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Naturwissenschaften 85, 507–511 (1998) Springer-Verlag 1998

Pheromone Precursor Synthesis Is Localized in the Metathorax of *Ips paraconfusus* Lanier (Coleoptera: Scolytidae)

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Received: 17 February 1998 / Accepted in revised form: 23 June 1998

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The aggregation pheromone of *Ips* spp. accumulates in the hindgut and is released while male beetles feed on the phloem of their host tree. However, a number of studies have failed to demonstrate the presence of a pheromone gland in this genus. By measuring the incorporation of [^{14}C]acetate into the pheromone precursors ipsenone and ipsdienone in various tissues in vitro, we have determined that pheromone precursor synthesis in male *I. paraconfusus* is closely associated with flight muscles in the metathorax. Northern blots hybridized with 3-hydroxy-3-methylglutaryl coenzyme A reductase cDNA show that transcript accumulation for this rate-limiting enzyme is also localized to the thorax. Tritiated ipsdienone is reduced to ipsenol and ipsdienol in the natural proportions in vivo, but not in vitro. It is possible that the final enantioselective reduction of ipsdienone and ipsenone may be localized to a site other than the thorax. The strategy for de novo pheromone production in *I. paraconfusus* is discussed.

Introduction

Male *Ips* spp. produce acyclic oxygenated monterpenoids as aggregation pheromone components de novo via the isoprenoid pathway [1–5] when colonizing their host tree. Male *I. paraconfusus* pheromone is a mixture of ipsenol and ipsdienol (10:1) and *cis*-verbenol [6]. The pheromone in male *Ips* spp. accumulates in the hindgut [7] and is released as the beetles feed on the phloem of their host tree. In the Coleoptera, pheromone biosynthesis may be localized to specialized glands [8–12], the fat body [13], or antennae [14]. However, although females of the elm bark beetles *Scolytus multistriatus* and *S. scolytus* both have accessory glands suggested as the site where pheromone synthesis, storage, and release occur [15, 16], studies over the past 30 years have failed to demonstrate the presence of a hindgut-associated pheromone gland in male *Ips* spp. or other scolytids [17–22]. Furthermore, the gut lumen does not contain enough mitochondria to account for the high production of pheromone [22].

In order to determine the site of pheromone synthesis in *I. Paraconfusus*, we used a novel in vitro assay [23] to measure the de novo synthesis of the pheromone precursors ipsenone/ipsdienone in various body regions and tissues of *I. paraconfusus*. In addition, we investigated the role of 3-hydroxy-3-methylglutaryl coenzyme A reductase (HMG-R), one of the key regulatory enzymes of the isoprenoid pathway [24], at the molecular level by northern blot analyses of selected tissues.

Insects

Ips paraconfusus were collected between December 1996 and March 1997 and handled as described [23].

Incubation of Bark Beetle Tissue and Collection of Volatiles

Male *I. paraconfusus* were treated topically with 8 μg juvenile hormone (JH III; Sigma) in one μl acetone and then fed on *P. jeffreyi* phloem rolls in film canisters for 48 h before being frozen at –80 °C (no longer than 3 weeks) for later use. The beetles were thawed and then dissected in a petri dish with phenylmethylsulfonyl fluoride (protease inhibitor; Sigma) in isotonic saline solution. All dissected tissues were immediately frozen on dry ice. They were then incubated in saline solution together with 1 MBq sodium [1–^{14}C]acetate (ICN), 20 μM 2-octynoic acid (fatty acid synthesis inhibitor; Aldrich), 5.6 μM NADPH (Sigma), and 20 mM malonate (citric acid cycle inhibitor; Fisher) [23]. Incubating entire homogenized beetles in different volumes of saline optimized the tissue concentration to 80 μg/μl. The volatiles produced during the incubation were collected, fractionated, identified, and assayed as described [23]. Ipsdienone and ipsenone coeluted on HPLC under our separation conditions.

Northern Blot Analysis

Heads, thoraces, and abdomens were isolated from 30 unfed male beetles 20 h after topical treatment with 5.4 μg JH III or acetone. Polyadenylated RNA was isolated using Quick-Prep Micro kits (Pharmacia), separated by glyoxal agarose gel electrophoresis (2 μg/lane) and transferred to nylon membrane (Hybond N, Amersham) using standard methods [25]. The blot was hybridized with a ^{32}P-labeled 1.2 kb cDNA fragment corresponding to the 3' one-third of *I. paraconfusus HMG-R* transcript (C. Tittiger, G.J. Blomquist, P. Ivarsson, C.E. Borgeson, and S.J. Seybold, in press) and washed under high stringency. The blot was also hybridized with ^{32}P-labeled mouse b-actin cDNA (Stratagene) and washed under moderate stringency. Following exposure using a BioRad Molecular Imager, densitometry was performed with Molecular Analyst software.

Preparation and Use of Tritium-Labeled Ipsdienone

Ipsdienone (*Lippia javonica* oil, obtained from Drs. D.L. Wood, University of California, Berkeley, USA, and J.P. Vité, University of Freiburg, Germany) was purified to 98% by constant pressure normal phase HPLC (mobile phase: pentane:acetone 99:1 at 4 ml/min, column: 10 mm x 50 cm Nucleosil 50-5; Alltech Associates). Radical inhibitors [3-*tert*-butyl-4- hydroxy-anisole and 2,6-di-*tert*-butyl-*p*-cresol (0.02% w/w)] were added to the pure extracts to stabilize ipsdienone and minimize side reactions, and all glassware was silanized. Tritiation of ipsdienone was performed at the National Tritium Labelling Facility, Berkeley, California. Tritiated water was prepared by allowing 10 Ci tritium gas to react with palladium oxide. Sodium metal (1 μmol) was added to the 100 μl water and the NaOT solution was stirred with 10 mg ipsdienone in 10 μl pentane for 24 h. Ipsdienone was extracted from the solution three times with pentane and the extract was dried with $MgSO_4$, sealed in glass ampoules and stored at –20° C until use. This exchange reaction gave ipsdienone labeled with tritium at carbon 5. The purity of [^{3}H]ipsdienone was 95% as determined by radio-HPLC. [^{3}H]Ipsdienone (200,000 dpm) was added to the incubation mixture (see above) with whole homogenized insects. The experiments were also carried out in vivo by injecting JH-treated beetles with 60,000 dpm [^{3}H]ipsdienone/beetle. Twenty beetles were placed in an airtight jar and volatiles were collected on Porapak Q for 24 h. The Porapak eluate was subsequently analyzed by radio-HPLC.

In vitro incubations of isolated tissues from male *I. paraconfusus* with [^{14}C]acetate revealed that the metathorax yielded the highest production of radiolabeled ipsenone/ipsdienone (ien/idn; Fig. 1). The alimentary canal, including the malpighian tubules, did not yield labeled ien/idn. Isolated fat body from the prothorax produced radiolabeled ien/idn in much lower amounts than the metathorax (Fig. 1). Replicated incubations of the isolated dorsal-ventral flight muscles showed the highest relative incorporation of ^{14}C into ien/idn, compared to fat body and abdomen (insert, Fig. 1).

Northern blot analyses showed that the 3.2 kb *HMG-R* transcript is present in all three body segments of adult males, with highest expression in thoracic tissue (Fig. 2). The signal was

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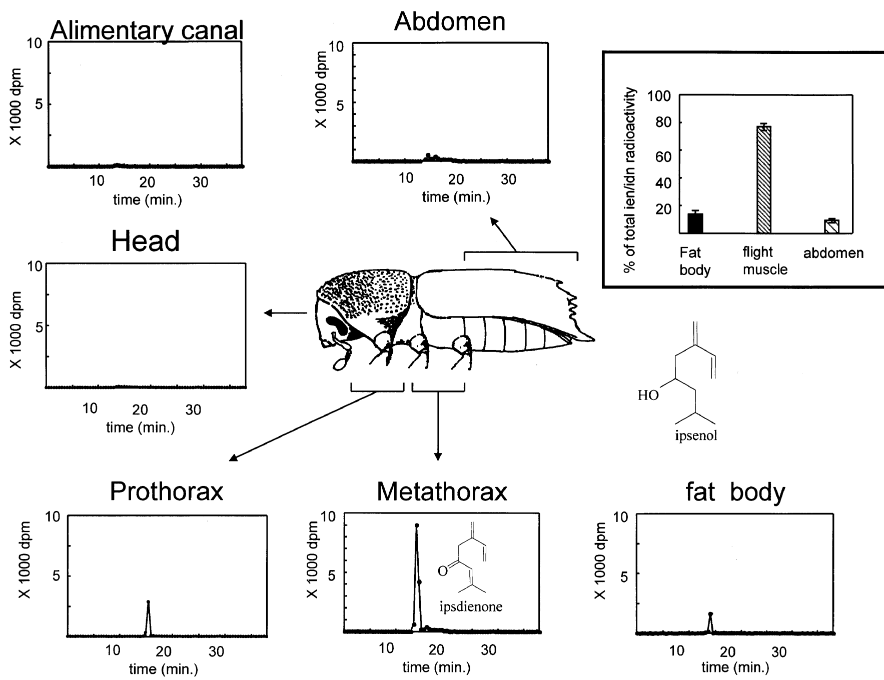

Fig. 1. Radio-HPLC analyses of ipsenone/ipsdienone resulting from in vitro assays incubating different tissues and body regions of male *I. paraconfusus* with [^{14}C]acetate. Column, Partisil PXS5/25 (Whatman); 25 × 0.5 cm. Mobile phase: hexane:acetone 99:1 for 15 min, 1% acetone/min for 5 min, and then isocratic for 30 min; flow rate 0.8 ml/min. Structures of ipsenone (main pheromone component) and ipsdienone are shown. *Insert*, relative amount of radioactivity found in ipsenone/ipsdienone from in vitro assay of fat body, flight muscle, and abdominal tissue of male *I. paraconfusus*. *Bars*, mean of three incubations (20 beetles/incubation); *error bars*, the 95% confidence interval

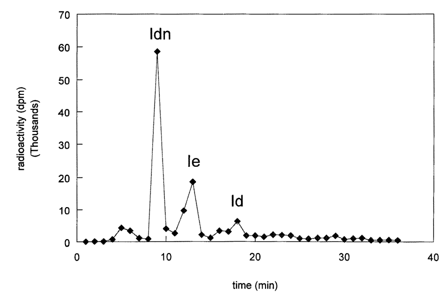

Fig. 3. Radiochromatogram of volatiles collected from male *I. paraconfusus* injected with [^{3}H]ipsdienone. *Idn*, Ipsdienone; *Ie*, ipsenol; *Id*, ipsdienol. Column, Partisil PXS5/25 (Whatman); 25 × 0.5 cm. Mobile phase: hexane:acetone 96:4; flow rate: 1 ml/min

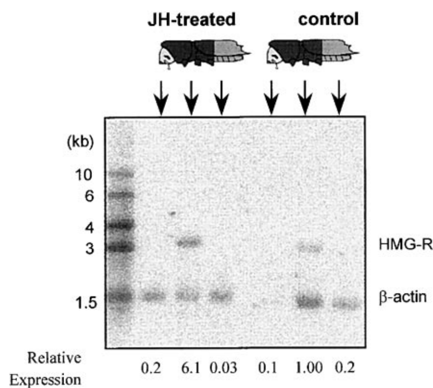

Fig. 2. Northern blot of polyadenylated RNA from body regions head, thorax, and abdomen) JH III (*JH*) or acetone (*C*) treated adult male *I. paraconfusus*. The approximate locations where the beetles were sectioned are shown in the diagrams. The blot was hybridized sequentially with a *HMG-R* cDNA fragment to test for HMG-R gene expression, and mouse b-actin to normalize the amount of RNA in each lane. *Left lane*, markers (Novagen; sizes kilobases). *Below each lane*, *HMG-R* transcript levels relative to the control thorax sample

6.1-fold higher in thoraces of JH III treated insects than in acetone-treated controls (Fig. 2).

Injection of male *I. paraconfusus* with [^{3}H]ipsdienone produced radiolabeled ipsenol and ipsdienol in the natural proportions (Fig. 3). No incorporation of radiolabel was detected in either ipsdienol or ipsenol recovered from in vitro experiments with [^{3}H]ipsdienone.

In vitro incubation of isolated tissues indicated that labeled pheromone precursors are produced mostly in the metathorax of male *I. paraconfusus*. Furthermore, isolated flight muscle showed the highest synthesis of ipsenone and ipsdienone relative to fat body and abdominal tissue. Northern blot analysis demonstrated that the transcript for HMG-R, a regulatory enzyme in the isoprenoid pathway, is induced over sixfold in the thorax of JH III treated males. Together, these data indicate that the pheromone producing tissue is closely associated with the flight muscles in the metathorax in male *I. paraconfusus*.

JH induces two temporally synchronized events: adult male beetles produce pheromone [26] and the flight muscles of both sexes degenerate [27–31]. As scolytids begin excavating a gallery, the flight muscles begin to degrade and are almost gone within 3–4 days [32, 33]. Degeneration of female flight muscle is thought to provide energy and amino acids for egg development. However, JH also initiates male flight muscles degradation [27, 31] and increases the amount of tissue degrading acid phosphatases in female *Dendroctonus pseudotsugae* flight muscle [30]. Degradation is not induced by denervation as it does in silkmoths, but rather that JH acts directly [30]

Pheromone production is also affected if *I. typographus* are allowed to fly before feeding on their host logs [34], suggesting a relationship between flight muscles and de novo pheromone production in *Ips* bark beetles.

In *I. pini*, feeding increases JH III production and initiates de novo pheromone production [4]. Since JH also triggers the degradation of flight muscle tissue [27], and feeding is not a prerequisite for pheromone production when beetles are treated with JH [26], the degradation of muscle tissue may serve both as a carbon source and energy supply for pheromone biosynthesis. All 20 amino acids from muscle proteins can be converted to either glucose or acetate. The glucose

could be converted to acetate, which can then enter the isoprenoid pathway for the synthesis of ipsenol and ipsdienol. Flight muscle tissue is found in the thorax and an increase in flux through the isoprenoid pathway in the thorax is supported by our observation of increased *HMG-R* transcript levels following JH III treatment.

When male *Ips paraconfusus* were injected with [^{3}H]ipsdienone in vivo, the ketone was converted to [^{3}H]ipsenol and [^{3}H]ipsdienol in the naturally occurring 10:1 proportion (Fig. 3). It has been demonstrated that male *I. paraconfusus* produces ipsenol and ipsdienol, when aerated with ipsdienone [35]. The conversion of [^{3}H]ipsdienone to the pheromone alcohols is consistent with an in vivo role of ipsdienone as the precursor to both ipsenol and ipsdienol. Why ipsdienone is not reduced to the alcohols in vitro, whereas this reduction works in vivo, remains to be explained. It is possible that a functioning circulatory system is necessary to transport the ketone to the site of reduction.

We thank Hiromi Morimoto at the National Tritium Labelling Facility, Berkeley, California, for his excellent help on tritiating ipsdienone. This work was made possible by grants from the Swedish Council for Forestry and Agricultural Research (SJFR 96.1035/94 T1) to PI and the United States Department of Agriculture (NRI-CGP grants 9502551 and 9702991) to SJS.

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BOOK REVIEWS

Strasburger – Lehrbuch der Botanik für Hochschulen. Von Sitte, P., Ziegler, H., Ehrendorfer, F., Bresinsky, A. Fischer, Stuttgart 1998, 34. Auflage, 1024 S., 1053 Abb., DM 138,–

Die neueste Auflage des Strasburger, die ungefähr zeitgleich mit dem 150. Geburtstag des Begründers des Lehrbuches der Botanik, Prof. Eduard Strasburger, erscheint, ist nun da. Noch dicker und noch schwerer ist das meist benutzte botanische Standardwerk nun geworden: Stolze 2694 g hat man nun zu stemmen, um das Buch auf den Schreibtisch zu wuchten.

Vier führende Professoren haben es erneut randvoll mit Information gefüllt, die von der Darstellung der Morphologie der Pflanzen über die Physiologie, Evolution und Systematik bis zur Geobotanik reicht; die gesamte Bandbreite der Botanik ist wieder dargestellt.

Der bewährte Aufbau des Lehrbuches ist gleichgeblieben, wenngleich inhaltlich vieles verändert und überarbeitet wurde und damit nun auch die sog. modernen Erkenntnisse der Molekularbiologie Eingang und Berücksichtigung fanden. Derartige Forschungsergebnisse führten auch dazu, daß die klassische und für Lernende und Lehrende nachzuvollziehende Einteilung in die Mono- und Dikotyledonen aufgegeben und durch die Klassifizierung in Magnoliopsida, Rosopsida und Liliopsida ersetzt wurde. Auch die Einteilung der Lebewesen wurde den nun allmählich akzeptierten Anschauungen folgend in Archaea, Bacteria und Eucarya vorgenommen. Die Biodiversitätsforschung fand als neues Forschungsgebiet Eingang in den geobotanischen Teil.

Wenn ein Lehrbuch den Anspruch hat, ein Gebiet so umfassend darzustellen, wie dies beim Strasburger der Fall ist, dann ist es naturgemäß nicht ganz einfach, die Informationsfülle entsprechend „an den Mann" zu bringen. Doch trotz der enormen Daten- und Faktenfülle ist es den Autoren wieder gelungen, eine gute Lesbarkeit des Textes zu erreichen; die Wichtigkeit bestimmter Passagen wird zusätzlich durch unterschiedliche Druckgrößen herausgestellt. Das integrierte deutsch/lateinische resp. lateinisch/deutsche Kreuzregister erleichtert das Auffinden von Suchbegriffen.

Die vielen Strichzeichnungen sind durch hervorragende mikroskopische Aufnahmen ergänzt. Die Bebilderung ist hauptsächlich schwarz-weiß gehalten; dies ist bei REM-Aufnahmen selbstredend, aber auch bei Makroaufnahmen von Pflanzenorganen tut der Verzicht auf Farbe in unserer reizüberfluteten Zeit durchaus gut.

Probleme hat man als Lehrender allerdings, will man gute für die Vorlesung zu benutzende Folien aus den Abbildungen fertigen, da teilweise rote Beschriftungen oder Pfeile in den Abbildungen verwendet wurden. Natürlich kann durch solch farbige Markierungen z.B. die Ambivalenz von Aminosäuren besser kenntlich gemacht oder ein Wirkungsgefüge didaktisch geschickter dargestellt werden, aber die partielle Reproduzierbarkeit leidet dementsprechend; vielleicht kann dies bei der nächsten Auflage so weit wie möglich wieder rückgängig gemacht werden.

Liest man die Originalzeilen des Verlages an den Begründer: „Hochverehrter Herr Professor Strasburger, mit aufrichtiger Freude ersehe ich, daß Sie nunmehr geneigt sind, unserem Plan eines Lehrbuchs der Botanik näher zu treten. Ich werde aufs äußerste bemüht sein, alles aufzubieten, um ein Musterbuch herzustellen. Ihr ganz ergebenster Gustav Fischer (Jena im Jahr 1893)", so kann man nur sagen, daß dies beiden Seiten gelungen ist: Der Strasburger ist erneut state of the art, und wird, obwohl klassisch deutsches Lehrbuch, mit den aufkommenden „anglo-amerikanischen" Lehrbüchern konkurrieren können. Der Strasburger ist eben neben dem anerkannten Lehrbuch auch ein unersetzliches Nachschlagewerk für botanische Belange. Er wird weiterhin eine der Säulen und Grundlage der meisten Vordiplom- und Diplomprüfungen in Botanik an deutschsprachigen Universitäten bleiben.

H. Pfanz (Essen)