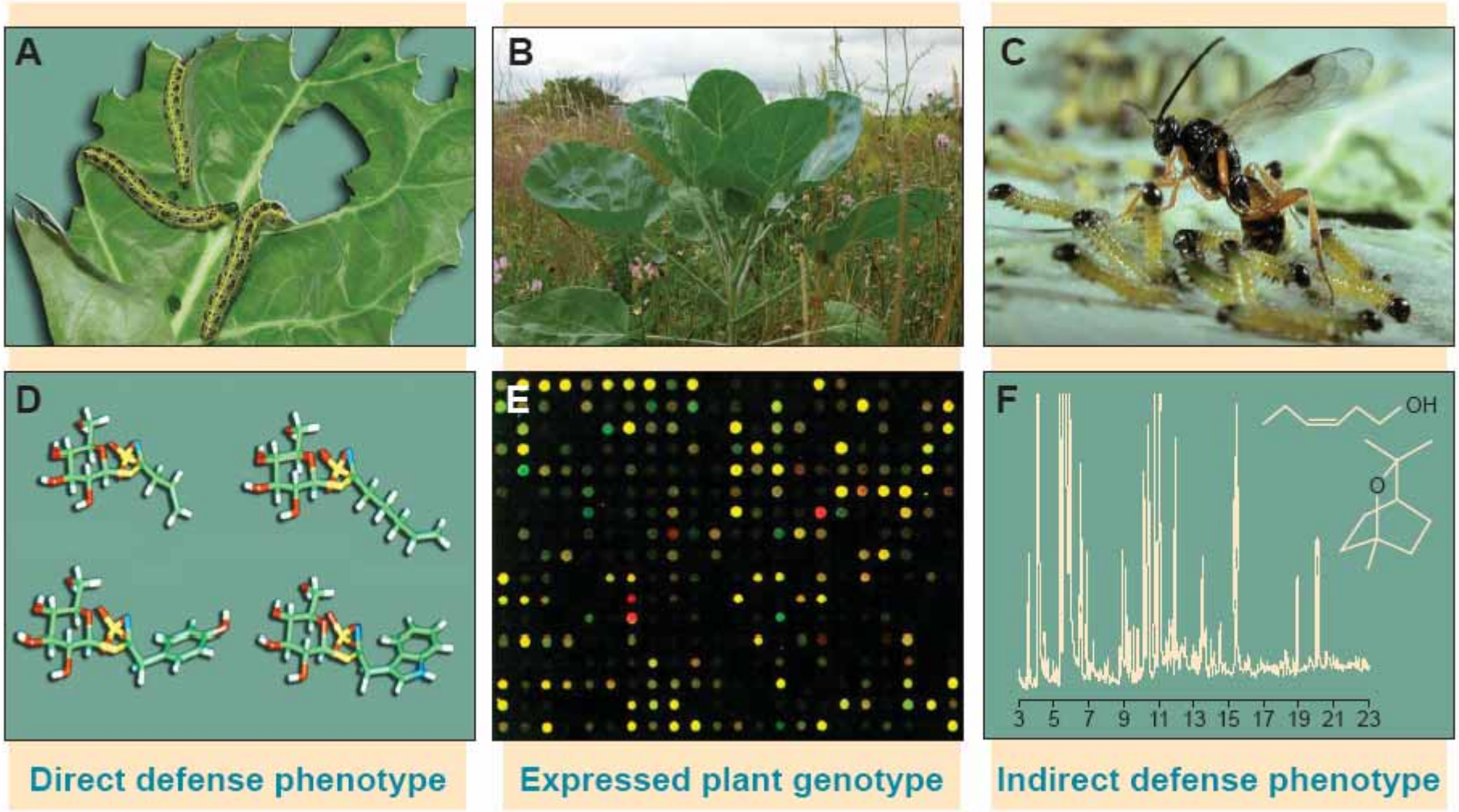
Multitrophische Interaktionen

Ecogenomics



Beating back the bugs. A tritrophic system consisting of plants, insect herbivores, and their natural enemies. This particular system comprises cabbage plants (*Brassica oleracea*) (**B**), herbivorous larvae of the cabbage white butterfly (*Pieris brassicae*) (**A**), and parasitoids, *Cotesia glomerata* (**C**), that attack *P. brassicae* caterpillars (**C**). Damage caused by caterpillars feeding on cabbage plants upregulates the expression of various genes in the plants, which are visualized as red spots in the microarray (**E**), and down-regulates the expression of other genes (green spots). Herbivory induces up-regulation of the biosynthesis of certain types of glucosinolates (**D**), toxic secondary metabolites characteristic of the Brassicaceae that mediate a direct defense against herbivorous insects. Additionally, the emission of dozens of volatile organic compounds, each represented by a peak in the gas chromatogram (**F**), is induced by herbivory. These herbivore-induced volatiles act as an indirect defense by attracting parasitoids that lay eggs in the caterpillars. Shown are the green-leaf volatile (Z)-3-hexen-1-ol and the terpenoid 1,8-cineole, representatives of two dominant classes of volatiles emitted by cabbage (**F**).

Tritrophische Interaktionen

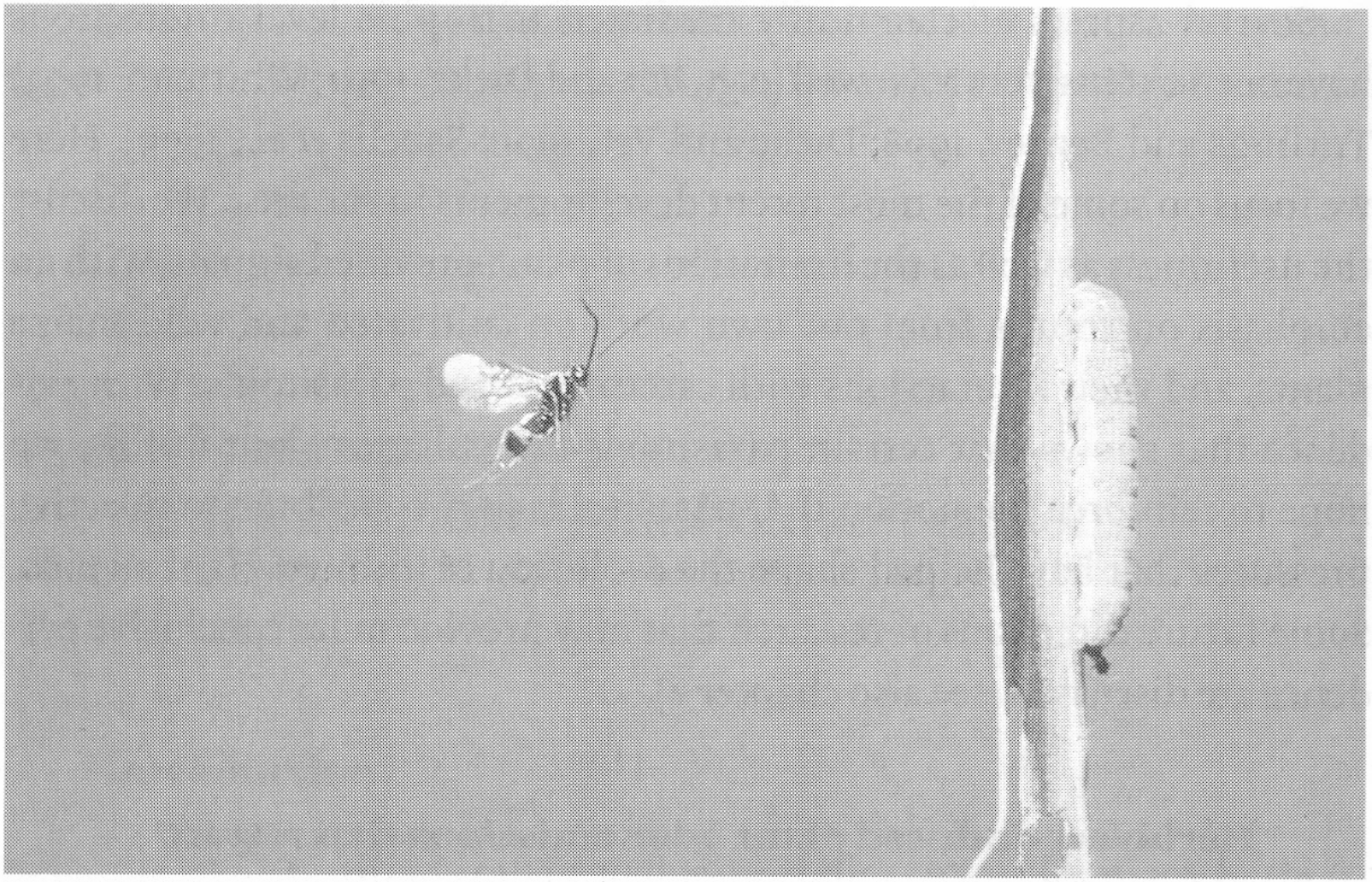


Fig. 7.1. A female *Cotesia marginiventris* approaching a maize seedling on which a potential host, a *Spodoptera exigua* larva, has been feeding.

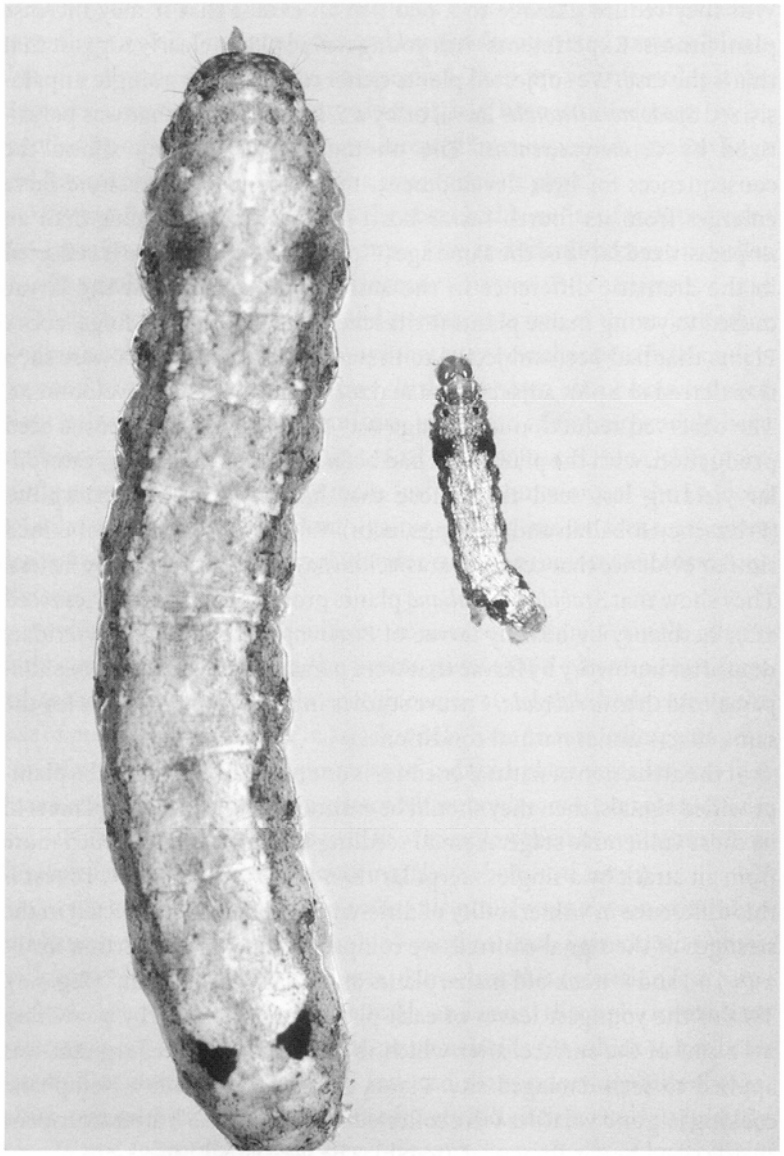


Fig. 7.5. Final size difference between a healthy, unparasitized *S. littoralis* larva (left) and a larva parasitized by *C. marginiventris* (right). (Photo by Yves Borcard.)

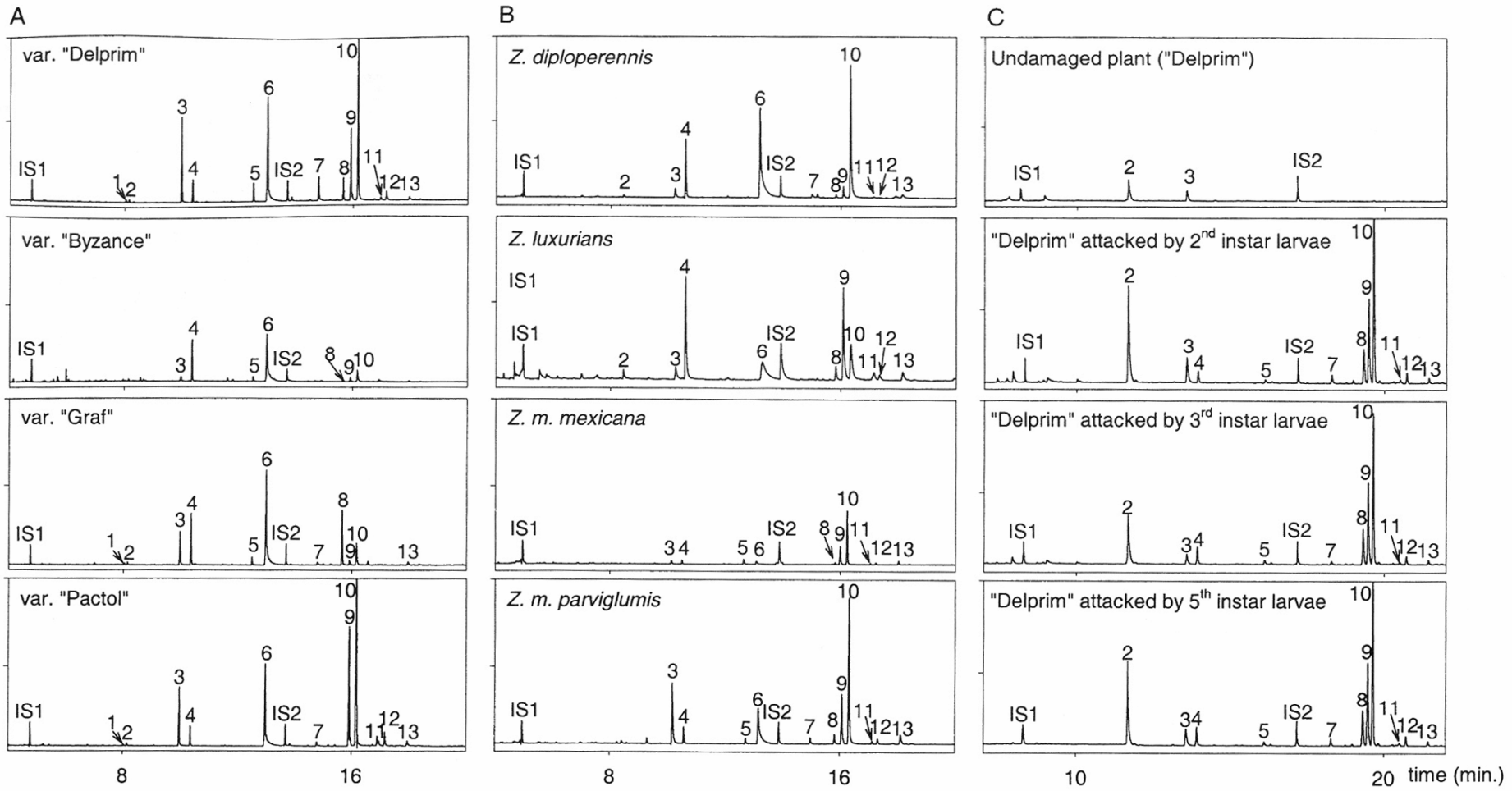
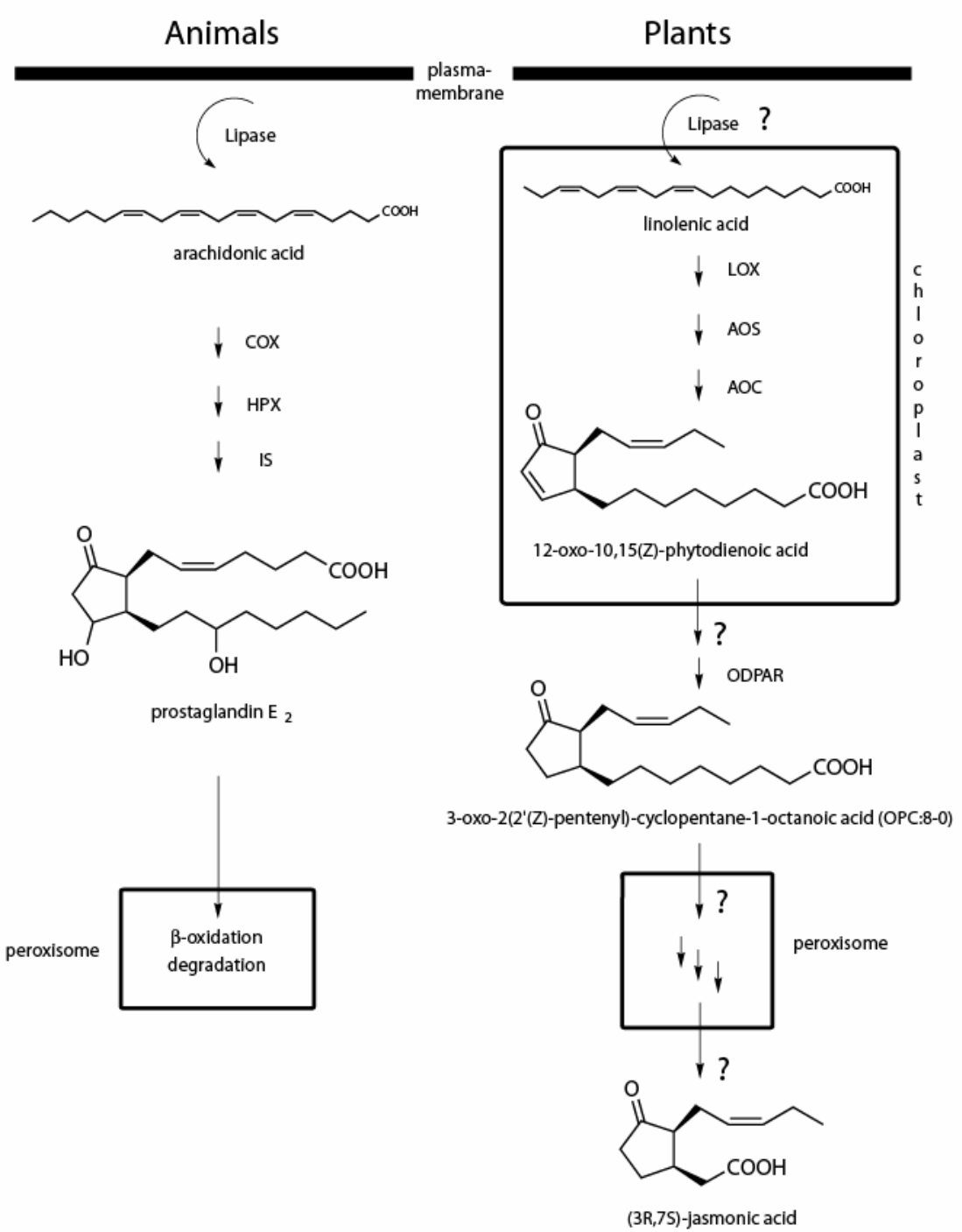


Fig. 7.3. Typical chromatographic profiles of volatiles collected from four different maize genotypes (A), four wild relatives of maize, teosintes (B), and from maize plants of the variety "Delprim" that were left undamaged or incubated in the regurgitant of either second, third, or fifth instar *Spodoptera littoralis* larvae (C). Odors were collected for 2 h about 14 h after a particular treatment was performed or started. For (A) and (B), 2 cm^2 of two leaves of each plant were scratched and 10 µl of *S. littoralis* regurgitant was applied to the damaged sites. The labeled peaks are: 1, β-myrcene; 2, (*Z*)-3–hexen-1–yl acetate; 3, linalool; 4, (3*E*)-4,8–dimethyl-1,3,7–nonatriene; 5, phenethyl acetate; 6, indole; 7, geranyl acetate; 8, β-caryophyllene; 9, (*E*)-α-bergamotene; 10, (*E*)-β-farnesene; 11, β-bisabolene; 12, unknown sesquiterpene; 13, (3*E*, 7*E*)-4,8,12–trimethyl-1,3,7,11–tridecatetraene. IS1 and IS2 represent the internal standards *n*-octane and nonyl acetate, respectively.


Animals
Plants
plasma-
membrane
Lipase
COOH
arachidonic acid
COX
HPX
IS
O
COOH
HO
OH
prostaglandin E 2
peroxisome
β-oxidation
degradation
Lipase ?
COOH
linolenic acid
LOX
AOS
AOC
O
COOH
12-oxo-10,15(Z)-phytodienoic acid
chloroplast
?
ODPAR
O
COOH
3-oxo-2(2'(Z)-pentenyl)-cyclopentane-1-octanoic acid (OPC:8-0)
?
peroxisome
?
O
COOH
(3R,7S)-jasmonic acid

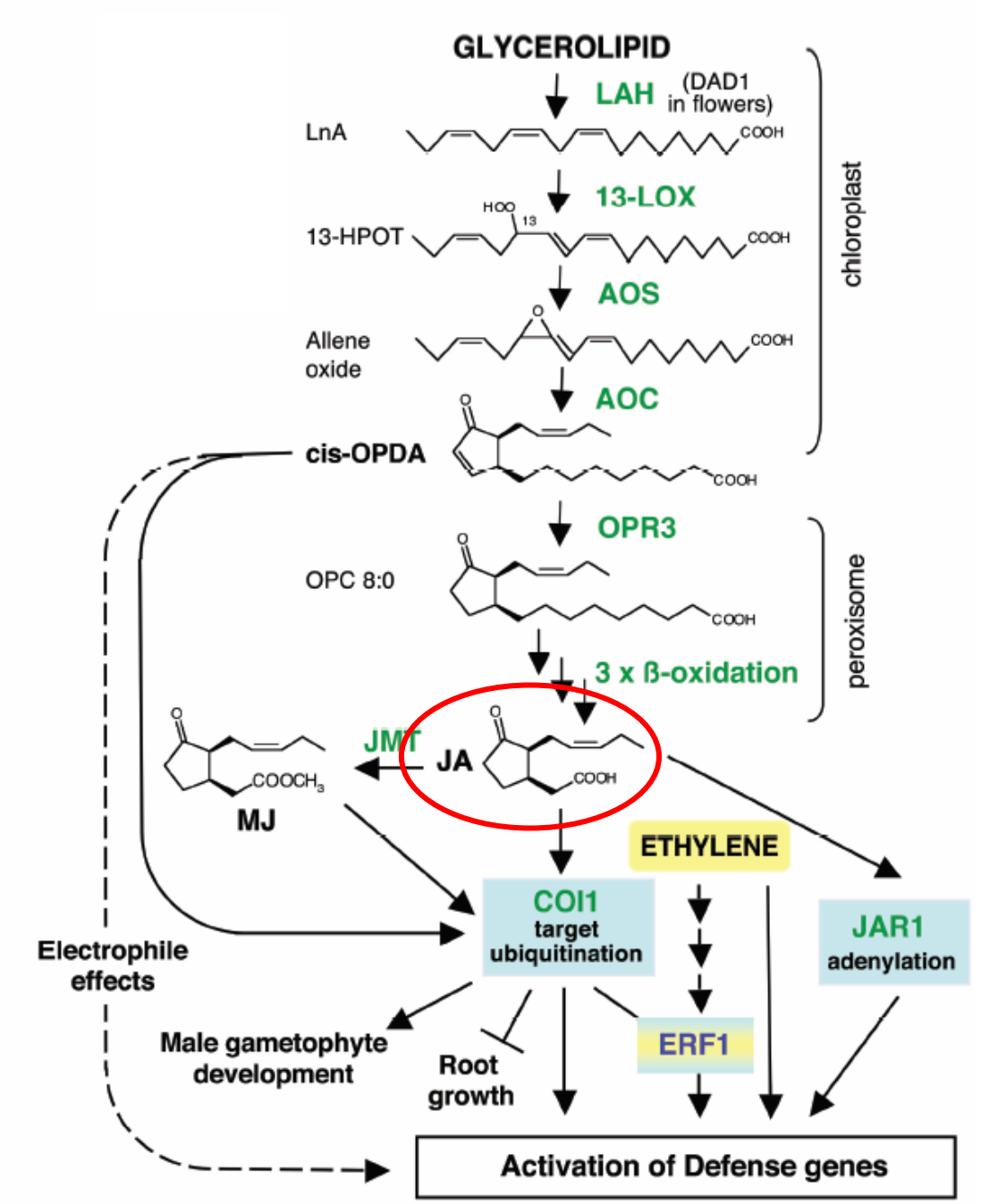
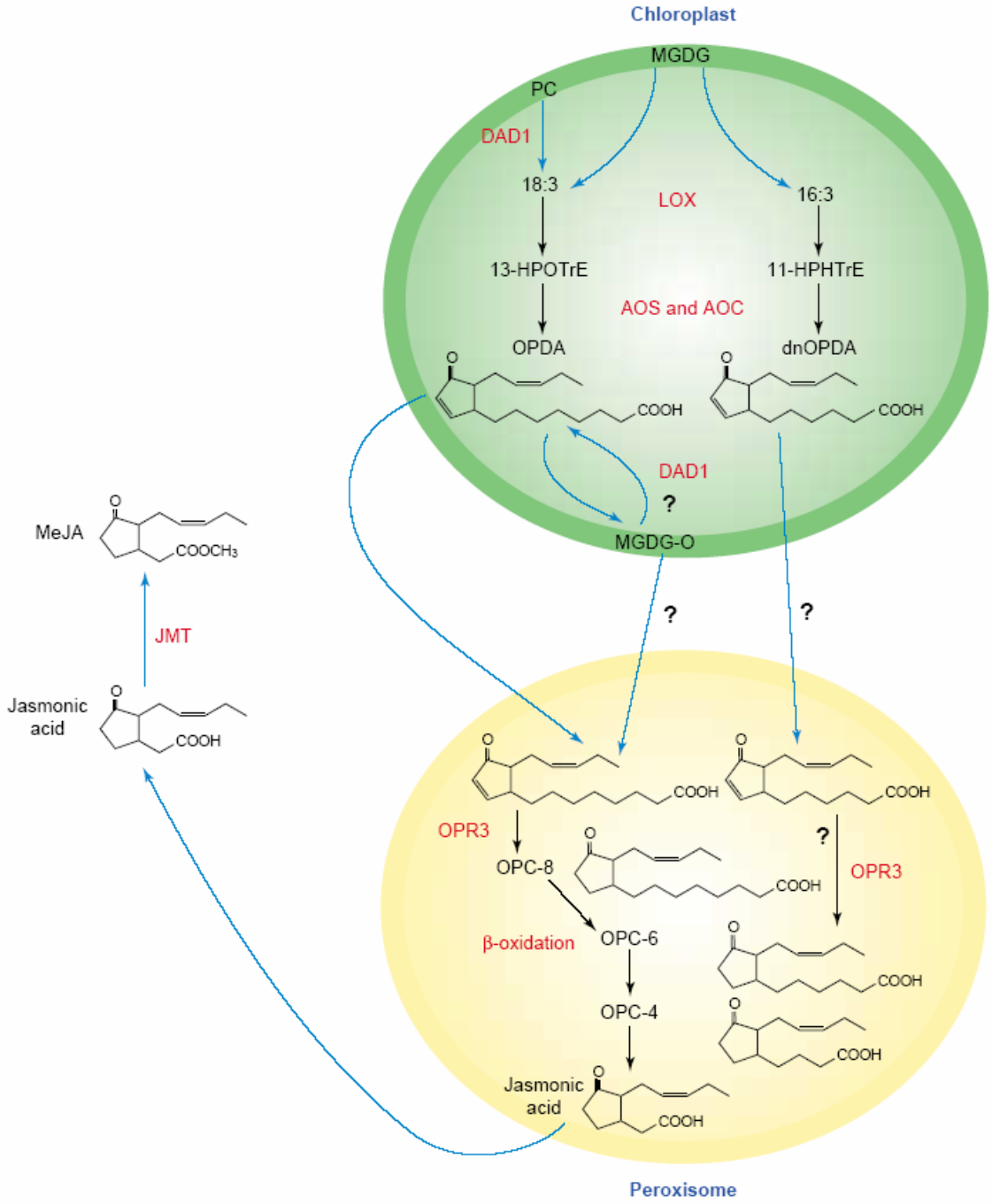
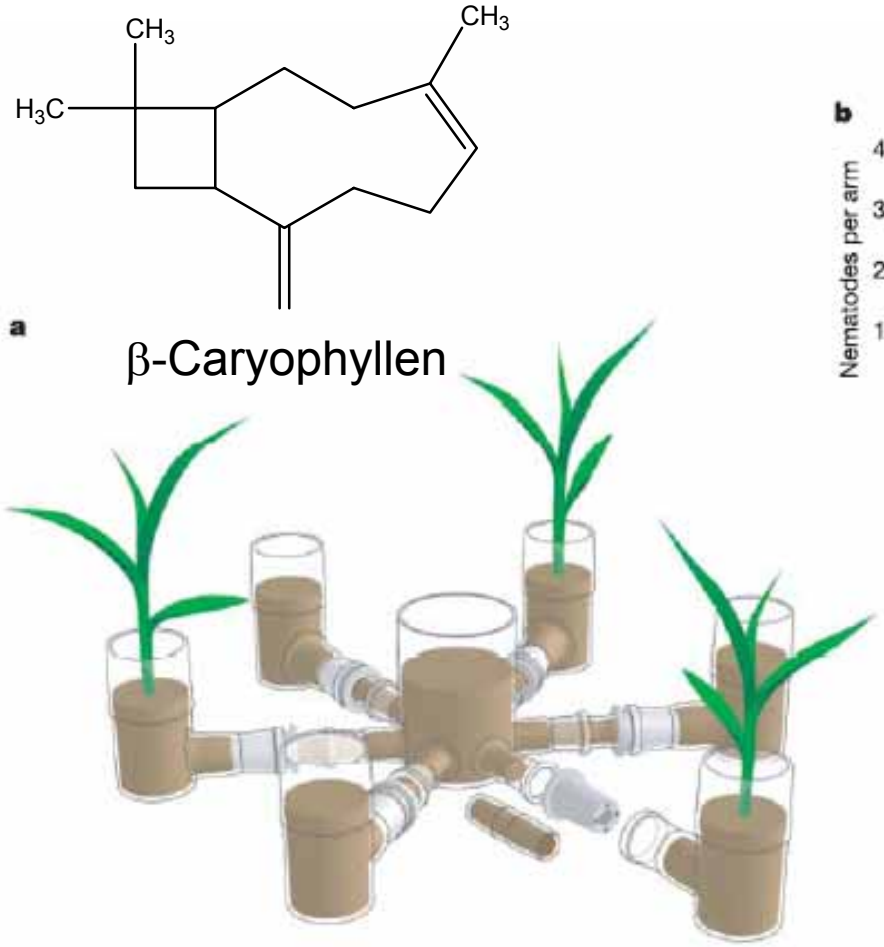
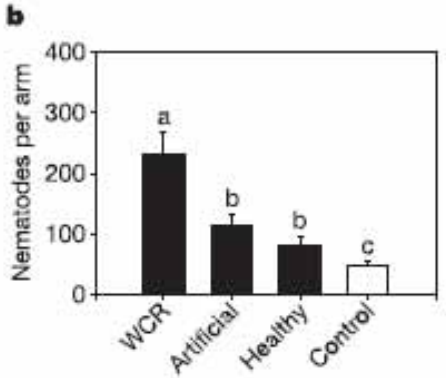


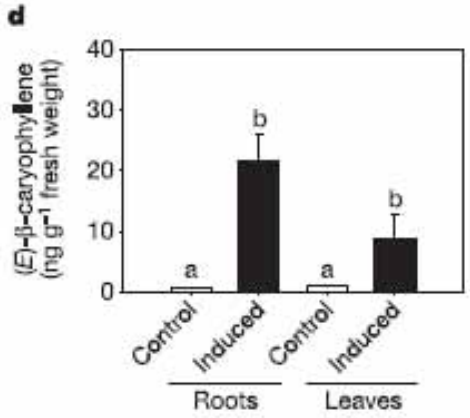
Fig. 3. Diversity of plant oxylipins formed in response to biotic aggressions. After mobilization by lipid acyl hydrolases (LAHs) from structural lipids, free fatty acids can be oxidized by at least three primary enzymatic systems (shown in color boxes), the best known being the lipoxygenase (LOX) pathway. LOXs generally introduce molecular oxygen onto carbon 9 or 13 (and are referred to as 9- or 13-LOX) in C18 unsaturated fatty acids, leading to 9- or 13-specific derivatives. LOX-generated fatty acid hydroperoxides may enter sub-branches, generating antimicrobial, cytotoxic, or signaling compounds. The profile of oxylipins formed depends on the enzymatic equipment of each plant species and on the type of stress that is encountered. In addition, a series of nonenzymatically derived, prostaglandin-like compounds (phytoprostanes) are formed under oxidative stress upon wounding or pathogen attack. AOS, allene oxide synthase; DES, divinyl ether synthase; EAS, epoxy alcohol synthase; FA, fatty acid; HPL, hydroperoxide lyase; LOX, lipoxygenase; a-DOX, a-dioxygenase.



Biosynthesis and intracellular fluxes of jasmonates in *Arabidopsis*.
Jasmonate biosynthesis originates in the chloroplast from 18:3 (octadecanoid pathway) and 16:3 (hexadecanoid pathway) fatty acids. The source for these is likely to be monogalactosydiacylglycerol (MGDG) (16:3 and 18:3) and, at least in flowers, phosphatidylcholine (only 18:3), as was shown by the substrate specificity of the lipase DAD1 [50]. Jasmonate biosynthesis terminates in the chloroplast with the cyclopentenone jasmonates **12-oxo-phytodienoic acid (OPDA)** and dinor OPDA (dnOPDA). Most OPDA was found to be esterified to membrane lipids (MGDG-O) and there might be continuous exchange of free and esterified OPDA in the chloroplast. The cyclopentenone jasmonates have to leave the chloroplast either to act as signals or to be further metabolized in the peroxisome, where reduction of the cyclopentenone ring and β-oxidation are thought to take place. Jasmonic acid and perhaps oxopentenyl-cyclopentanes (OPCs) leave the peroxisome to act as signals, and jasmonic acid can be methylated in the cytosol to its volatile counterpart methyl jasmonate (MeJA). This is a model of jasmonate biosynthesis and intracellular fluxes in Arabidopsis, and is based on many experimental findings, especially enzyme-location studies. Enzymatic steps are shown in red and fluxes as blue arrows; question marks indicate that there is no experimental evidence for these steps. Abbreviations: AOC, allene oxide cyclase; AOS, allene oxide synthase; DAD1, defective in anther dehiscence 1(phospholipase A1); 11-HPHTrE, 11(*S*)-hydroperoxy-7(*Z*),9(*E*),13(*Z*)-hexadecatrienoic acid; 13-HPOT*r*E, 13(*S*)-hydroperoxy-9(*Z*),11(E), 15(*Z*)-octadecatrienoic acid; JMT, S-ade-nosyl-*L*-methionine–jasmonic acid carboxyl methyl-transferase; MGDG-*O*, sn1- *O*-(12-oxophytodi-enoyl)-sn2-*O*-(hexadecatrienoyl)-monogalactosyl diglyceride; OPDA, 12-oxophytodienoic acid; OPR, OPDA reductase; 16:3, 7(*Z*),10(*Z*),13(*Z*) hexadecatrienoic acid; 18:3, 9(*Z*), 12(*Z*), 15(*Z*) octadecatrienoic acid (linolenic acid).







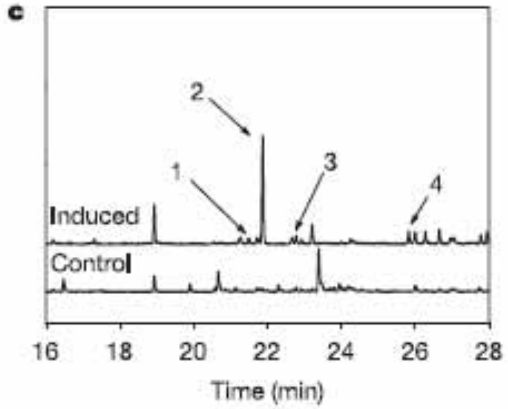
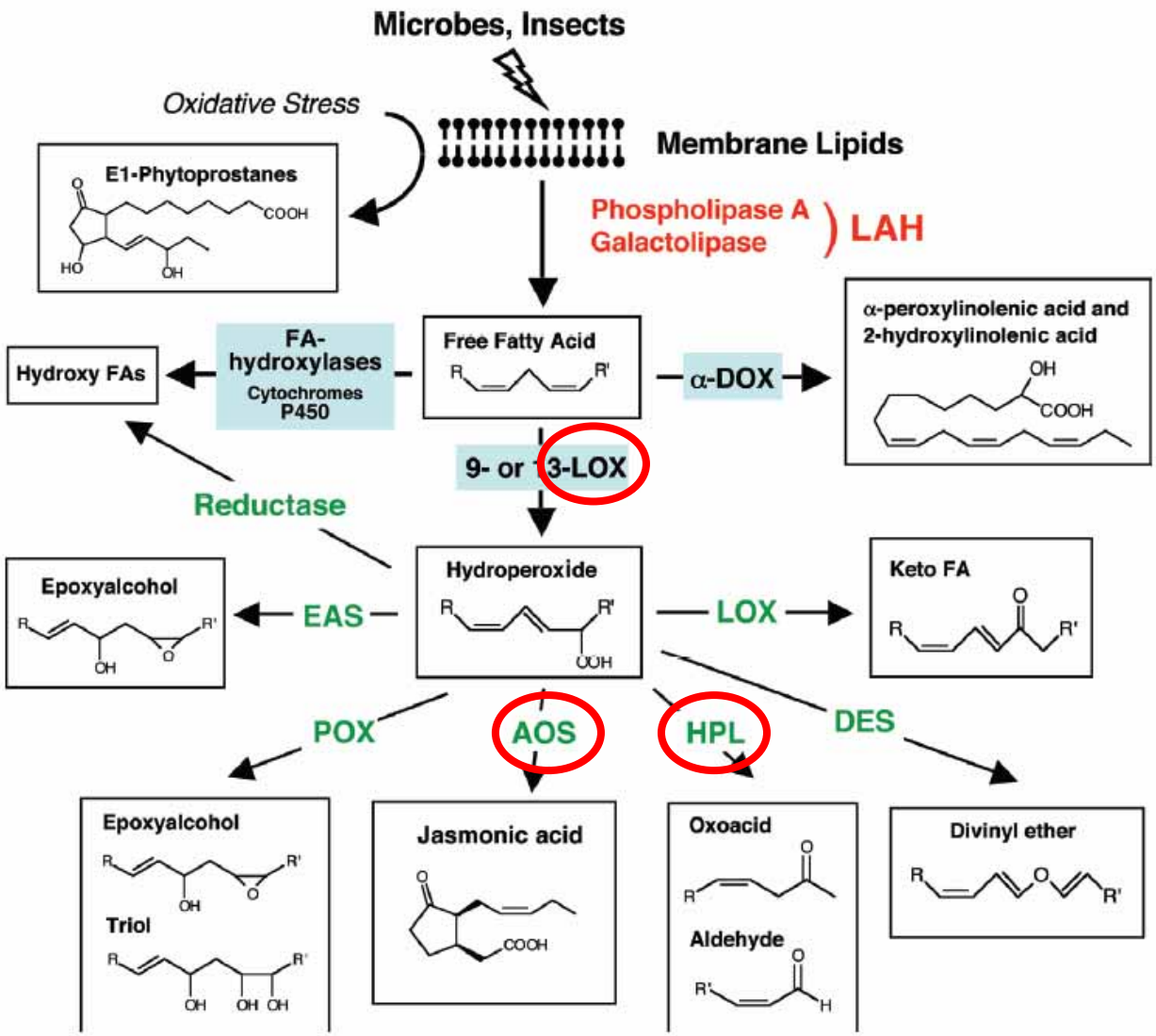


Figure 1 Attraction of entomopathogenic nematodes to a WCR-induced root signal. **a**, Drawing of a newly designed belowground six-arm olfactometer in which nematode attraction was tested. **b**, Choices between plants: the average number of nematodes recovered from olfactometer arms that were connected to pots holding either a maize plant with WCR-damaged roots, mechanically damaged roots or undamaged roots ($n = 12$). For each replicate, the total number of nematodes that went to the three control pots (only moist sand) were summed and divided by three. **c**, Typical chromatographic traces obtained from the roots of a healthy plant and of a WCR-damaged plant. The labelled peaks are as follows: 1, unknown sesquiterpene; 2, (*E*)-β-caryophyllene; 3, α-humulene; 4, caryophyllene oxide. **d**, Quantification of (*E*)-β-caryophyllene in roots and leaves from healthy and WCR-damaged maize plants ($n = 6$). Letters above bars indicate significant differences. Error bars indicate standard errors.

Nicotiana attenuata

gene knockouts



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B

	Genotype		
	as-*lox*	**as-*aos***	**as-*hpl***
Jasmonic acid	strongly reduced	reduced	slightly increased
(*Z*)-3-hexenal	-	slightly increased	strongly reduced
Nicotine	strongly reduced	-	-
Proteinase inhibitors	reduced	reduced	reduced
Terpenoids	strongly reduced	reduced	-
Resistance (*Manduca*)	reduced	-	slightly increased

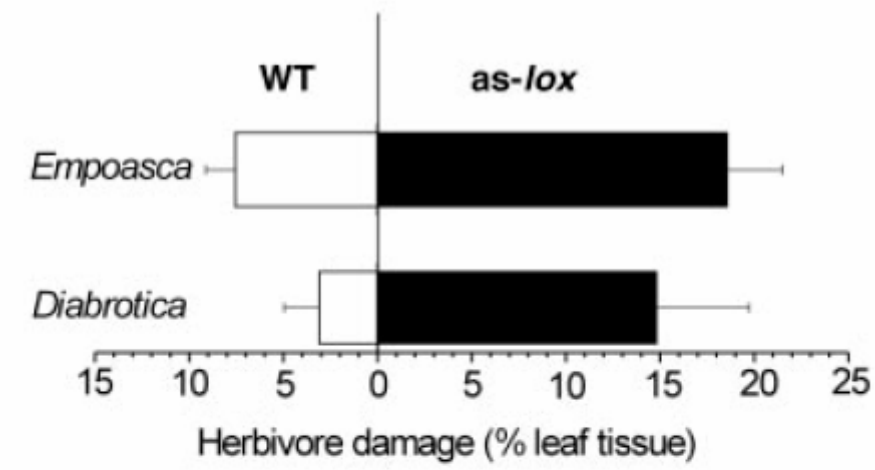
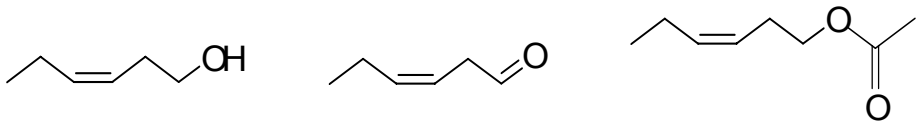


Fig. 4. Mean (+SEM) leaf tissue damage on wild-type (WT) and as-*lox* plants after 3 days of attack by *Empoasca* sp. leafhoppers or *D. undecimpunctata* leaf beetles, respectively. Ten *Empoasca* and two *D. undecimpunctata*, respectively, were allowed to choose between a WT and an as-*lox* plant that had been potted together and covered with insect mesh. Both experiments were replicated 10 times.



Z-3-HOL Z-3-HAL Z-3-HAC

Table 1. Amount of GLV (in ng) released by source plants upstream from receiver plants during periods of treatment

		CIV	GLV	Control
30 min	Z-3-HAL	356 ± 95	4,872 ± 633	ND
	Z-3-HOL	108 ± 53	2,736 ± 546	ND
	Z-3-HAC	595 ± 569	3,720 ± 1,052	ND
Overnight	Z-3-HAL	2,177 ± 470	653 ± 339	44 ± 37
	Z-3-HOL	1,210 ± 128	3,137 ± 245	44 ± 30
	Z-3-HAC	3,540 ± 833	4,102 ± 663	207 ± 184

Data are from caterpillar-infested corn plants (CIV), cut leaf material (GLV), and control plants during the 30-min and overnight incubation period. Data represent mean ± SD ($n = 4$). ND, not detected.

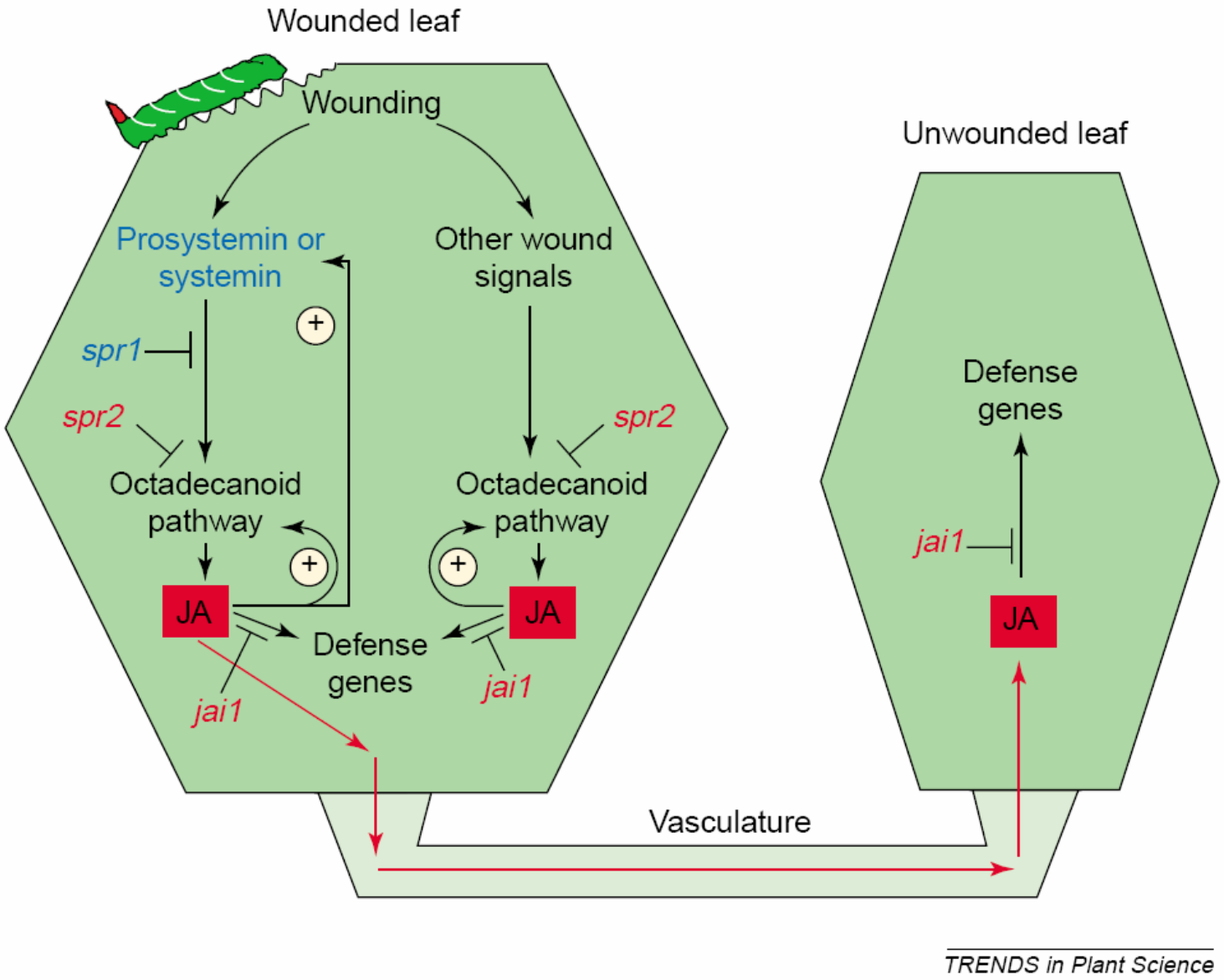


Fig. 2. Hypothetical processes involved in the systemic wound response in tomato plants. Wounding results in processing of systemin from prosystemin. Systemin activates jasmonic acid (JA) synthesis in a *Spr1*-dependent manner. Jasmonic acid is also synthesized in response to additional local wound signals such as oligogalacturonides, hydraulic and electrical signals. The mutant *spr2* is blocked in jasmonic acid biosynthesis, possibly in an enzyme functioning in the octadecanoid pathway. Expression of defense genes in wounded and unwounded leaves in response to jasmonic acid requires *Jai1*. Jasmonic acid produced in wounded leaves in response to systemin is translocated to distant unwounded leaves. Jasmonic acid also establishes positive feedback loops (+) by activating expression of genes coding for prosystemin and for enzymes functioning in jasmonic acid biosynthesis (octadecanoid pathway). This results in amplification of the long-distance signal.

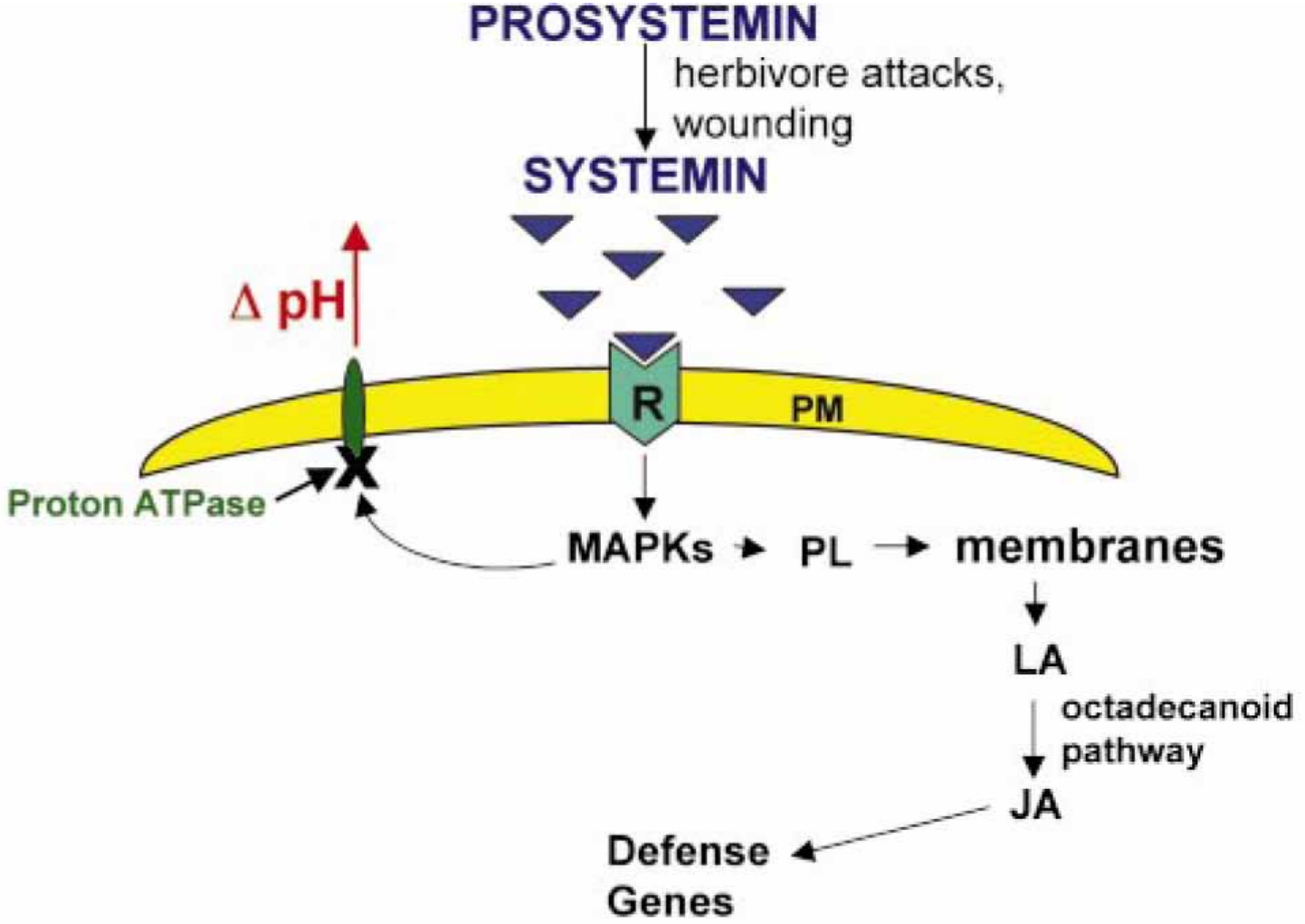
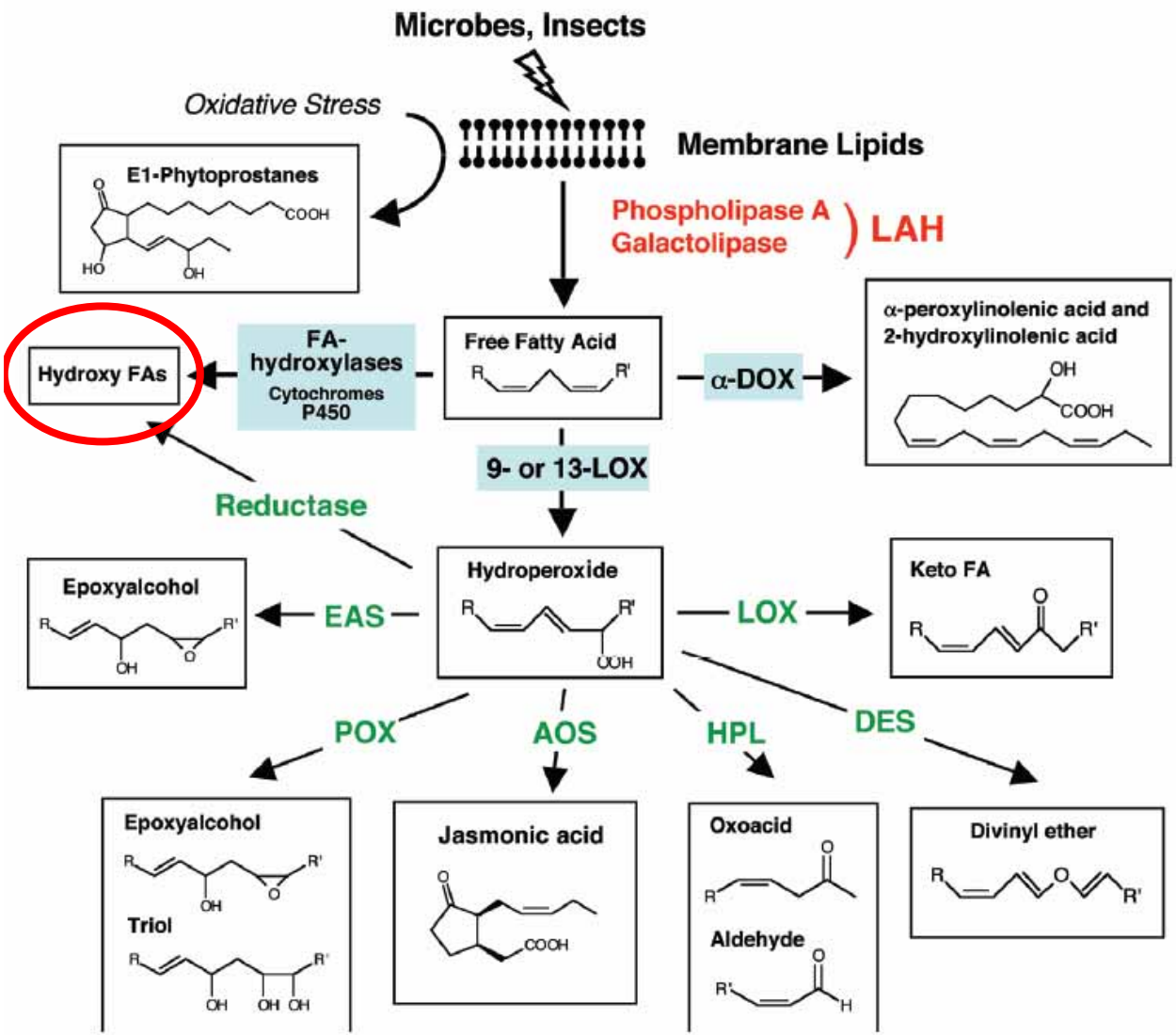


Fig. 1. A simplified diagram of the systemin signaling pathway. The pathway shows several key steps of the signaling pathway, and in particular the steps leading to the blockage of a proton ATPase that leads to the alkalinization of the extracellular medium, which is the basis of the assay developed to identify signaling peptides.



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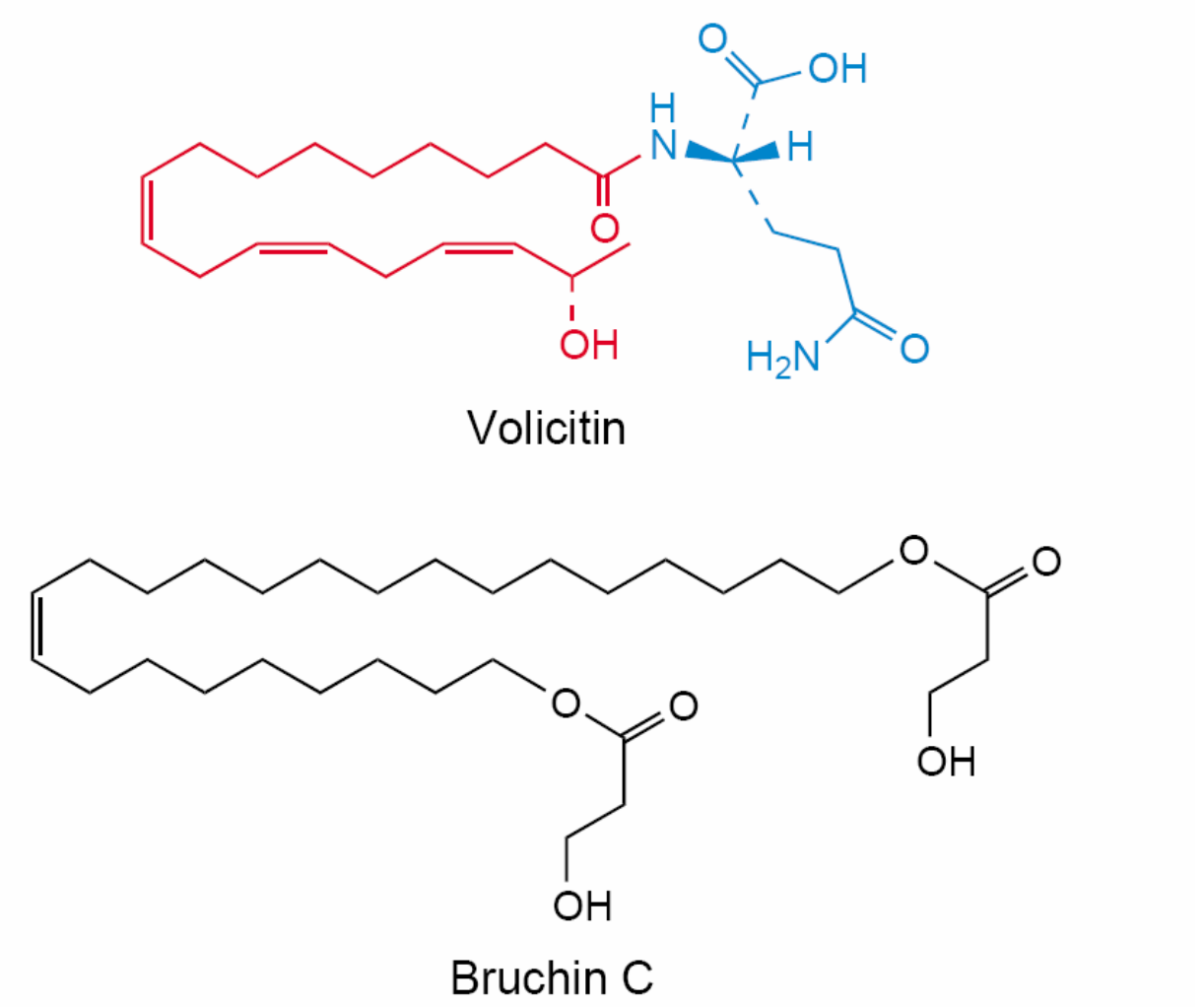


Fig. 3. Fatty acid-based signals from insects. Plants do not sense insects only by the physical injury caused by herbivory. Two recent examples, volicitin and bruchins, show that plant–insect interactions are mediated by complex chemical signalling. Volicitin, N-17(S)-hydroxylinolenoyl-Lglutamine, was isolated from oral secretions of beet army worm and is composed of 17(S)-hydroxy linolenic acid (red) and L-glutamine (blue). Volicitin triggers the release of a specific blend of volatiles by the plant and this attracts parasitic insects to the herbivore. Bruchins occur in pea and cowpea weevils. Bruchins are mono- and diesters of C22–C24 α,ω-diols with 3-hydroxypropanoic acid. The diol moiety is probably fatty acid derived. Bruchins have highly mitogenic activity and promote callus formation when applied to pea pods.

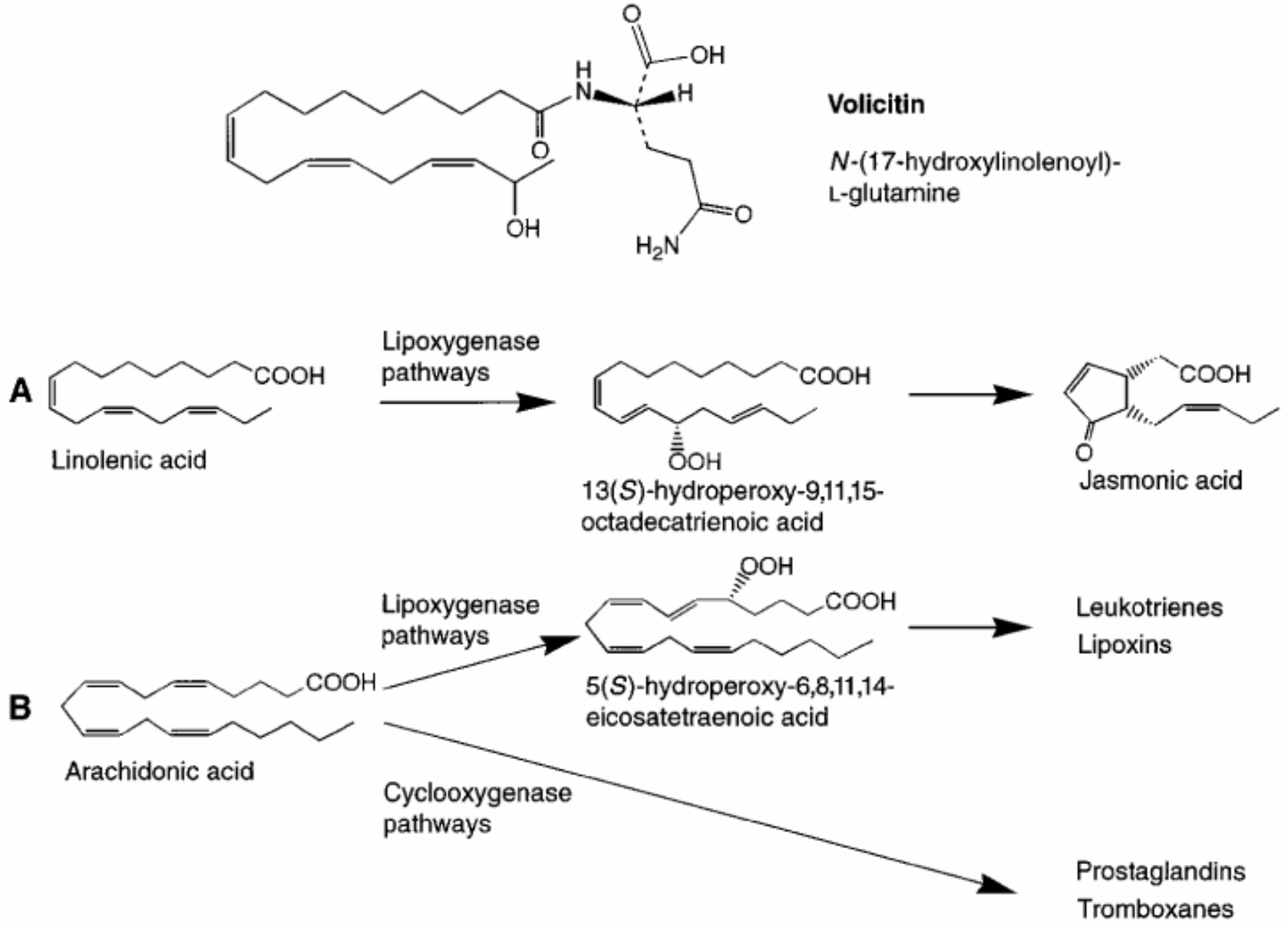


Fig. 1. Structure of volicitin. (**A**) The biosynthetic pathway leading to jasmonic acid in plants and (**B**) the biosynthetic pathways leading to prostaglandins and leukotrienes in animals.

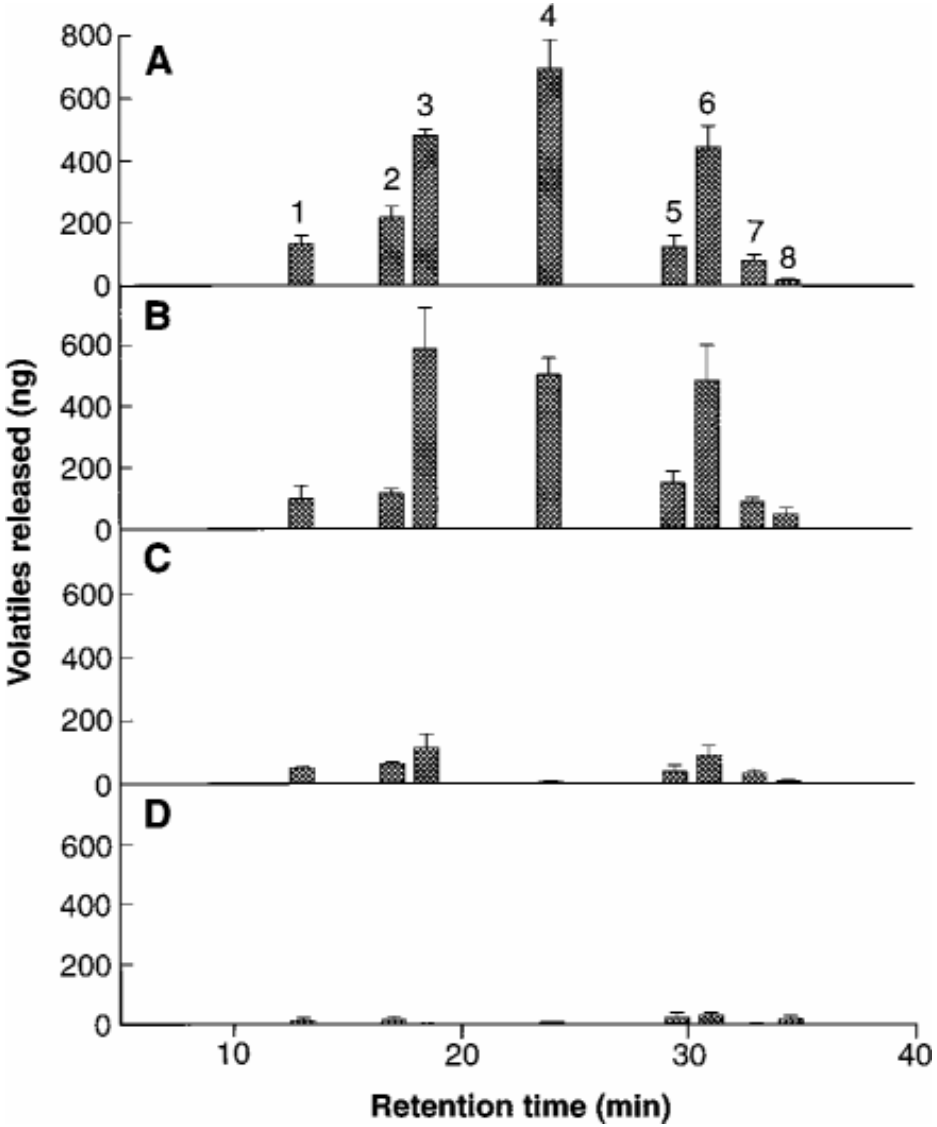
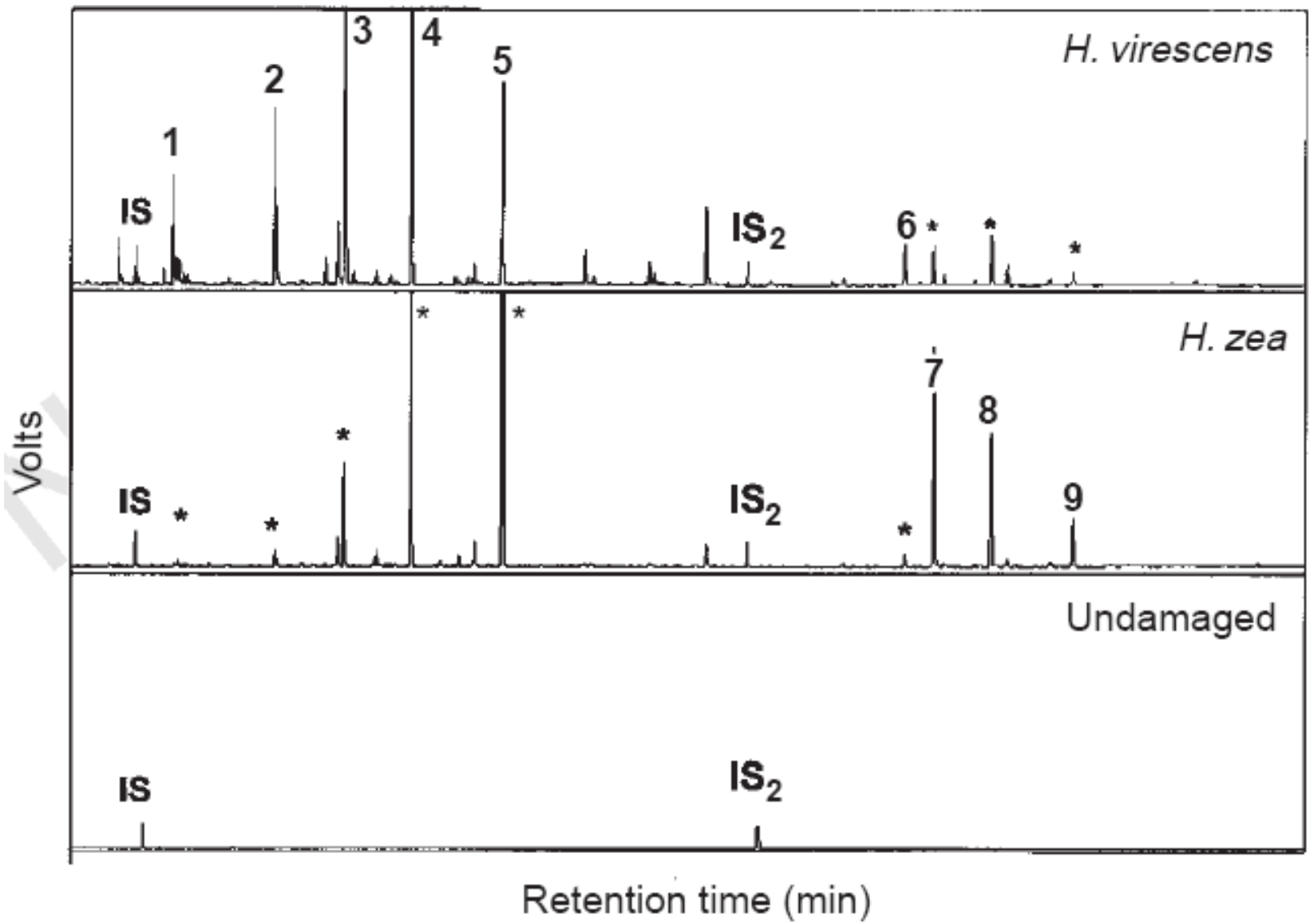


Fig. 2 (**left**). Average amount (nanograms per 2 hours) (*n* 5 4) of volatiles collected from three intact loana corn seedlings that had been artificially damaged and treated with (**A**) 15ml of BAW oral secretion per seedling on the damage sites, (**B**) 15 ml of oral secretion equivalents of pure natural volicitin,
(**C**) 15ml of buffer (*8*), or (**D**) undamaged control plants. At 9:00 p.m. a 1-cm^2 area of the second leaf of three-leaf seedlings was scratched with a clean razor blade and the test solution immediately rubbed over the damaged site.
The next morning at 9:00 a.m. the seedlings were cut off above the root, and volatiles were collected and analyzed as described (*7, 8*). Bars with the same retention time in each graph represent the following compounds: 1, hexenyl acetate; 2, linalool; 3, (*E*)-4,8-dimethyl-1,3,7-nonatriene; 4, indole; 5,
a-*trans*-bergamotene; 6, (*E*)-b-farnesene; 7, (*E*)-nerolidol; 8, (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene.


H. virescens
H. zea
Undamaged
IS
IS2
1
2
3
4
5
6
7
8
9
*
Volts
Retention time (min)

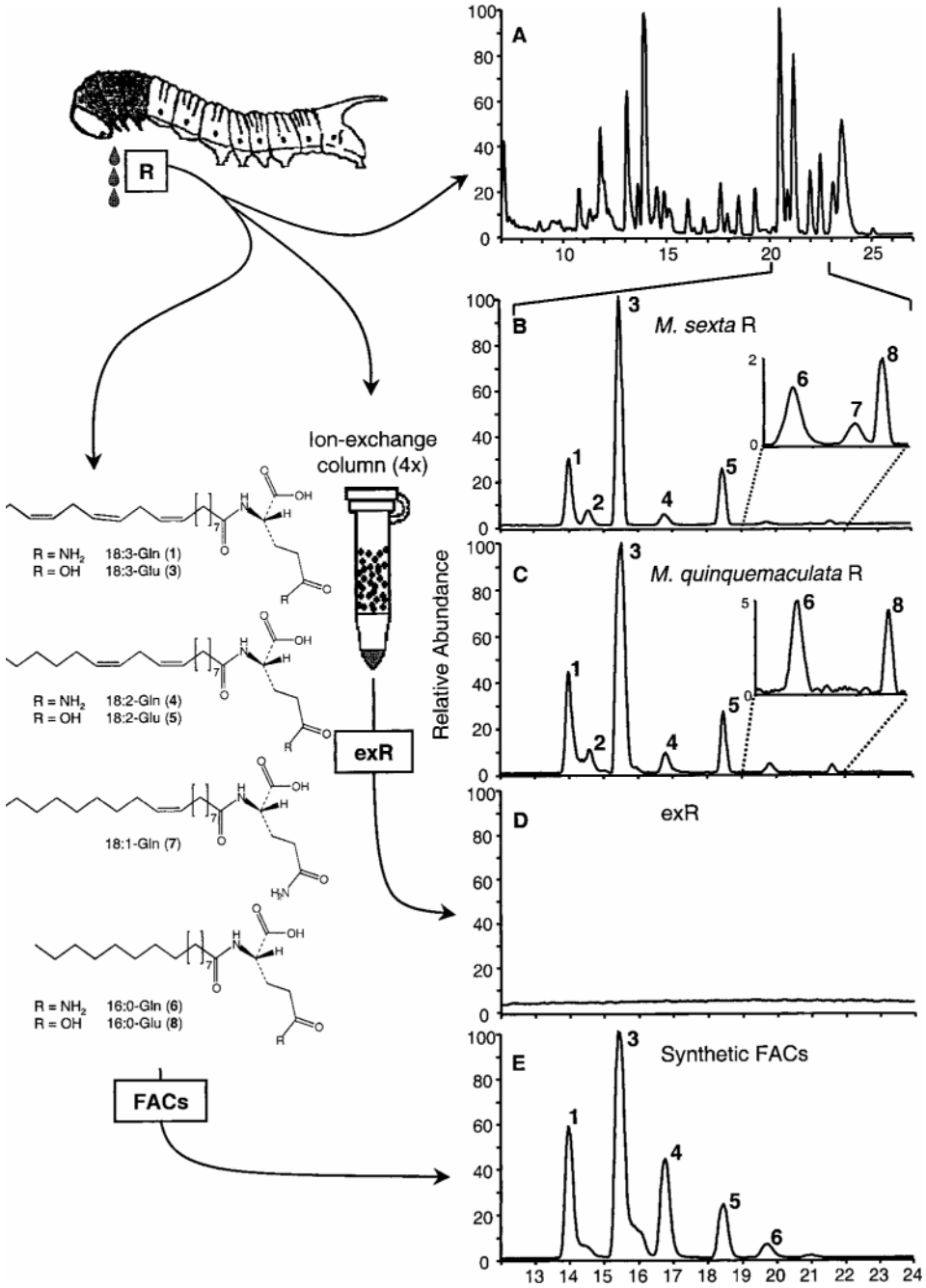


Figure 1. Scheme of experimental setup of the ion-exchange approach and structures of identified FACs (left) and HPLC-MS-Base peak profiles of 10-mL injections of test solutions (right): **A**, oral secretions and regurgitant (R) from *M. sexta* larvae. HPLC gradient (C18): CH3CN/H2O; 0.5% (v/v) HAc; 0.7 mL/min: 0% (v/v) CH3CN, 20 to 25 min 100% (v/v) CH3CN. Separation of the FACs in *M. sexta* (**B**) and *M. quinquemaculata* (**C**) R: HPLC gradient (C18): CH3CN/H2O; 0.5% (v/v) HAc; 0.7 mL/min: 40% (v/v) CH3CN, 7 min 68% (v/v) CH3CN, 18 min 80% (v/v) CH3CN, 28 min 100% (v/v) CH3CN. **1**, N-linolenoyl-L-Gln; **2**, unidentified; **3**, N-linolenoyl-L-Glu; **4**, N-linoleoyl-L-Gln; **5**, N-linoleoyl-L-Glu; **6**, N-palmitoyl-L-Gln; **7**, N-oleoyl-L-Gln; and **8**, N-palmitoyl-L-Glu. Base peak profiles of ion-exchanged M. sexta R (**D**) and mixture of synthetic FACs at concentrations found in M. sexta R (E) analyzed with the HPLC gradient as in B and C.

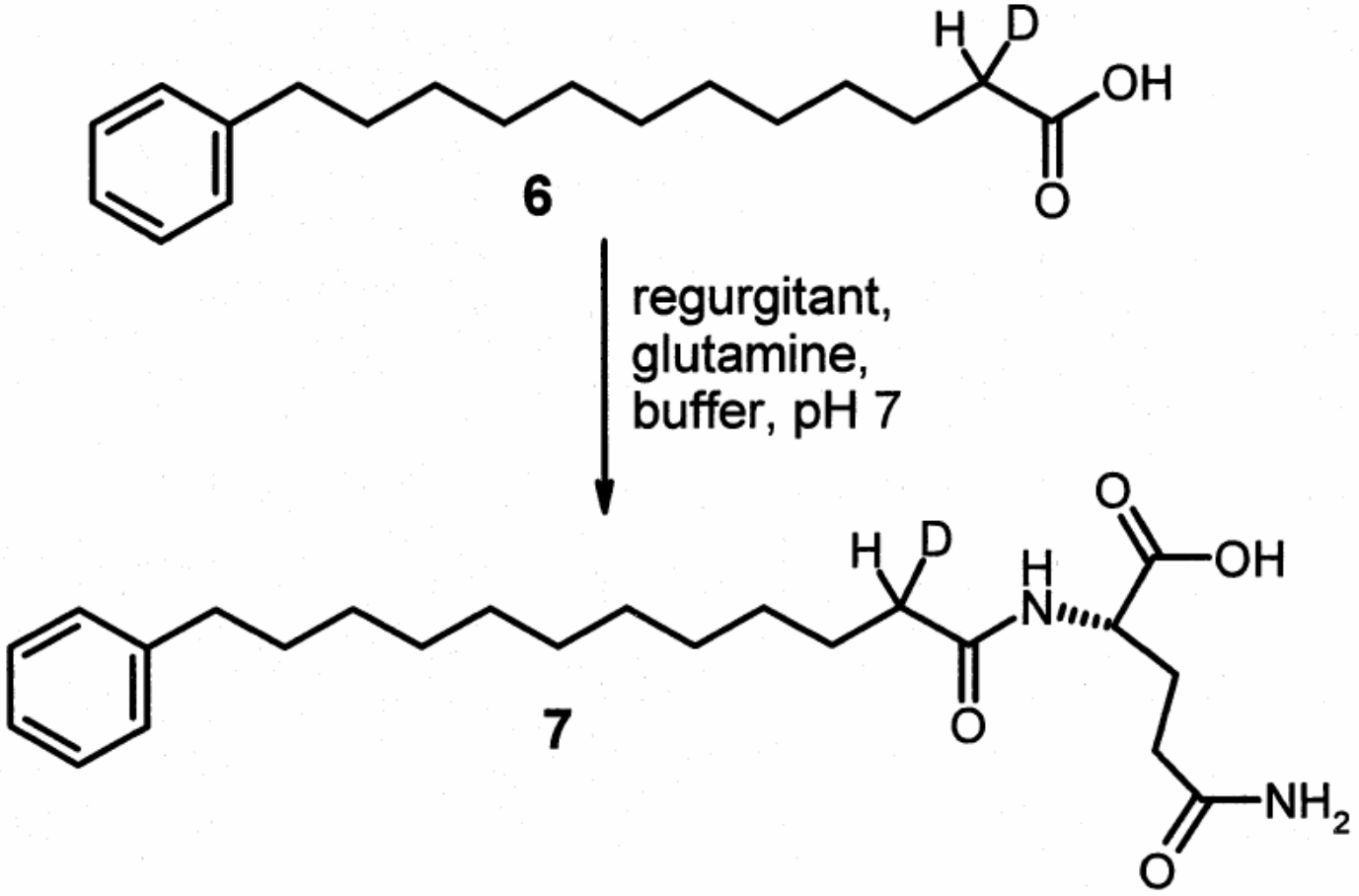
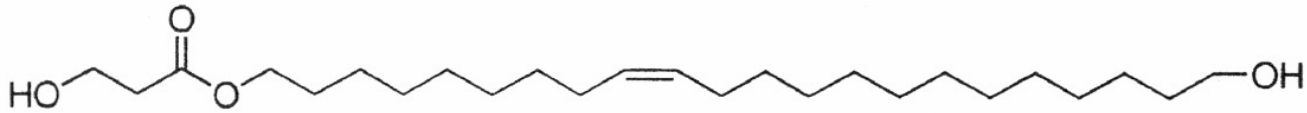
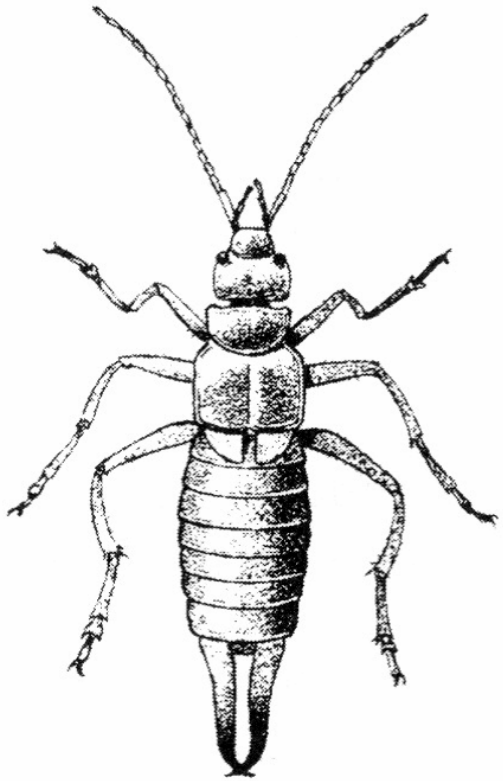


Fig. 2 *In Vitro* Formation of *N*-12-Phenyldodecanoylglutamine (**7**) from Labelled Phenyldodecanoic Acid (**6**) and L-Glutamine by Microorganisms from the Regurgitant of *S. exigua*.



bruchin A, stimulates neoplastic growth in peas



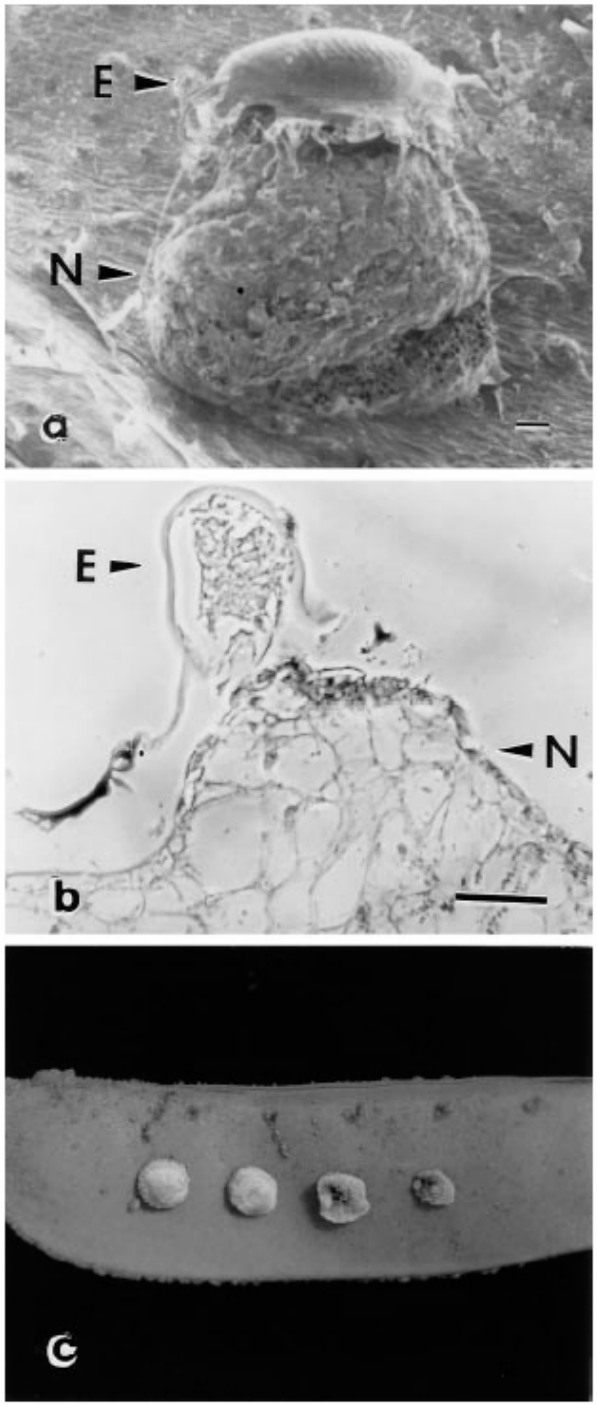
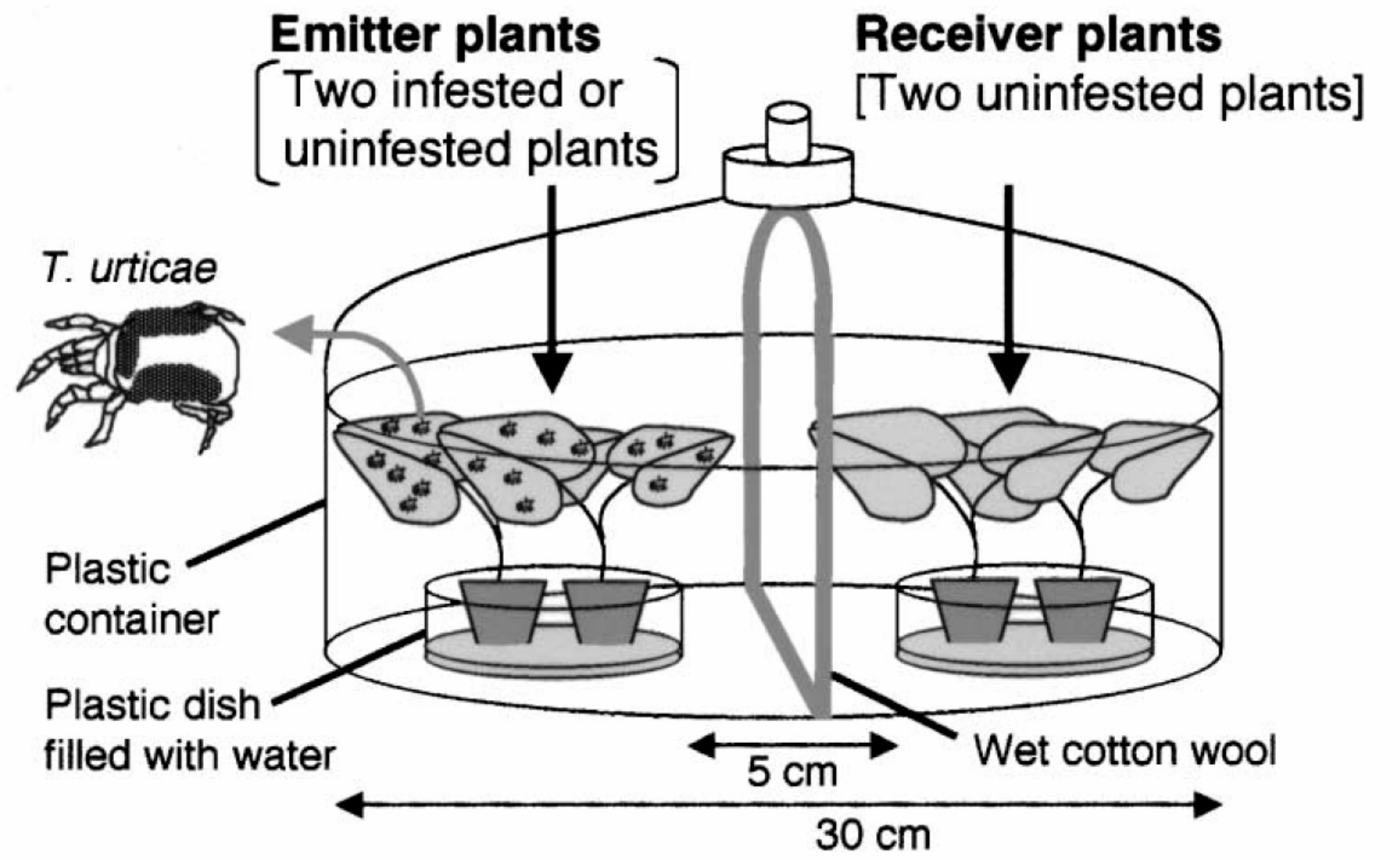


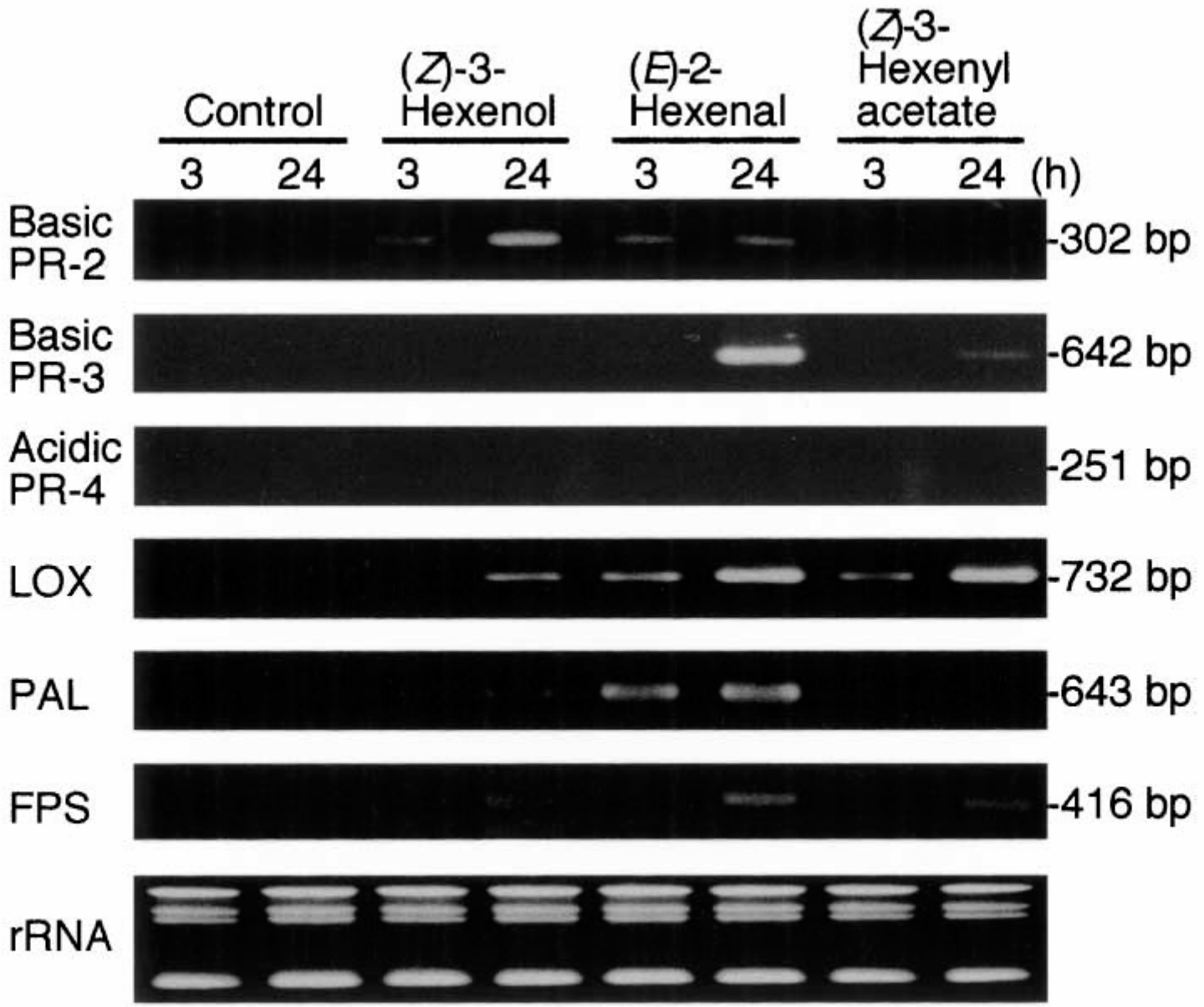
Fig. 1. Stimulation of cell division on pods of an *Np* pea line (a derivative of C887-332) by several treatments.

(***a***) Scanning electron micrograph showing the response of a pod from an *Np* pea line to oviposition by a pea weevil. The pod was obtained from a field-grown plant several days after oviposition. E, egg; N, neoplastic tissue formed in response to oviposition.

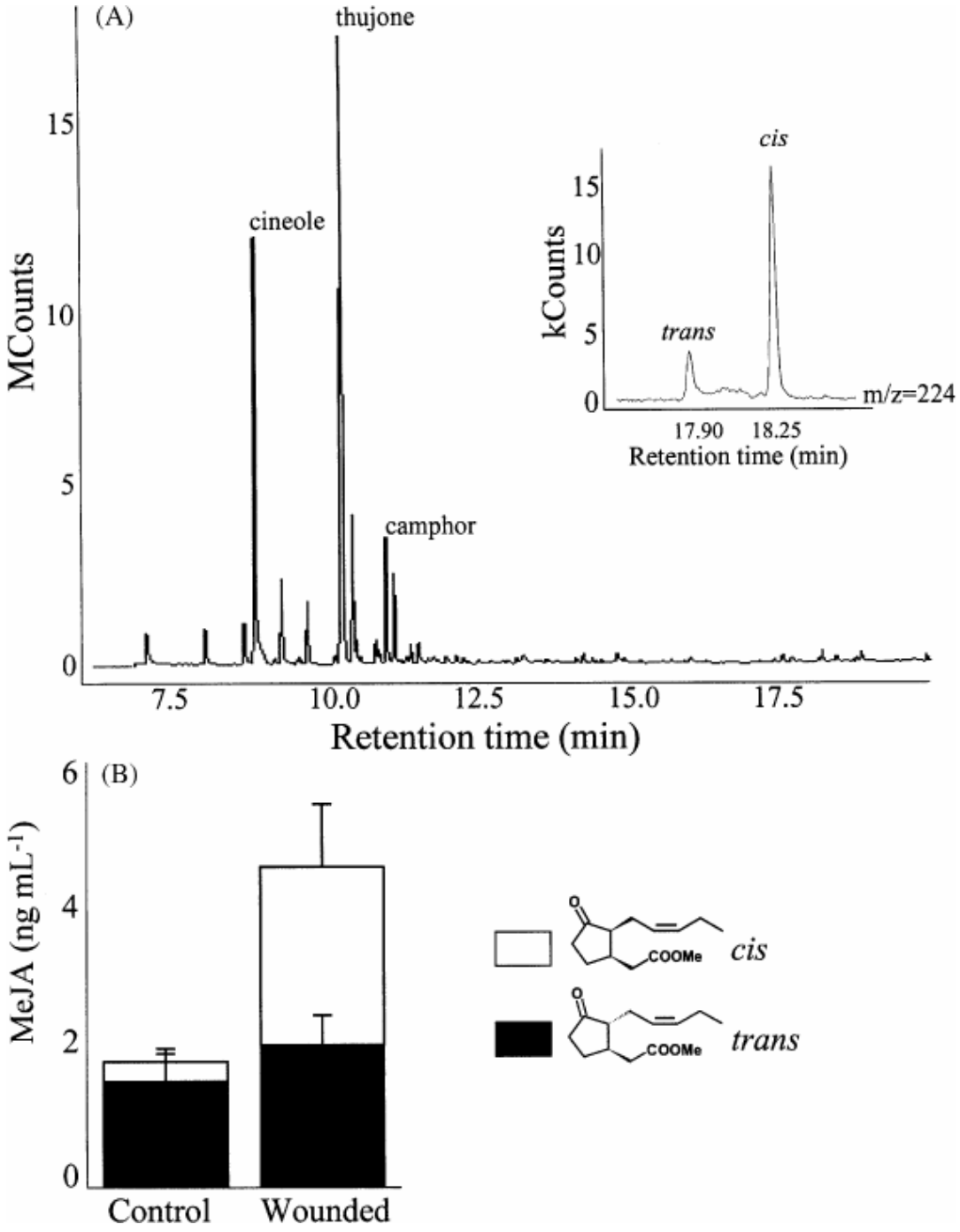
(***b***) Cross section through a pod showing neoplastic tissue formed in response to pea weevil oviposition. Pod was harvested and fixed 8 days after oviposition.

(***c***) Neoplasms present 1 week after application of various amounts of **2** (bruchin B), a compound present in extracts from the cowpea and pea weevil. Amounts applied as 1-ml drops in 50% (volyvol) ethanol were (from left) 10, 5, 1, 0.5, and 0.0 pg. (Bars 5/100 mm.)


Emitter plants
Two infested or uninfested plants
Receiver plants
[Two uninfested plants]
T. urticae
Plastic container
Plastic dish filled with water
Wet cotton wool
5 cm
30 cm



g. 3. Each of the three synthetic vapors shown here elicited the expression of defense genes. Tw infested leaves were enclosed in a glass container together with a piece of cotton wool containing (*Z*)-3 xenol, (*E*)-2-hexenal or (*Z*)-3-hexenyl acetate, dissolved in dichloromethane, for 3 or 24 h.


(A)
thujone
cineole
camphor
MCounts
15
10
5
0
7.5
10.0
12.5
15.0
17.5
Retention time (min)
cis
trans
kCounts
15
10
5
0
m/z=224
17.90
18.25
Retention time (min)
(B)
MeJA (ng mL-1)
6
4
2
0
Control
Wounded
COOMe
cis
COOMe
trans

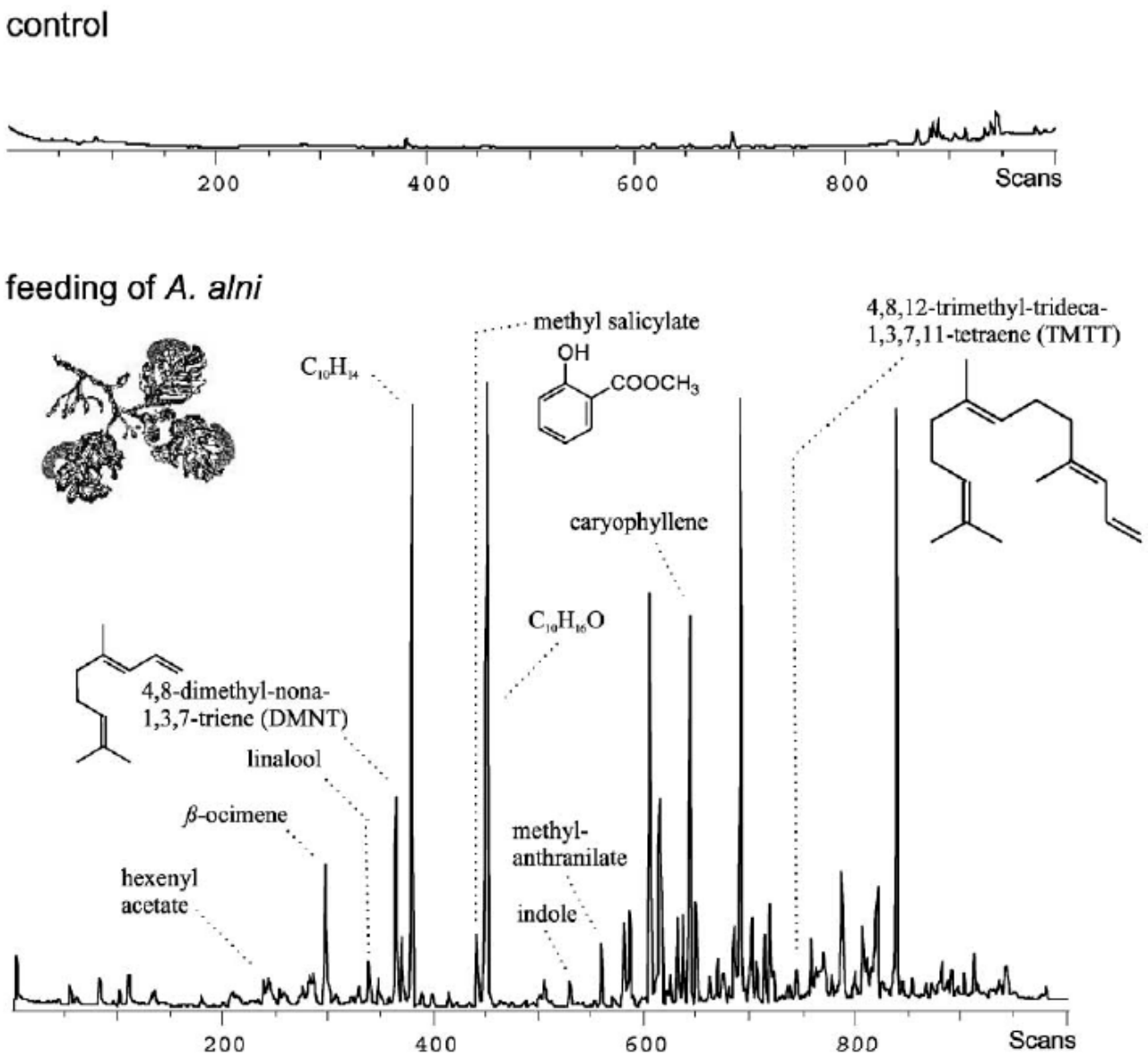


Fig. 2. Gaschromatographic profile of the alder volatiles emitted after feeding by *Agelastica alni*. In response to herbivory,black alder leaves released a blend of volatiles comprising the following compounds: monoterpenes (e.g. β-ocimene,linalool), sesquiterpenes (e.g. b-caryophyllene, b-farnesene,α-humulene), homoterpenes (e.g. 4,8-dimethylnona-1,3,7-triene, 4,8,12-trimethyltrideca-1,3,7,11-tetraene), fatty acid derivatives (e.g. 3-hexenyl acetate,decanal) and aromatic compounds such as 2-methyl anthranilate,methyl salicylate and indole. Control: gaschromatographic profile of undamaged alder leaves.

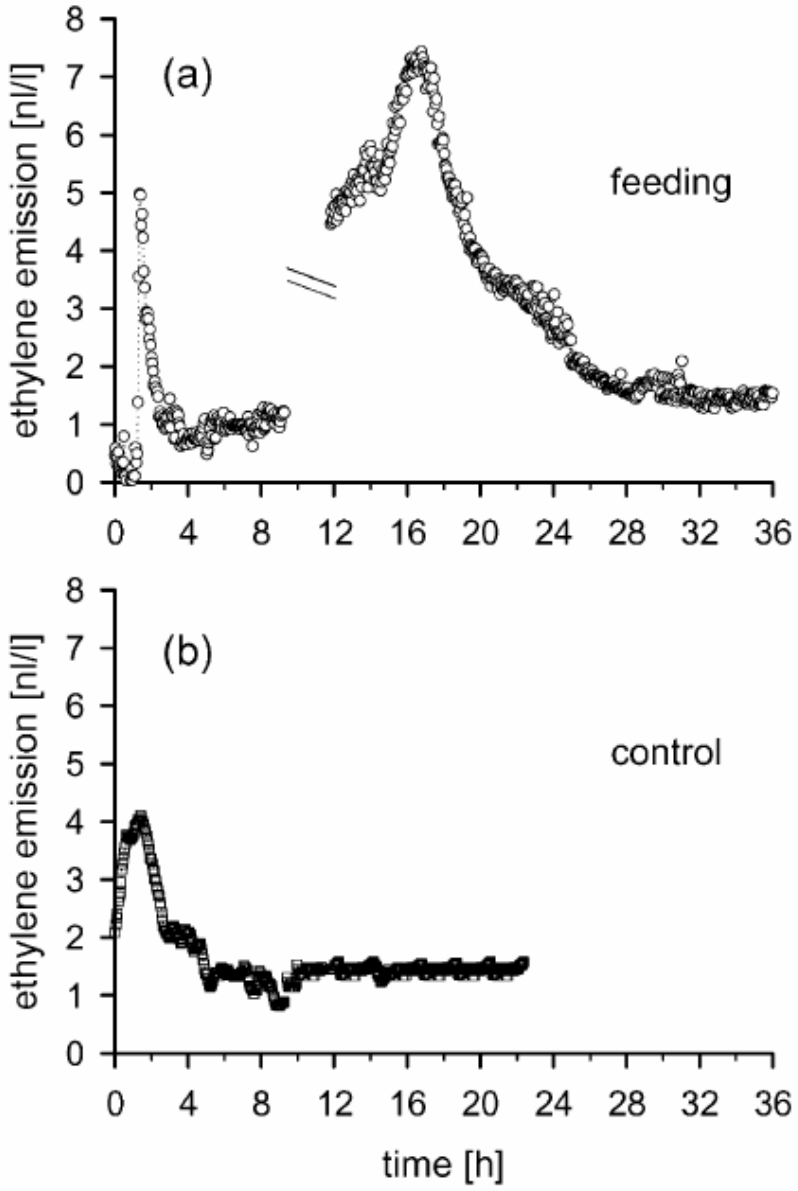


Fig. 3. Ethylene emission (nl/l) from *Alnus glutinosa* plants during feeding of *Agelastica alni* adults, measured by photoacoustic laser spectroscopy: (a) feeding of *A. alni*. Data measurement for the ethylene emission due to the beetles' feeding was shortly interrupted (as indicated by the double line); (b) control (undamaged leaves).

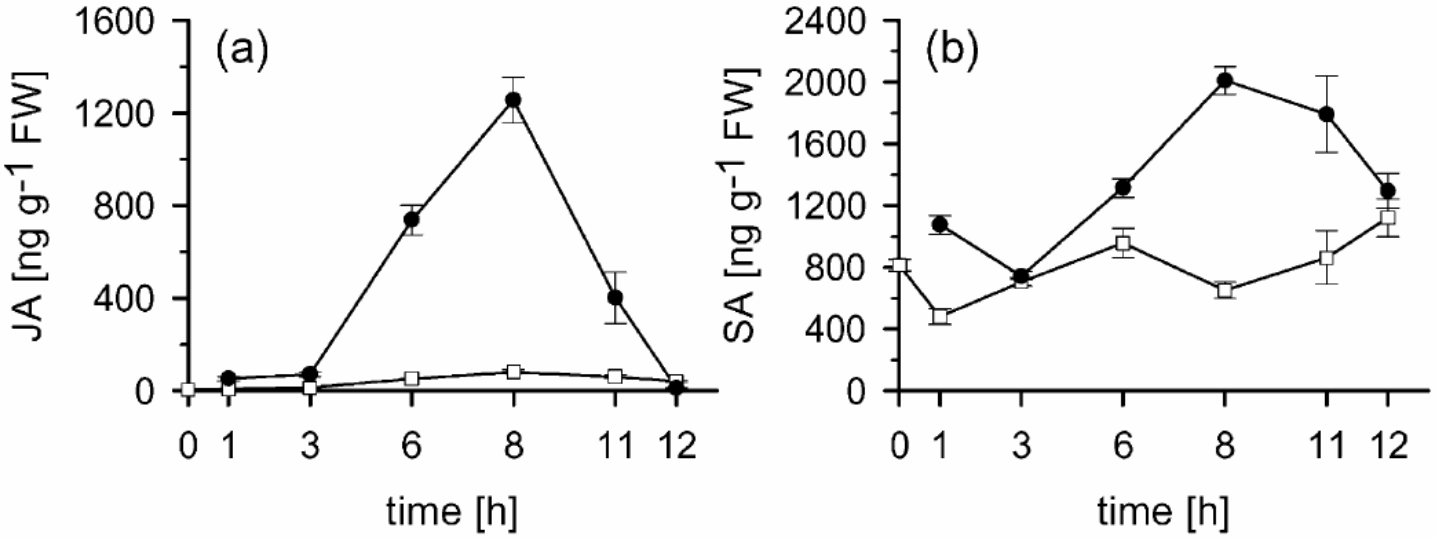
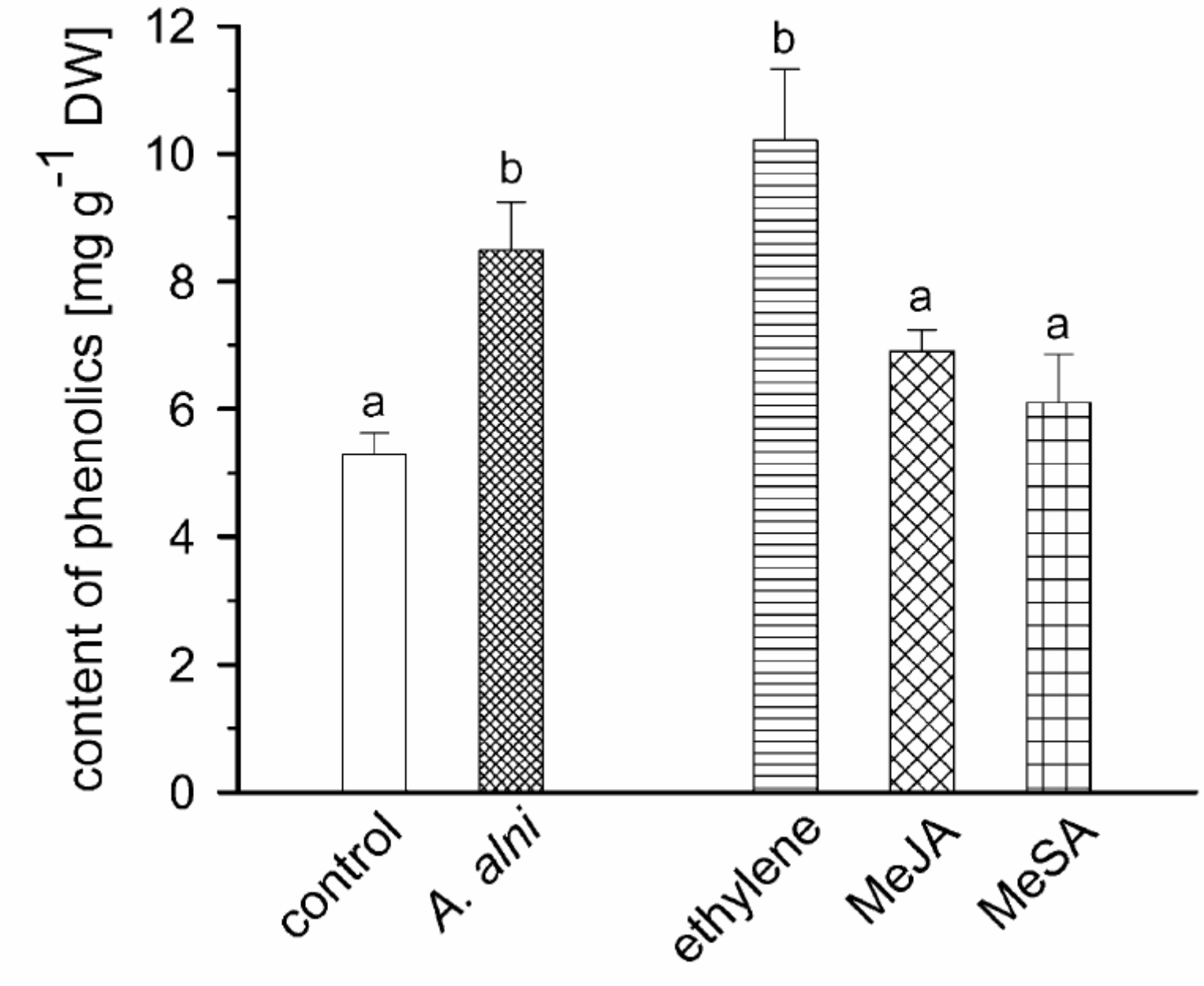


Fig. 4. Jasmonic acid (JA) and salicylic acid (SA) concentrations of black alder leaves wounded at time 0 with feeding of *Agelastica alni* larvae, and leaves without herbivores (=control). Leaves from four alder plants were harvested at each time: (a) JA concentration is expressed as ng JA per g leaf FW and; (b) SA concentration is expressed as ng SA per g leaf FW. Arithmetic means $\pm$ one standard error is shown ($n = 4$). (□) Control; (●) feeding of *A. alni*. FW= fresh weight.


content of phenolics [mg g-1 DW]
12
10
8
6
4
2
0
a
b
b
a
a
control
A. alni
ethylene
MeJA
MeSA

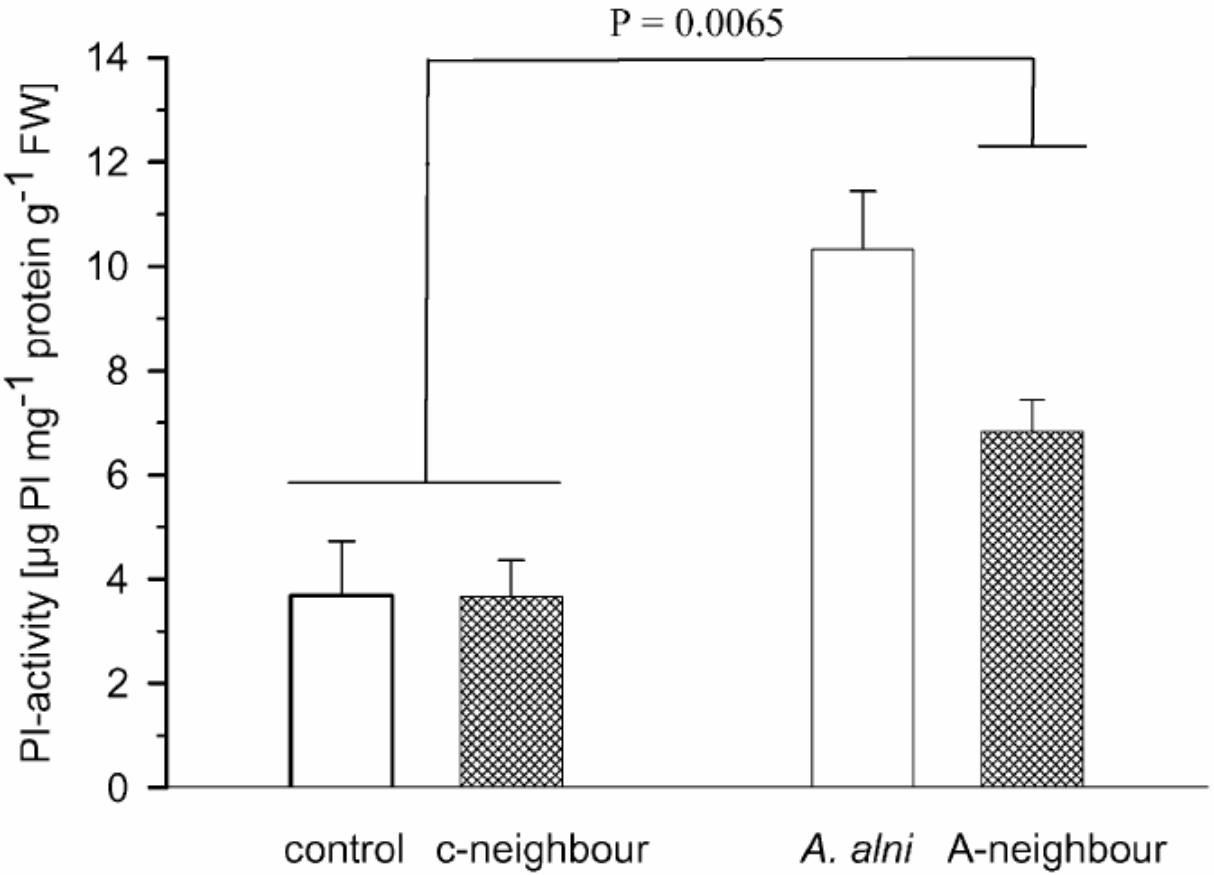


Fig. 8. Proteinase inhibitor (PI) activity of undamaged alder leaves influenced by volatiles emitted by leaves damaged by *A. alni* larvae (A-neighbour) in an airtight container. The control leaves (C-neighbour) were associated with only undamaged leaves. PI activity ($\mu g\,PI\,mg^{-1}$ protein g^{-1} FW) was monitored by radial diffusion assay after 72 h of incubation. Arithmetic means + one standard error are given ($n = 6$). FW = fresh weight. Undamaged leaves ("A-neighbour") neighbouring damaged leaves ("*A. alni*") showed a significant difference from control leaves ("Control and C-neighbour"): $t = 3.12$, $n = 18$, $p = 0.0065$ (or "A-neighbour" vs. "C-neighbour": $t = 3.22$, $n = 12$, $p = 0.009$). Damaged leaves and their undamaged neighbours did also differ ("*A. alni*" vs. "A-neighbour"): $t = 2.85$, $n = 12$, $p = 0.017$.

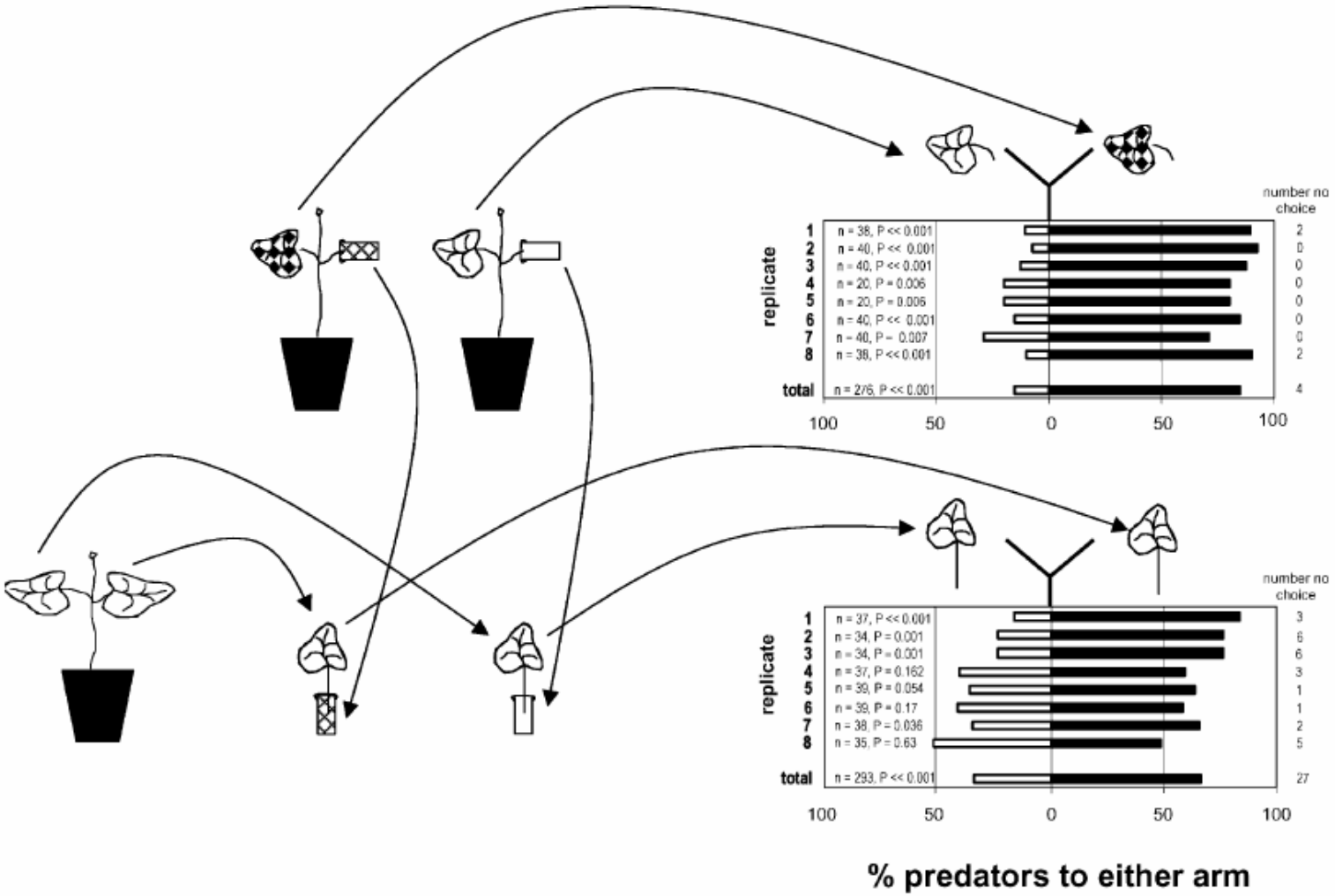


Fig. 2. Collection of systemic elicitor from the petiole of the primary leaves of lima bean plants that were infested with spider mites on the other primary leaf. The elicitor solution is used to incubate uninfested leaves from an uninfested lima bean plant for three days. Subsequently, the elicitor-treated and control uninfested leaves were used as odour sources in a Y-tube olfactometer. The responses of adult female predatory mites are shown for each of the replicate experiments and for the combined data. The data were analysed with a binomial test; '*n*' represents the number of predators that made a choice. The number of predators that did not make a choice is indicated on the right of the graph.

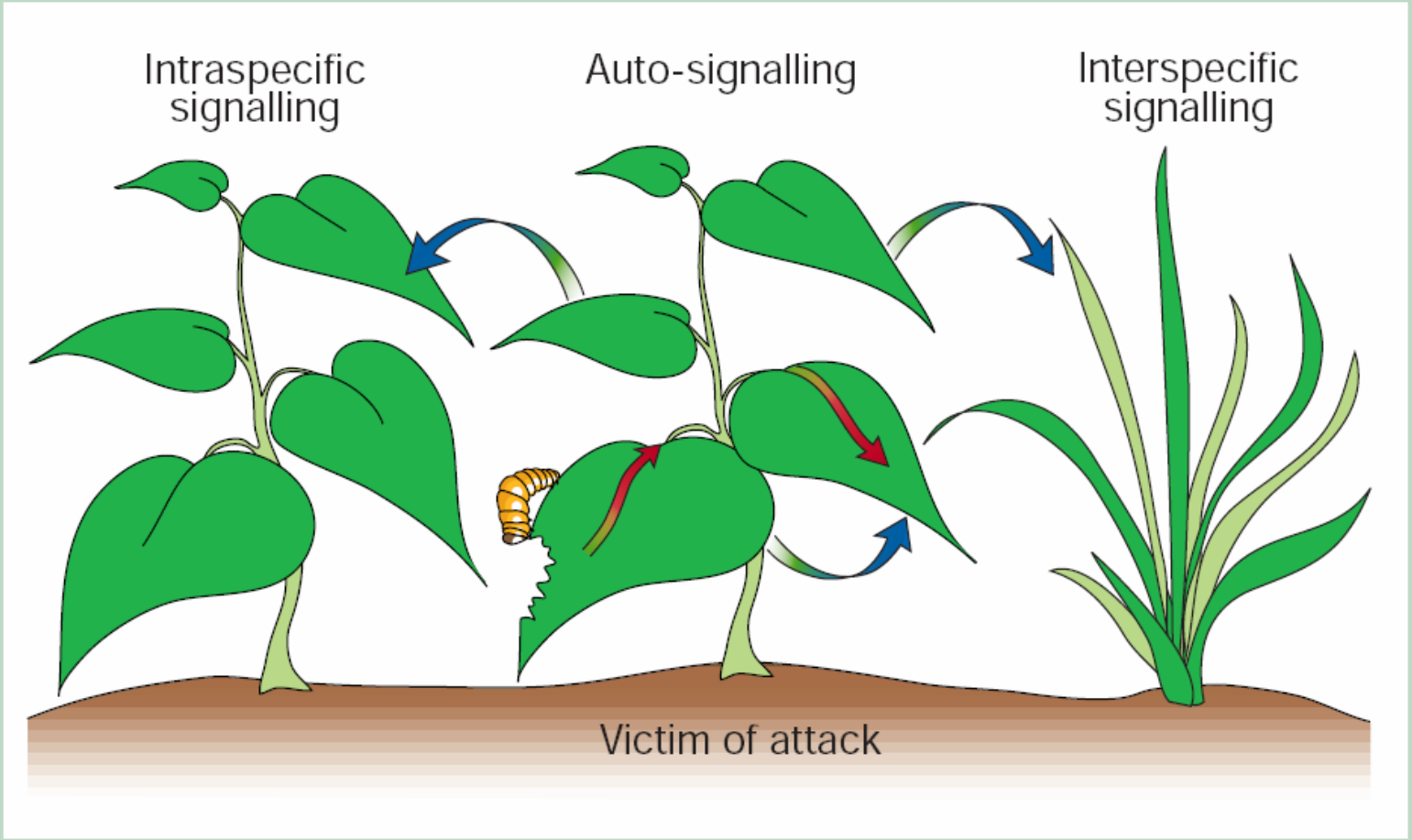


Figure 2 Communicating danger with airborne signals. Four modes of signalling from or within diseased or wounded plants are indicated: signalling to healthy congeners, signalling to members of other species, or auto-signalling either within (arrow in leaf) or outside the plant body. Good evidence exists for plant-to-plant airborne signalling in the laboratory, but field studies are limited.

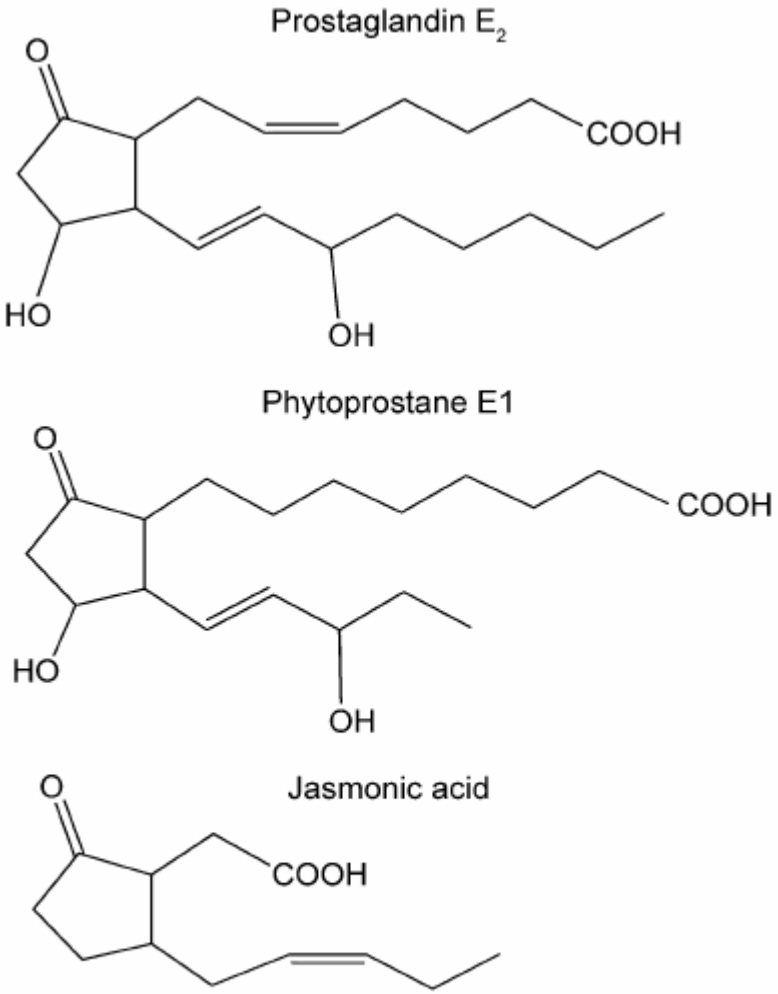
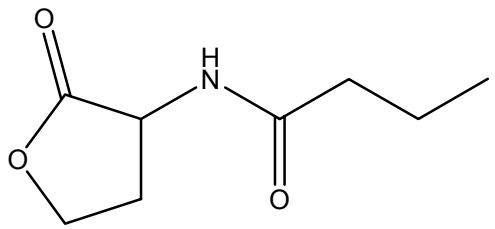
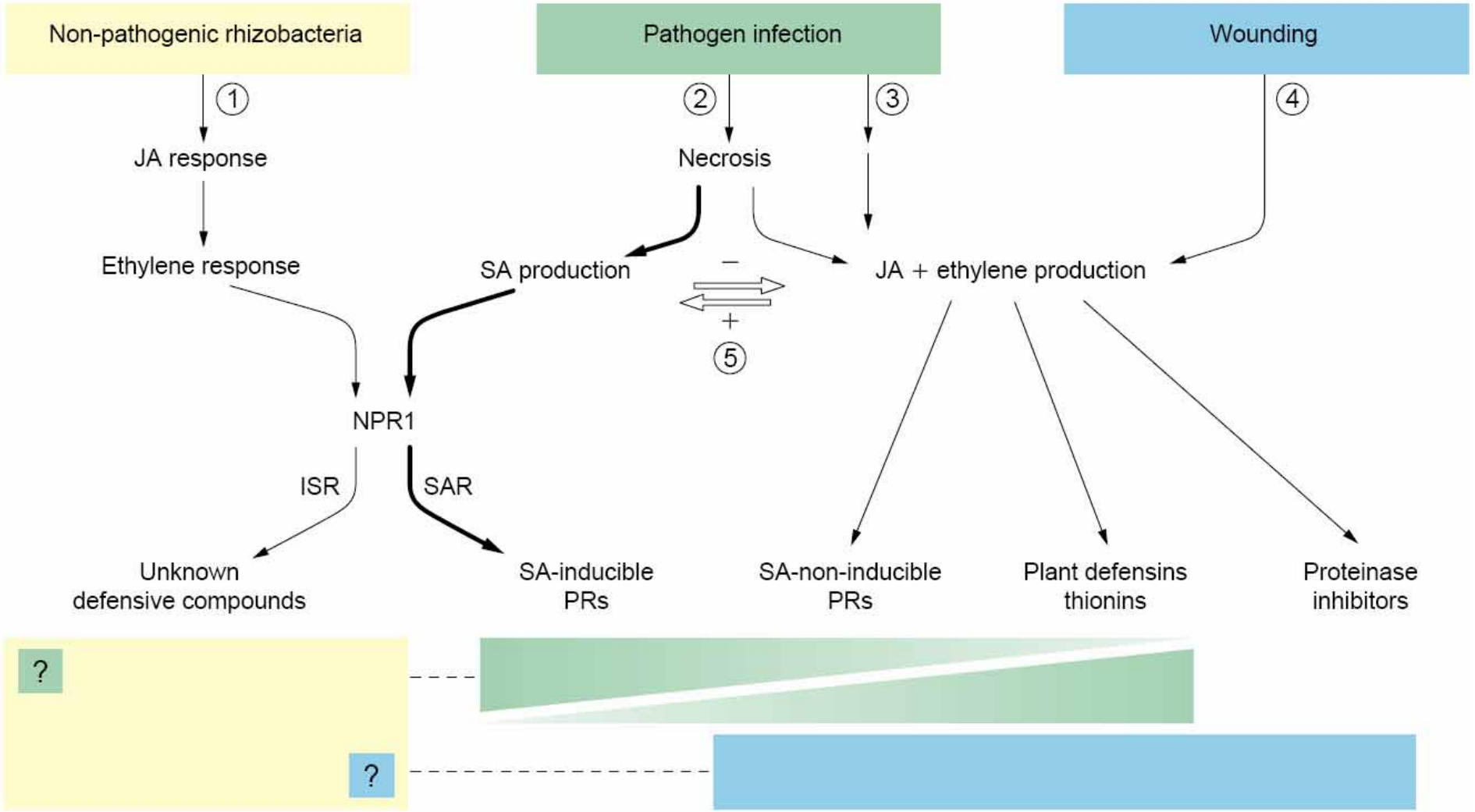


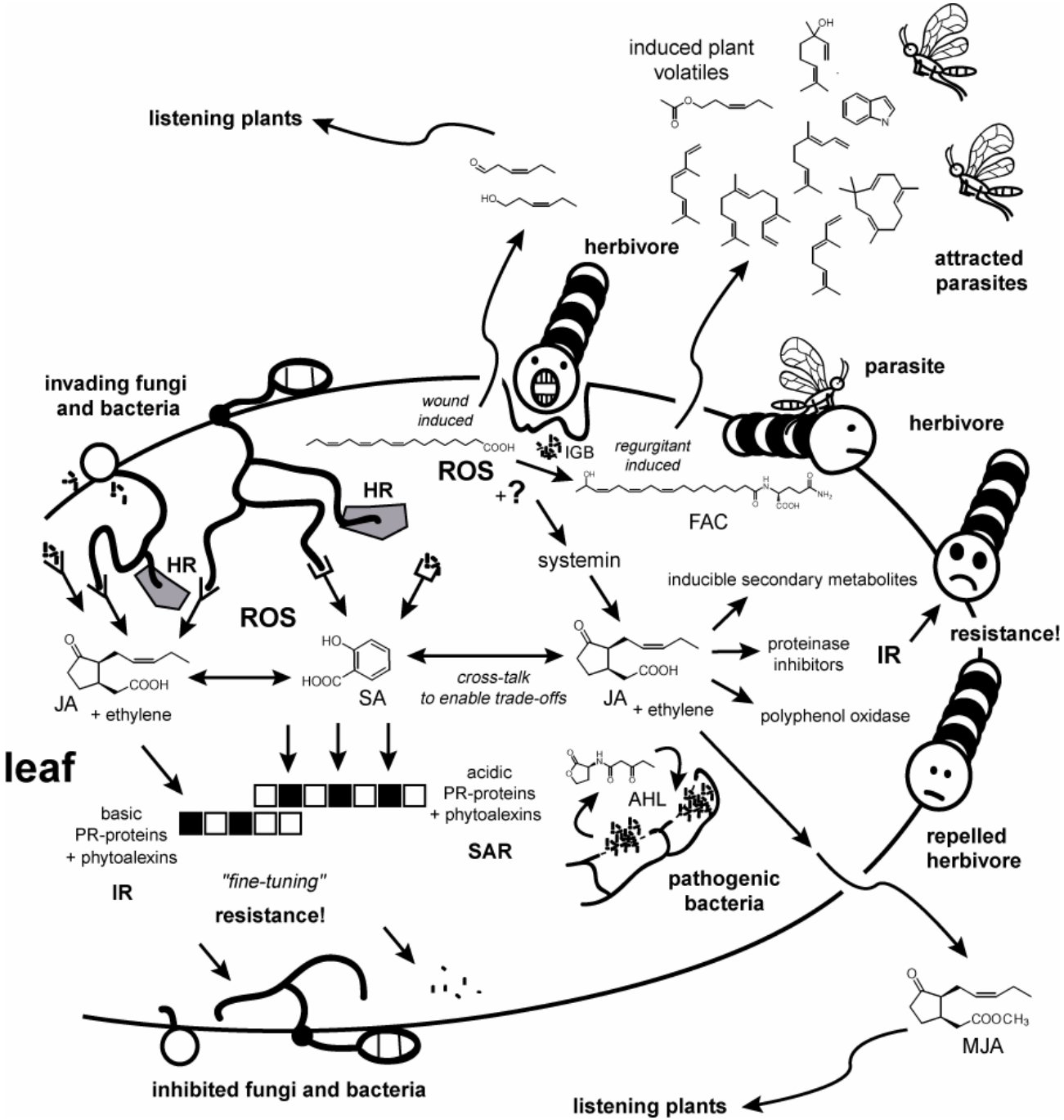
FIG. 1. Structures of prostaglandin E_2 (PGE_2) from invertebrates used in this study, phytoprostane E1 (a plant prostaglandin), and jasmonic acid (a plant wound hormone).

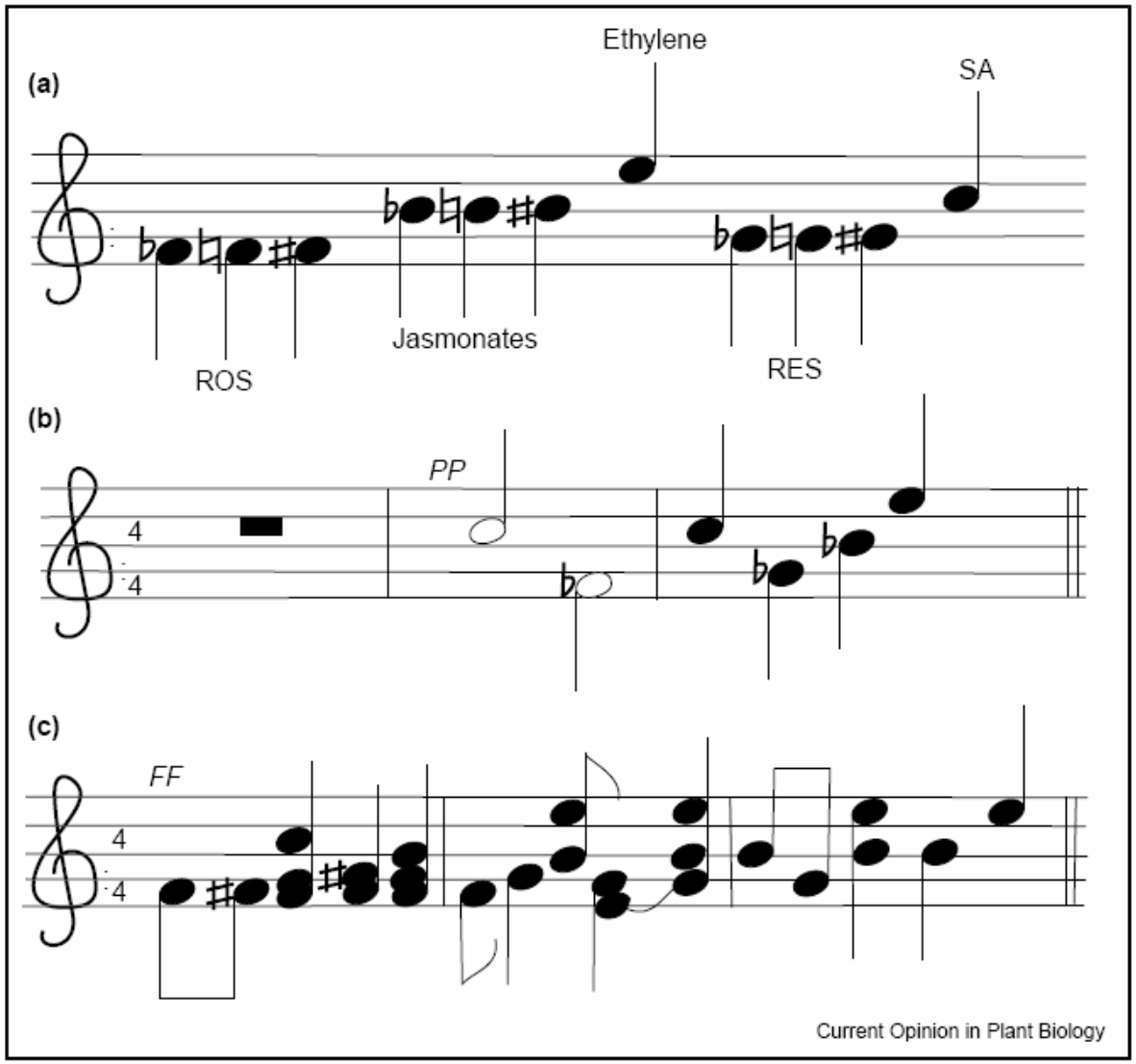


Quorum Sensing bei Bakterien!

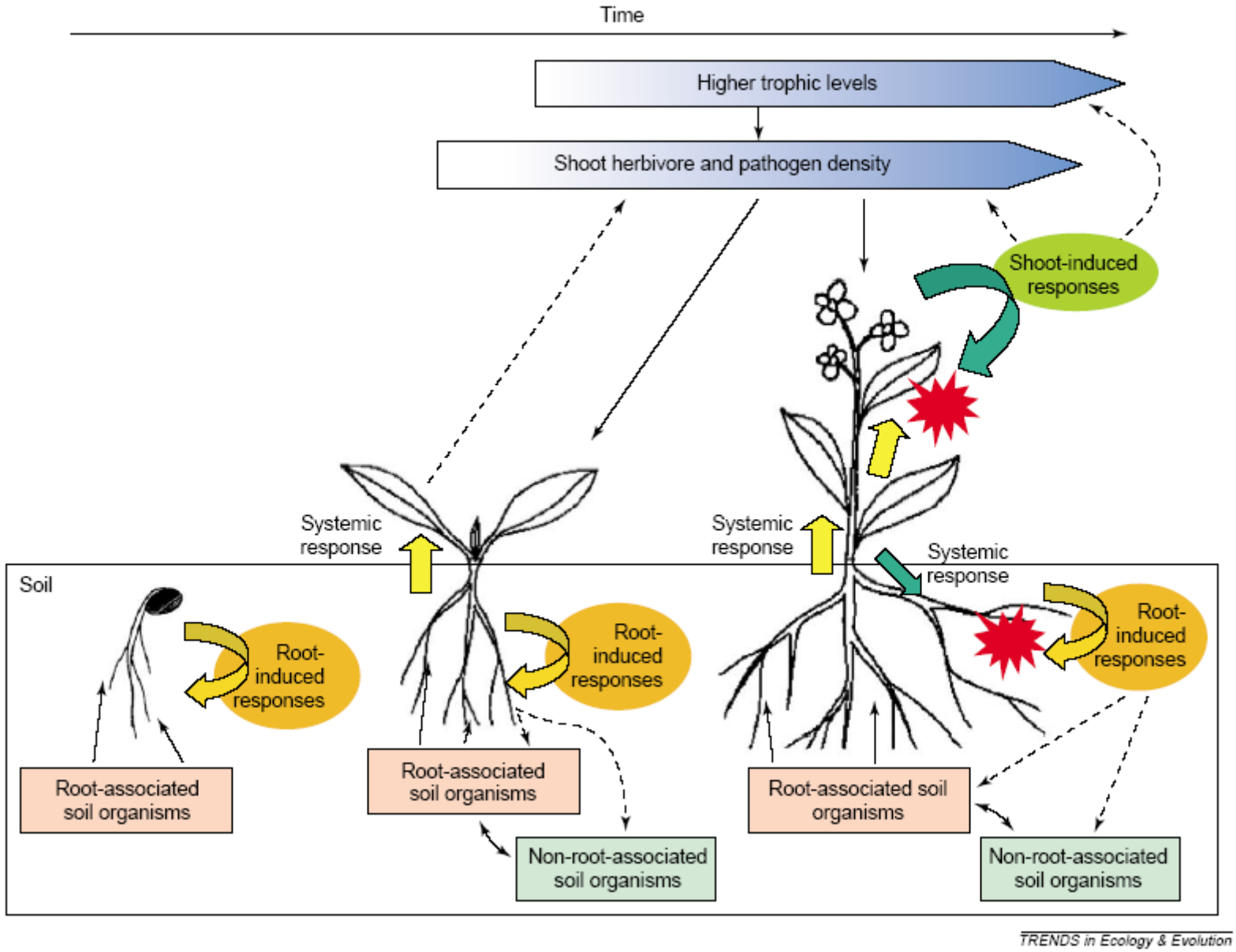


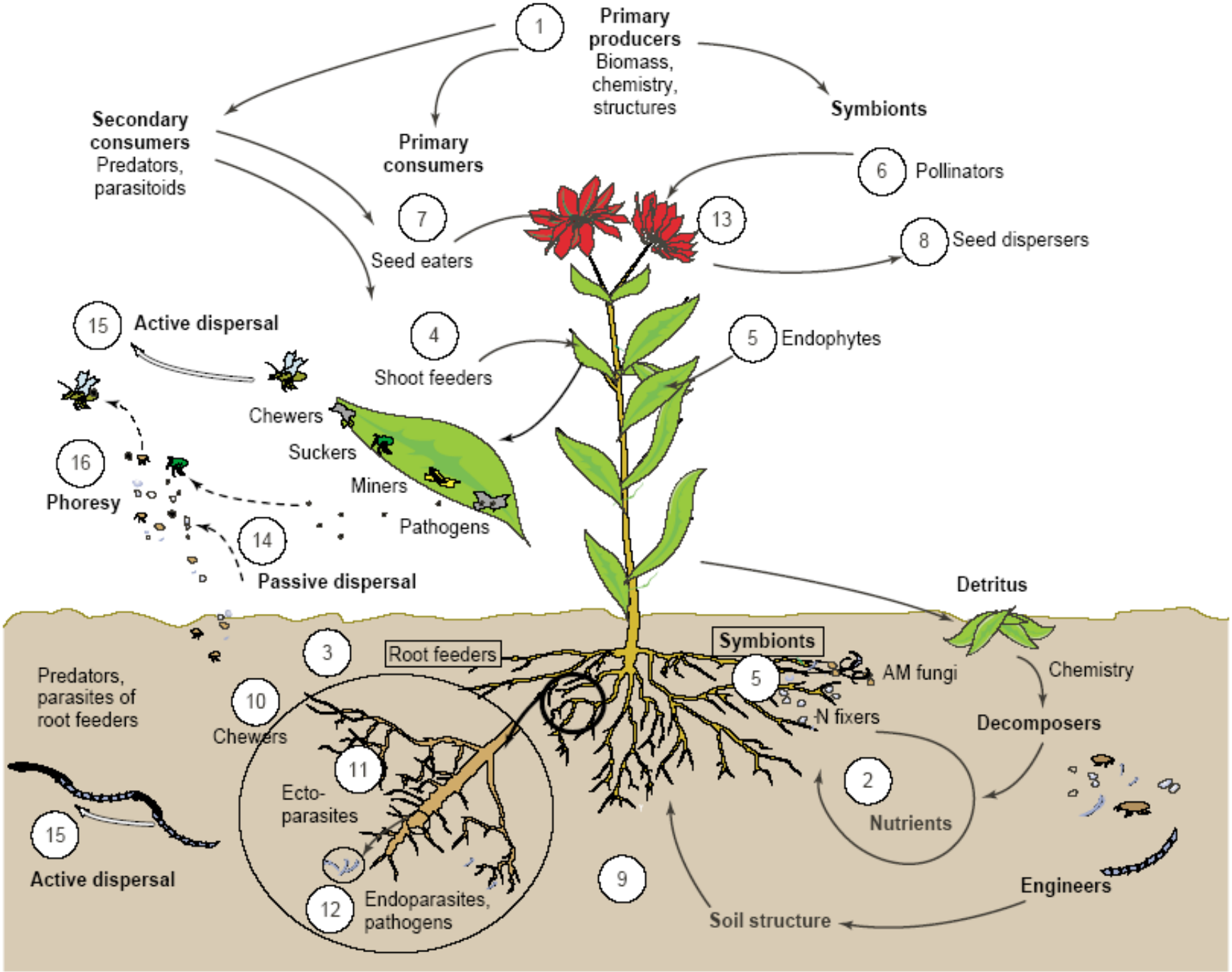
JA, Jasmonsäure; SA, Salicylsäure;
SAR, **S**ystemic **A**cquired **R**esistence; ISR, **I**nduced **S**ystemic **R**esistence


induced plant volatiles
listening plants
herbivore
attracted parasites
parasite
herbivore
invading fungi and bacteria
wound induced
IGB
regurgitant induced
ROS
+?
FAC
HR
HR
ROS
systemin
inducible secondary metabolites
proteinase inhibitors
polyphenol oxidase
IR
resistance!
JA
+ ethylene
SA
cross-talk to enable trade-offs
JA
+ ethylene
leaf
basic PR-proteins + phytoalexins
IR
"fine-tuning"
resistance!
acidic PR-proteins + phytoalexins
SAR
AHL
pathogenic bacteria
repelled herbivore
inhibited fungi and bacteria
MJA
listening plants



The interplay of low-molecular-mass signals in defense. Increasing evidence suggests that all of the low-molecular-mass signals illustrated in the figure intervene in response to attack, and that these signals or families of signals interact to control gene expression. **(a)** Each type of signal is given one or more note, a single note for ethylene and SA (including other SA-related signals) or several notes for complex families of signals (ROS, RES and jasmonates). Unassigned notes (not shown) indicate the possibility that more signals will be discovered in the future. **(b)** Representation of the host response to a compatible biotroph. **(c)** Representation of the host response to a virulent necrotroph or an avirulent pathogen. Other scores would exist for chewing or sucking insects.


Time
Higher trophic levels
Shoot herbivore and pathogen density
Shoot-induced responses
Systemic response
Systemic response
Systemic response
Soil
Root-induced responses
Root-induced responses
Root-induced responses
Root-associated soil organisms
Root-associated soil organisms
Root-associated soil organisms
Non-root-associated soil organisms
Non-root-associated soil organisms
TRENDS in Ecology & Evolution



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