites, a disk was cut from each leaf with a #4 cork borer (63.6 mm^2)and put immediately into 1 ml of 2N HCl for extraction of phenolic compounds. Total phenolic concentration was determined by the Prussian Blue method described by Budini et al. (1980). Phenolic concentration was computed as equivalents of quercitin per leaf disk. The remainder of the leaf was weighed and put into cold 30% ethanol to extract monoterpenes. Monoterpenes were extracted by the method of DeAngelis (1981), and analyzed by gas chromatography as described in the caption for Figure 2. The relationship between peppermint secondary metabolites and spider mite biology was analyzed by linear and multiple regression. The dependent variables were number of eggs per leaf, development time, and number of immature mites caught in the Tack-Trap. Independent variables were total phenolic concentration; amount of total monoterpenes; amount of pulegone, menthone, 1,8-cineole, and menthol; and the percent contribution to the total oil of pulegone, menthone, 1,8-cineole, and menthol. Data were analyzed within each leaf strata, and pooled for all leaf strata.

EXPERIMENT 2. Spider mite response to the vapors of individual monoterpenes was tested by confining two-day old female twospotted spider mites on Tack-Trap ringed lima bean disks in vermiculite filled 150 mm diameter petri dishes containing the monoterpenes to be tested in a small cup in the center (Dabrowski and Rodriguez 1971). Petri dish lids were elevated with a circular band of wire screen to produce

Figure 2. GC chromatogram of pentane fraction. Peppermint leaf sample (0.097 g fresh weight). Sample volume = 0.2 ml; 0.05 ml injected with a 10:1 split ratio. Hewlett Packard 5710 A gas chromatograph equipped with flame ionization detector. Column: 0.2 mm x 25 m flexible silica W.C.O.T. capillary, AT-1000 coated. Carrier gas flow through the column 1 cc/min helium, with make-up to the detector at 30 cc/min, hydrogen at 30 cc/min, air at 220 cc/min. Peak area integration done on an HP 3380 A reporting integrator using internal standard method of calibration. 800 ng n-tridecane was added to samples as an internal standard. Temperature programming: 16 min isothermal at 65 C, 2^{0}C/min to 100^{0}C and held for 8 min. Injection port temp. 250^{0}C, detector temp. 300^{0}C. Labelled peaks account for 95% of the extracted oil.

Figure 2


recorder response
retention time (min.)
10
20
30
α-pinene
β-pinene
1,8-cineole
internal std.
menthone
t-sabinene hydrate
isomenthone
neomenthol
menthol
pulegone
piperitone

a 5 mm air space between the edge of the lid and the base. Three females were put on each of six, 17 mm diameter leaf disks per dish, and kept at 25°C under a 16 hour photoperiod. The number of eggs and mites were counted 72 hours later. The monoterpenes tested were 1%, 5%, and 10% solutions of menthol, menthone, and pulegone, each dissolved in propylene glycol. Propylene glycol alone served as the control. A second experiment was conducted in which the wire screens were excluded, thus sealing the chambers. Only 5% solutions of monoterpenes were tested in the sealed chambers.

RESULTS

Four leaves, varying in age and growth form, from 20 peppermint plants were analyzed for secondary metabolite content and spider mite reproductive success. The concentration of phenolic compounds and monoterpenes varied considerably between the four leaf strata tested, and to a lesser extent among leaves within the same strata (Tables 1 and 2).

The phenolic content of upper lateral leaves was not comparable to the other leaf strata due to an error in the collection of spectrophotometer data. Values for upper lateral leaves were necessarily excluded from all analyses involving phenolic concentraton. Upper lateral leaf data were included in comparisons of monoterpene content among leaf strata, but were excluded in analyses of monoterpene influence on spider mites.

Four monoterpenes, 1,8-cineole, menthone, pulegone, and menthol, composed between 80-90% of the total oil in all leaves analyzed, and were the only monoterpenes considered in detail. The monoterpene compostion of essential oil from upper and lower lateral leaves was not significantly different, and was composed mainly of menthone and pulegone (Table 1). Comparison of the two mainstem leaves showed

TABLE 1. Means $\bar{x}$ (S.E.) of monoterpene composition for each leaf strata

LEAF STRATA	TOTAL MONOTERPENE[2] µg/gm/Fr. wt.	% CINEOLE	% MENTHONE	% PULEGONE	% MENTHOL	n
TOP MAINSTEM	2554.4(570.6)a[1]	11.5(0.8)a	44.1(3.9) a	24.2(5.1) a	20.2(3.8)a	20
BOTTOM MAINSTEM	1400.8(281.8)b	11.6(1.3)a	22.3(5.6) b	39.0(6.3) b	27.1(5.7)b	20
UPPER LATERAL	5368.6(1749.0)c	12.0(3.5)a	52.6(10.9)c	35.4(10.1)b	> 5.0	40
LOWER LATERAL	5174.8(975.9)c	13.4(2.0)a	54.6(8.3) c	32.1(8.8) b	> 5.0	24

[1]Means in the same column followed by the same letter are not significantly different using the Student-Newman-Keuls test (p=.05).

[2]Total oil content was estimated by summing values for 1,8-cineole, menthone, pulegone, and menthol; menthol content was not included for lateral leaves.

Table 2. Means $\bar{x}$(S.E.) of total phenolic concentration for each leaf strata.

LEAF STATA	PHENOLIC CONCENTRATION (mg/disk)	n
TOP MAINSTEM	0.017(0.006) a[1]	20
BOTTOM MAINSTEM	0.024(0.006) b	20
LOWER LATERAL	0.040(0.014) c	24

[1]Means followed by the same letter are not significantly different using the Student-Newman-Keuls test (p=.05).

that the relatively older bottom mainstem leaves had higher menthol and lower menthone content than the top mainstem leaves (Table 1).

Spider mite reproductive success was measured in terms of the total number of eggs laid on each leaf, the percent of immatures caught in the Tack-Trap enclosures, and the development time from larva to adult; all were influenced by leaf strata (Table 3). In oviposition tests, a differential number of female mites were caught in the Tack-Trap enclosures on different leaf stata. Only 20% of the mites on top mainstem leaves and 28% of mites on bottom mainstem leaves were caught in the Tack-Trap, while 68% were caught on upper lateral leaves and 75% on lower lateral leaves. Thus, the total number of eggs laid per leaf was dependent on both the loss of female mites due to repellency, and the average number of eggs laid by each female.

Overall, mite reproductive success was lowest on lower lateral leaves (fewest number of eggs per leaf, highest percentage of immatures caught in the Tack-Trap, and longest development times), intermediate on upper lateral and bottom mainstem leaves, and highest on top mainstem leaves (highest number of eggs per leaf, lowest percentage of immatures caught in the Tack-Trap, and shortest development times).

Regression analysis of pooled data for all leaves from

Table 3. Means $\bar{x}$(S.E.) of _T. urticae_ biology parameters on different leaf strata.

LEAF STRATA	EGGS PER LEAF	% NYMPHS CAUGHT IN TACK-TRAP	DEVELOPMENT TIME (DAYS)	n
TOP MAINSTEM	84.7(20.1) a[1]	29.4(0.13) a	9.1(0.7) a	20
BOTTOM MAINSTEM	52.4(17.6) b	38.7(0.18) a	9.7(0.9) ab	20
UPPER LATERAL	55.5(23.2) b	56.9(0.23) b	10.3(1.4) b	20
LOWER LATERAL	24.9(17.0) c	84.6(0.20) c	11.8(1.7) c	12

[1]Means in the same column followed by the same letter are not significantly different using the Student-Newman-Keuls test (p=0.05).

all leaf strata revealed a strong relationship between the phenolic concentration of leaves and the reproductive success of twospotted spider mites confined on those leaves. As phenolic concentration of leaves increased, the number of eggs laid on each leaf decreased ($p < 0.001$; Fig. 3), the percentage of immatures caught in the Tack-Trap enclosures increased ($p < 0.001$; Fig. 4), and the time required to complete development increased ($p < 0.001$; Fig. 5).

These relationships between the concentration of phenolic compounds and mite reproductive success were also apparent among the leaves of a particular leaf stratum. The relationship between the number of eggs laid per leaf and phenolic concentration was significant for leaves within each stratum tested ($p < 0.05$; Fig. 3). The relationship between phenolic concentration and the percent of immatures caught in the Tack-Trap and development time were significant only for bottom mainstem leaves ($p < 0.05$; Figs. 4 and 5).

A consistant relationship was not apparent between the monoterpene composition of leaves and the biology of spider mites on those leaves. Neither immature growth rate nor the number of immature mites caught in the Tack-Trap enclosures were significantly related to quality or quantity of monoterpenes tested. Some linear regressions of the number of eggs laid per leaf and various monoterpene components

Figure 3. Effect of concentration of total phenolic compounds on the number of eggs laid per leaf. Pooled data for all leaf strata; each point represents one leaf. Total phenolic concentration is measured in mg. quercitin equivalents per 63.6 mm^2 leaf disk. $r = -0.73$, $p < .001$, $n = 50$.

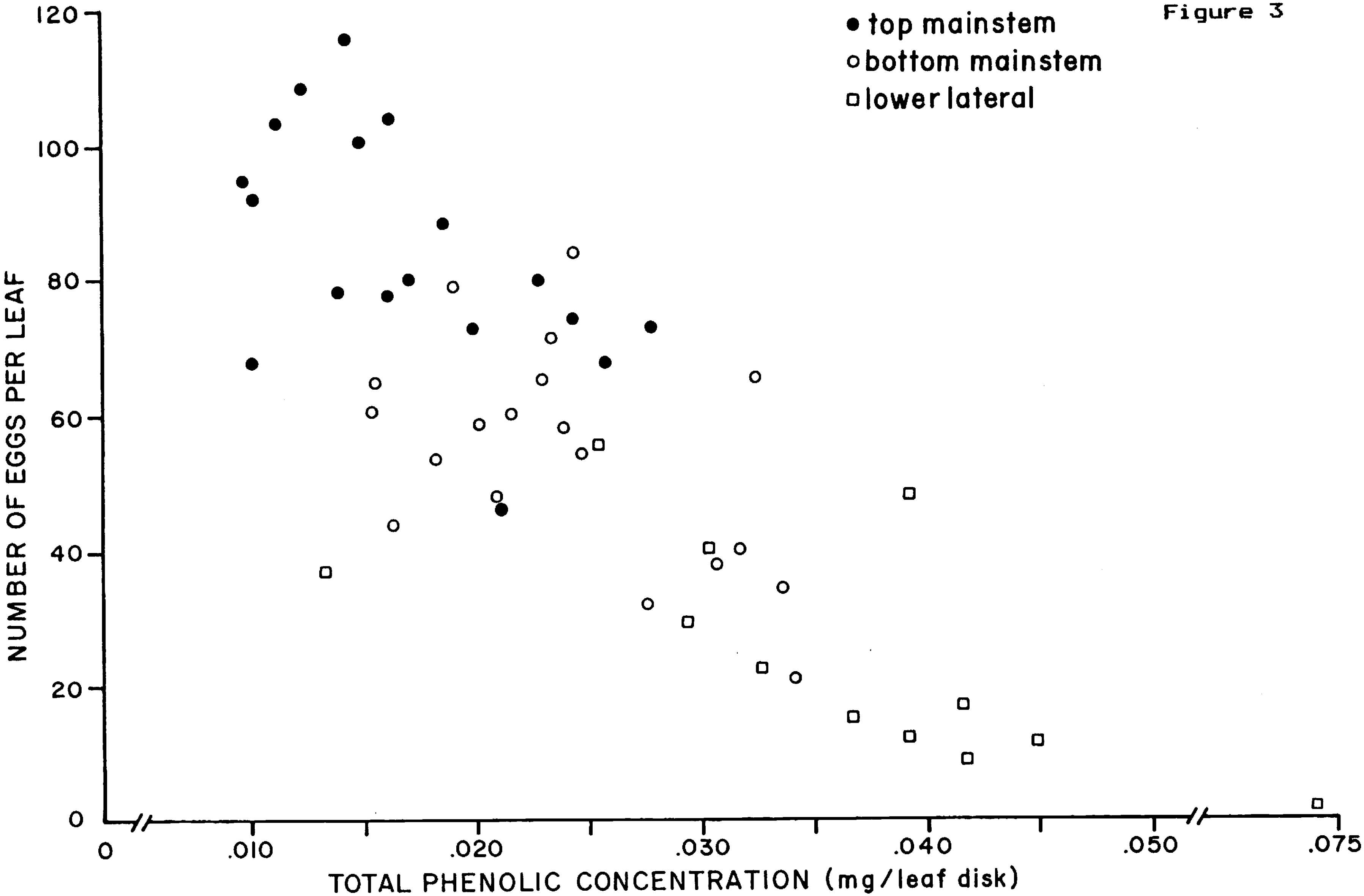
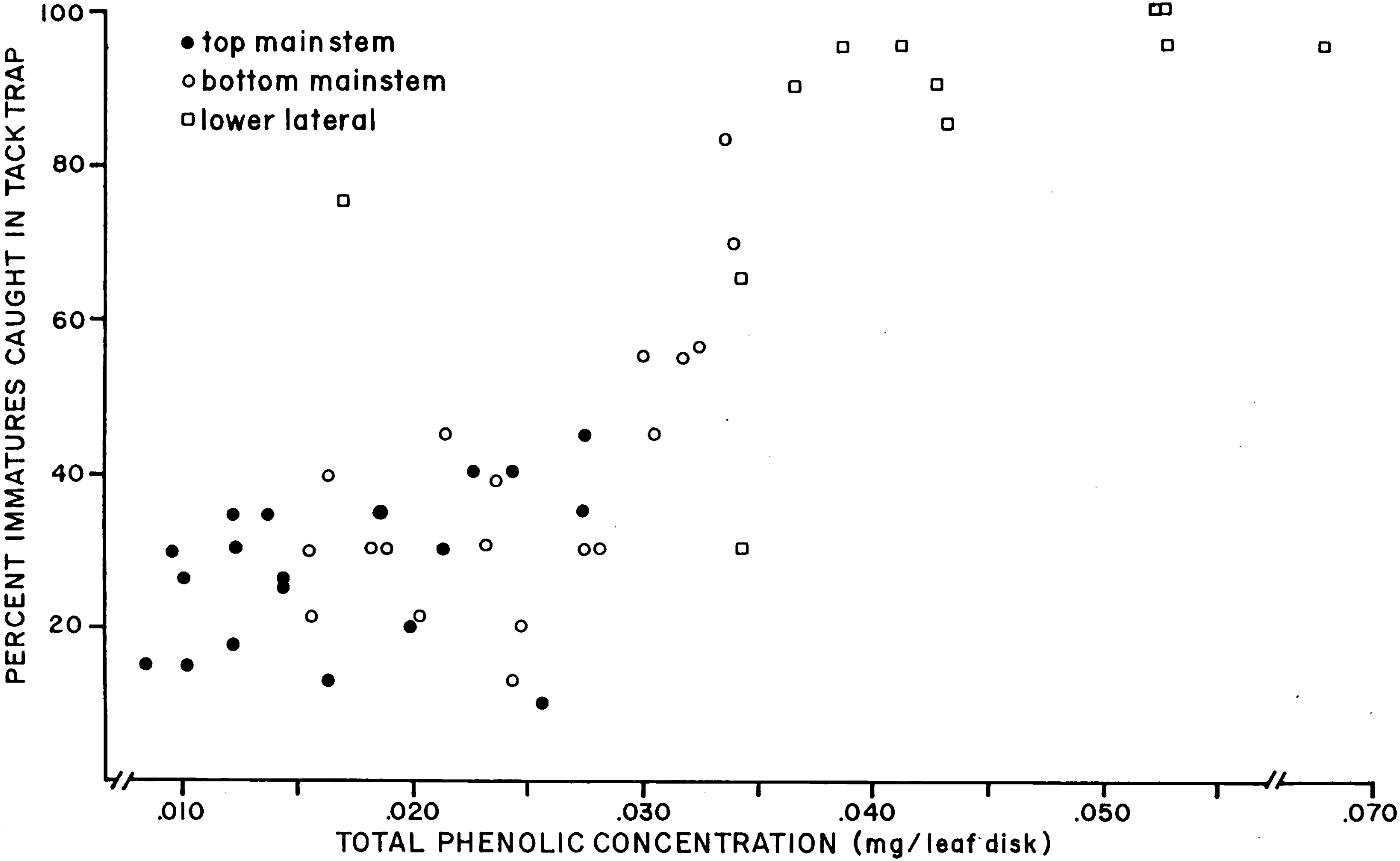


Figure 3
● top mainstem
○ bottom mainstem
□ lower lateral
NUMBER OF EGGS PER LEAF
0
20
40
60
80
100
120
0
.010
.020
.030
.040
.050
.075
TOTAL PHENOLIC CONCENTRATION (mg/leaf disk)

Figure 4. Effect of concentration of total phenolic compounds on percentage of immature T. urticae caught in Tack-Trap enclosures. Pooled data for all leaf strata; each point represents one leaf. Total phenolic concentration is measured in mg. quercitin equivalents per 63.6 mm^2 leaf disk. $r=0.83$, $p<.001$, $n= 50$.

Figure 4



100
80
60
40
20
PERCENT IMMATURES CAUGHT IN TACK TRAP
• top mainstem
○ bottom mainstem
□ lower lateral
.010
.020
.030
.040
.050
.070
TOTAL PHENOLIC CONCENTRATION (mg/leaf disk)

Figure 5. Effect of concentration of total phenolic compounds on length of development from larva to adult. Pooled data for all leaf strata; each point represents one leaf. Total phenolic concentration is measured in mg. quercitin equivalents per 63.6 mm^2 leaf disk. $r=0.57$, $p<.001$, $n= 45$.

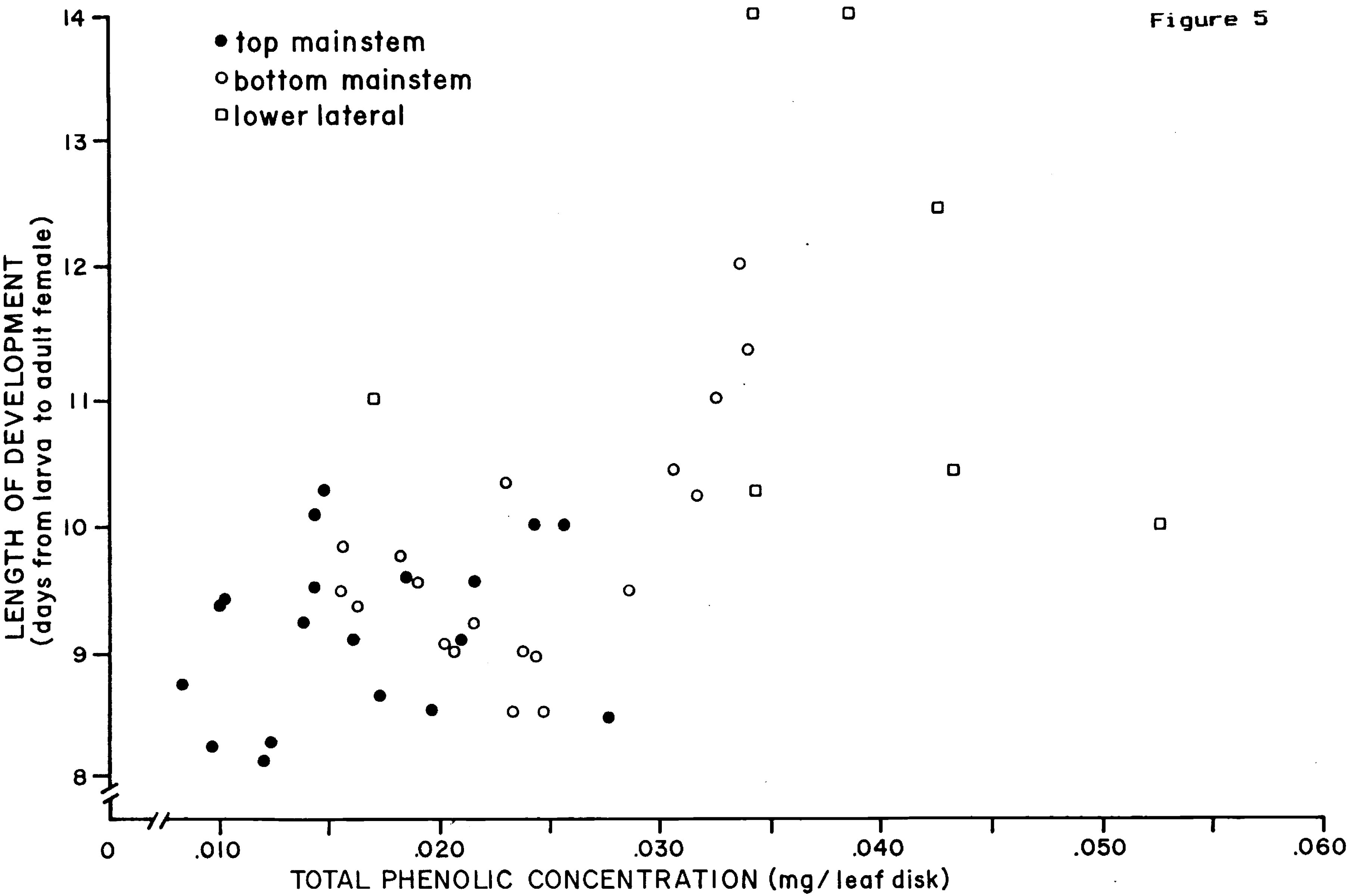

top mainstem
bottom mainstem
lower lateral
LENGTH OF DEVELOPMENT
(days from larva to adult female)
14
13
12
11
10
9
8
0
.010
.020
.030
.040
.050
.060
TOTAL PHENOLIC CONCENTRATION (mg/ leaf disk)

Figure 5

were statistically significant; the significant regressions are given in Table 4. None of the relationships between monoterpenes and oviposition in Table 4 were significant in multiple regression models that included total phenolic concentration due to positive correlations between the concentration of total phenolic compounds and the amount of various monoterpenes (Table 4).

In experiments to determine the effects of individual monoterpene vapors on twospotted spider mites, there were no significant effects on mite oviposition or the number of females caught in the Tack-Trap by vapors of 1% solutions of menthone, menthol, or pulegone in ventilated petri dishes. Vapors of a 5% pulegone solution in ventilated dishes significantly reduced ovipostion (36% fewer eggs per leaf than the control; $p<0.001$), but did not affect the number of females caught in the Tack-Trap. Vapors of a 10% pulegone solution also reduced oviposition (31% fewer eggs per leaf than the control; $p<0.025$), but had no effect on the number of females caught in the Tack-Trap. Menthone and menthol vapors of 5% and 10% solutions did not significantly reduce mite oviposition, or affect the number of females caught in the Tack-Trap.

In enclosed petri dishes, vapors of all monoterpenes tested had adverse effects on spider mite survival and oviposition (Table 5). Because these petri dishes were

Table 4. Pearson correlation coefficients (r) between monoterpene components, and phenolic concentration and number of eggs per leaf.

LEAF STRATA		EGGS PER LEAF	PHENOLIC CONC. MG/DISK
BOTTOM MAINSTEM LEAVES	Total Monoterpenes (µg/gm Fr wt.)	−0.67 **	+0.47
	1,8-Cineole (µg/gm Fr wt.)	−0.61 **	+0.34
	Pulegone (µg/gm Fr wt.)	−0.58 *	+0.26
	Menthol (µg/gm Fr wt.)	−0.62 **	+0.53 *
	Menthone (% of total oil)	+.053 *	−0.21
LOWER LATERAL LEAVES	Pulegone (µg/gm Fr wt.)	−0.60 *	+0.42
	1,8-Cineole (% of total oil)	+0.60 *	−0.60 **
POOLED DATA FOR ALL LEAF STRATA	Total monoterpenes (µg/gm Fr wt.)	−0.35 **	+0.43 **
	1,8-Cineole (µg/gm Fr wt.)	−0.32 **	+0.40 **
	Menthone (µg/gm Fr wt.)	−0.31 *	+0.35 *
	Pulegone (µg/gm Fr wt.)	−0.40 **	+0.55 ***

* $p<0.05$
** $p<0.01$
*** $p<0.001$

Table 5. Effects of vapor from 5% solutions of monoterpenes on *T. urticae* females after 72 hours.

TREATMENT	EGGS PER DISK	% FEMALES DEAD	% FEMALES IN TACK-TRAP
CONTROL	62.0 a[1]	6 a	6 a
MENTHOL	32.2 b	39 b	11 a
MENTHONE	18.8 c	17 c	0 a
PULEGONE	7.7 c	89 d	11 a

[1]Means in the same column followed by the same letter are not significantly different using the Student-Newman-Keuls test (p=0.05).

sealed, vapors in these dishes probably were near saturation. Pulegone vapors at this concentration were found to be highly toxic to twospotted spider mites; no mites survived on the leaf disks after 72 hours. Menthol vapor caused death of 39% of the mites, whereas only 17% of the mites died in the presence of menthone vapor.

DISCUSSION

The wide variety of secondary metabolites produced by plants are part of a highly coevolved system of herbivore defense (Whittaker and Feeny 1971, Feeny 1976, Rhoades and Cates 1976). Peppermint produces relatively large amounts of two classes of compounds that can potentially inhibit herbivore feeding and growth--phenolic compounds such as condensed tannins (Herrmann and Kucera 1967), flavones, and phenolic acids (Stanislaw et al. 1975); and essential oil consisting mainly of monoterpenes such as menthol, menthone, menthofuran, pulegone, and 1,8-cineole.

Phenolic compounds, especially condensed tannins, act to inhibit feeding and reduce the nutritional value of ingested plant material. The strong affinity of phenolic hydroxyl groups for binding proteins can make proteins in ingested plant tissue unavailable to herbivores, and can inactivate herbivore digestive enzymes, further reducing the nutritional value of the ingested plant tissue (Swain 1979, Harborne 1979). Flavones have been shown to be important as both insect feeding attractants and repellents (Schoonhoven 1972, Swain 1979).

Monoterpenes serve defensive functions through olfactory repellence and direct toxicity (Mabry and Gill

1979). Qualitative differences in monoterpene compositional types of Satureja douglasii (Labiatae) have been associated with differential consumption by herbivores. Types characterized by high pulegone content (52% of total oil) were least damaged by herbivores, while plants characterized by high camphor and carvone content (28% and 29% of total oil, respectively) sustained the most damage (Rice et al. 1978).

In this study there was a significant difference in the distribution of secondary metabolites among the leaf strata, with the greatest differences occurring between lateral and mainstem leaves (Table 1 and 2). Lateral leaves, which were still expanding at the start of the experiment, contained nearly twice the concentration of total phenolic compounds per disk and amount of essential oil per gram of leaf tissue as the fully mature mainstem leaves. Lateral leaves had high levels of menthone and pulegone, which is typical of young leaves (Battaile and Loomis 1961, Burbott and Loomis 1967). The reduction observed in menthone content, decreasing from lateral leaves to top mainstem leaves to bottom mainstem leaves, and concomitant rise in menthol in these leaves is expected during maturation (Battaile and Loomis 1961, Burbott and Loomis 1967).

Leaf strata had a significant impact on all parameters of spider mite reproductive success measured (Table 3).

Lateral leaves were clearly more repellent to both adult and immature twospotted spider mites than were mainstem leaves. An inhibition of feeding on lateral leaves was reflected in the tendency for fewer eggs to be laid and immature development to be slower on lateral leaves than mainstem leaves. The important difference between leaf strata was probably the secondary metabolite content of leaves (Tables 1 and 2). The phenolic concentration of leaves appeared to have a greater influence on twospotted spider mites than did either the total amount of essential oil or its monoterpenoid composition.

Variation in phenolic concentration both within plants (between leaf strata) and between plants (among leaves of a particular stratum) was significantly correlated with spider mite reproductive success. The large number of immature mites caught in the Tack-Trap enclosures on leaves with a high phenolic content (Fig. 4) may indicate that phenolic compounds in peppermint are acting as feeding deterrents. Rodriguez (1969) has shown that non-feeding spider mites are more active than feeding mites, and thus more likely to be caught in a sticky enclosure. An inhibition of feeding on leaves with a high level of phenolic compounds will reduce the growth rate of twospotted spider mites and could account for the increased development time of immatures, and the lower number of eggs laid per leaf on leaves with high phenolic content (Figs. 3 and 5). Condensed tannins could reduce the digestibility of ingested peppermint leaf tissue by binding with proteins, and contribute to the reductions observed in oviposition and development rates of twospotted spider mites (Swain 1979, Harborne 1979).

Phenolic compounds have been shown to inhibit feeding of twospotted spider mites on an artificial diet. The addition of various phenolic compounds to a sucrose diet reduced intake and increased the number of mites caught in the sticky enclosure around the feeding cell (Dabrowski and Rodriguez 1972). Caffeic acid, a major phenolic compound of peppermint (Herrmann and Kucera 1967, Stanislaw et al. 1975), was ranked as one of the more detrimental, of 14 phenolics tested, to twospotted spider mites (Dabrowski and Rodriguez 1972). High levels of condensed tannins in cotton leaves have been associated with resistance to twospotted spider mites (Lane and Schuster 1981).

The monoterpene content of leaves did not appear to have a substantial influence on spider mite reproductive success in this study. Some regressions between leaf monoterpene content and the number of eggs laid on those leaves were significant; however, in multiple regressions with the concentration of total phenolic compounds, monoterpene content did not influence mite oviposition over and above the influence of phenolic compounds. The positive correlation between quantity of essential oil and quantity of phenolic compounds was probably the major factor resulting in the relationships seen between the number of eggs laid per leaf and monoterpene content (Table 4).

Both monoterpenes and phenolic compounds may act as herbivore repellents or toxins, but only phenolic compounds appeared to influence spider mites in this study. This may be because of a difference in the degree of contact between twospotted spider mites and these two classes of secondary metabolites. Phenolic compounds are found in plant cells mainly in the vacuoles (Esau 1977), and contribute to the cellular sap ingested by twospotted spider mites feeding on peppermint leaves. Peppermint essential oil, on the other hand, is sequestered in glandular trichomes on the leaf surface, and may be largely avoided by spider mites feeding on mesophyll cells in the leaf interior. There is some evidence of peppermint essential oil synthesis and accumulation in nonglandular cells (Loomis and Croteau 1973), but it is not known how much this nonglandular secretion contributes to the total oil content of a leaf.

While monoterpenes may not be directly ingested by twospotted spider mites, monoterpenes evaporating from glandular trichomes would be present in vapor form at the leaf surface (Reitsema et al. 1961). Monoterpene vapor did show some toxic effect to spider mites feeding on bean leaves in the petri dish experiment. Pulegone was more toxic, and was effective at lower concentrations, than either menthone or menthol (Table 5). Clearly, pulegone vapor can be toxic to spider mites, but mite response to individual monoterpenes at the concentration tested in petri dishes may not be a good representation of how mites would respond to vapors on peppermint leaf surfaces. For example, Rodriguez et al. (1976) found that strawberry essential oils were generally repellent to twospotted spider mites at high concentration, while attractive at low concentration.

CONCLUSIONS

The anti-herbivore potential of pulegone and menthol was demonstrated in the experiment on the effects of monoterpene vapor on twospotted spider mites. Twospotted spider mites feeding on peppermint leaves, however, did not appear to be influenced by monoterpenes. Peppermint monoterpenes, sequestered in glandular trichomes on the leaf surface, may be largely avoided by twospotted spider mites feeding on mesophyll cells in the leaf interior. Further investigation is needed to determine if spider mites are ingesting any monoterpenes, and whether the monoterpene vapor around peppermint leaves can affect mites.

The concentration of phenolic compounds in peppermint leaves had a significant effect on twospotted spider mites. High levels of phenolic compounds in peppermint leaves probably acted as a feeding deterrent, and resulted in an increased number of both adult and immature twospotted spider mites caught in the Tack-Trap, slower development of immatures, and reduced numbers of eggs laid per leaf. The Tack-Trap enclosures used in this experiment were mainly designed to measure the effect of leaf repellency. This experiment does not examine the potential of phenolic compounds, especially condensed tannins, to reduce the digestibility of peppermint leaf tissue by binding with proteins, but this could also be a factor in the reductions observed in the number of eggs laid per leaf and immature development rate. Further investigation is needed to identify the phenolic compounds in peppermint, and to analyze the effects of isolated peppermint phenolic compounds on twospotted spider mites.

The results of this experiment indicate that twospotted spider mite reproductive success is influenced by the age and growth form of peppermint leaves, and that the variation in the concentration of total phenolic compounds in different age leaves may be a major factor affecting twospotted spider mites. Phenolic compounds may be important in determining the vertical distribution of twospotted spider mites on peppermint plants.

The potential of peppermint phenolic compounds to inhibit feeding of twospotted spider mites could be important in the management of this pest. Peppermint plants with an increased level of phenolic compounds may not only inhibit feeding and thus reduce growth rate of twospotted spider mites, but could also increase the resistance of peppermint to verticillium wilt (Sheppard and Peterson 1976). High levels of phenolic compounds, which can act as feeding deterrents to humans as well as to mites, would probably not affect the quality of the distilled essential oil. Phenolic compounds are not usually steam distillable

(Robinson 1980), and so would be left behind with the plant wastes after the distillation of the essential oil.

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