NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, tests publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

ISBN 0-315-46741-X

UNIVERSITÉ D'OTTAWA
UNIVERSITY OF OTTAWA

ABSTRACT

A series of field and laboratory experiments was undertaken to identify some of the cues involved in host selection by *Monochamus scutellatus* and other conifer-feeding beetles. Field trapping was carried out near Chalk River, Ontario. The importance of visual cues for the attraction of beetles was studied by using three visually distinctive trap designs. Two specially designed traps (sticky stovepipe traps and flight interception traps) and one commercially available trap (Lindgren multiple funnel traps) were baited with conifer monoterpenes and ethanol to capture beetles. Sticky stovepipe traps had a clear vertical silhouette, multiple funnel traps had an irregular silhouette, while the flight interception traps offered few visual cues to approaching insects. Of the more than 6000 beetles captured, 75% were captured by stovepipe traps, 15% by interception traps and 11% by multiple funnel traps. Dominant families were the Scolytidae (accounting for 14.5% of all beetles captured), Elateridae (14.4%), Lampyridae (12.1%), Cerambycidae (12.0%), Cleridae (10.5%), Curculionidae (9.3%), Staphylinidae (4.0%), and Buprestidae (3.4%), with other families accounting for 19.8% of captures. Conifer-feeding species in the families Buprestidae, Melandryidae, Cerambycidae, Scolytidae, and Curculionidae and their predators (Cleridae) all were captured in greatest numbers by the sticky stovepipe traps, with the interception traps generally capturing the fewest numbers. The superior performance of the sticky stovepipe traps appears to be due to the clear vertical silhouette which they offer to approaching insects.

Field trapping experiments using sticky stovepipe traps and Lindgren multiple funnel traps were carried out in order to verify the effects of conifer monoterpenes (α–pinene, β–pinene, myrcene, limonene, camphene and 3–carene) and ethanol on beetle attraction. Several species of conifer-feeding beetles were attracted to the monoterpenes or to monoterpenes and ethanol, including species in the families Cerambycidae (*Asemum striatum, Acmaeops proteus, Xylotrechus undulatus, M. scutellatus*), Curculionidae (*Pissodes strobi, Hylobius pales*) and Scolytidae (*Dryocetes autographus, Ips grandicollis*). Synergism between monoterpenes and ethanol was evident for *M. scutellatus*, *H. pales*, and *D. autographus*. Species of Buprestidae gen[illegible] did not respond to the monoterpenes or to ethanol. Species of

Cleridae (*Thanasimus dubius, Enoclerus nigripes rufiventris, Enoclerus nigrifrons gerhardi*) which are predators of conifer borers were attracted to the monoterpenes. While α–pinene appeared to account for most of the effects observed, monoterpenes other than α–pinene clearly synergised attraction to ethanol for *D. autographus*. Attraction of beetles to commercial turpentine and ethanol did not differ significantly from attraction to a pure monoterpene blend and ethanol.

A bioassay chamber and a test protocol were developed to evaluate the suitability of different substrates for oviposition by *M. scutellatus*. Most oviposition occurred in late afternoon and early evening. Field-collected females laid preferentially on white spruce, followed by red pine, white pine, and balsam fir. The presence of volatiles of red pine, white spruce, or aspen in the chambers did not affect oviposition. In no case did females lay in the bark of non-host species. No difference was found in the number of eggs laid in red pine with or without bark scales. Females oviposited equally in the outer bark and in the phloem of hosts. These results indicate that contact chemical cues probably play a major role in the evaluation of oviposition sites by female *M. scutellatus*.

Host selection by *M. scutellatus* therefore appears to involve attraction in response to monoterpenes and ethanol acting synergistically and to tree silhouette. After landing, contact chemical cues are used to evaluate host suitability. Attraction of conifer-feeding beetles and of their clerid predators in response to monoterpenes and to visual cues appears to be a generalised phenomenon.

RÉSUMÉ

Une série d'expériences sur le terrain et en laboratoire fut entreprise afin d'identifier certains des stimuli qui entrent en jeu dans le processus de sélection d'hôte par *Monochamus scutellatus* et d'autres coléoptères associés aux conifères. Le piégeage fut fait près de Chalk River, Ontario. L'importance des stimiuli visuels pour l'attraction des coléoptères fut étudiée en utilisant trois types de pièges à caractères visuels particuliers. Deux modèles de pièges développés pour ces travaux (piège collant à tuyaux de poêle et piège à interception) et un piège disponible commercialement (piège à entonnoirs multiples Lindgren) furent appâtés avec des monoterpènes de conifères et de l'éthanol afin de capturer des coléoptères. Les pièges collants à tuyaux de poêle avaient une silhouette verticale nette, les piège à entonnoirs multiples Lindgren avaient une silhouette irrégulière, et les pièges à interception étaient peu visibles pour les insectes qui s'en approchaient. Plus de 6000 coléoptères furent pris, avec 75% des spécimens capturés par les pièges à tuyaux, 15% par les pièges à interception et 11% par les pièges à entonnoirs. Les familles dominantes étaient les Scolytidae (14.5% des coléoptères capturés), Elateridae (14.4%), Lampyridae (12.1%), Cerambycidae (12.0%), Cleridae (10.5%), Curculionidae (9.3%), Staphylinidae (4.0%) et Buprestidae (3.4%), les autres familles comptant pour 19.8% des captures. Les espèces de Buprestidae, Melandryidae, Cerambycidae, Scolytidae et Curculionidae inféodées aux conifères, ainsi que leurs prédateurs (Cleridae), furent prises en plus grand nombre dans les pièges à tuyaux, et en plus petit nombre dans les pièges à interception. La performance supérieure des pièges à tuyaux semble attribuable à la silhouette verticale nette qu'ils offrent aux insectes qui s'en approchent.

Les pièges collants à tuyaux et les pièges à entonnoirs multiples furent utilisés dans des expériences sur le terrain afin de vérifier les effets des monoterpènes des conifères (α–pinène, β–pinène, myrcène, limonène, camphène et 3–carène) et de l'éthanol sur l'attraction des coléoptères. Plusieurs espèces de coléoptères inféodées aux conifères furent attirées par les monoterpènes ou par les monoterpènes et l'éthanol, y compris des espèces dans les familles Cerambycidae (*Asemum striatum, Acmaeops proteus, Xylotrechus undulatus, M. scutellatus*), Curculionidae (*Pissodes strobi, Hylobius pales*) et Scolytidae (*Dryocetes autographus, Ips*

grandicollis). Un synergisme entre les monoterpènes et l'éthanol fut mis en évidence pour *M. scutellatus*, *H. pales*, et *D. autographus*. Les espèces de Buprestidae n'étaient pas attirées par les monoterpènes ou l'éthanol. Les espèces de Cleridae (*Thanasimus dubius*, *Enoclerus nigripes rufiventris*, *Enoclerus nigrifrons gerhardi*) qui sont prédateurs des xylophages furent attirées aux monoterpènes. Quoique l'α–pinène semblait à lui seul susciter la plupart des effets observés, des monoterpènes autres que l'α–pinène agissaient de façon synergique avec l'éthanol pour attirer *D. autographus*. L'attraction des coléoptères à la térébenthine de commerce et à l'éthanol ne se distinguait pas de façon significative de l'attraction à un mélange de monoterpènes purs et à l'éthanol.

Une chambre à essai et un protocole expérimental furent développés afin d'évaluer la valeur de différents substrats offerts pour l'oviposition par *M. scutellatus*. La ponte eut lieu surtout en fin d'après-midi et en soirée. Les femelles recueuillies en forêt pondaient de préférence sur l'épinette blanche, puis sur le pin rouge, le pin blanc et le sapin baumier. La présence dans la chambre à essai de substances volatiles de pin rouge, épinette blanche ou tremble n'eut aucun effet sur la ponte. Les femelles ne pondaient jamais dans l'écorce d'espèces non-hôtes. Un nombre égal d'oeufs fut pondu dans les écorces de pin rouge avec ou sans écailles. Les femelles pondaient aussi bien dans l'écorce externe que dans le liber des essences hôtes. Ces résultats indiquent que des stimuli chimiques de contact jouent probablement un rôle de premier ordre dans l'évaluation du milieu de ponte par *M. scutellatus*.

La sélection de l'hôte par *M. scutellatus* semble donc se composer de l'attraction sous l'effet synergique de monoterpènes et éthanol et l'effet de la silhouette de l'arbre. Suite à l'arrivée de l'insecte sur l'arbre, des substances chimiques non volatiles servent à évaluer l'hôte. L'attraction des coléoptères inféodés aux conifères et de leurs prédateurs Cleridae en réponse aux monoterpènes et aux stimuli visuels semble être un phénomène répandu.

Acknowledgements

I thank Dr. B.J.R. Philogène and Dr. J.T. Arnason, Department of Biology, University of Ottawa, for their useful comments and for giving me considerable liberty in carrying out this research; their supportive attitudes towards all their students is much appreciated. I also thank the staff of the Petawawa National Forestry Institute for permission to carry out field experiments on their land and for discussions regarding selection of sites; the staff of the the Agriculture Canada Biosystematics Research Centre for verifying or carrying out identifications of insect species; Dr. M. Alvo, Department of Mathematics, University of Ottawa, for discussions regarding statistical analyses of data; and the Department of Biology support staff, especially André Richer and Nino Cavacciuti for their good-natured technical assistance.

I also would like to express my thanks to my entire family which has provided so much helpful support, both direct and indirect, over the years. To Suzanne, Ani and Alexis, I am especially grateful for the patience (and endurance) which they have shown.

This research was supported by a grant from N.S.E.R.C. to B.J.R. Philogène.

TABLE OF CONTENTS

List of tables

List of figures

INTRODUCTION

Monochamus scutellatus (Say) is the most prevalent cerambycid beetle feeding on conifers in Canada. Like other cerambycids, its larvae attack the wood of their hosts, and help promote degradation of dead trees. However, their activity results in serious degrade of the wood for the lumber industry and poses a threat to wood exports.

Most beetles feeding on conifers are in fact secondary insects, attacking moribund or dead trees. This is largely due to the healthy conifers' ability to produce resin which acts as an efficient defence against invading organisms. For beetles adapted to attacking weakened trees, chemical components of the resin may in fact be used as cues to locate hosts. Studies of host selection by certain species of Scolytidae have shown that monoterpenes present in host bark can act as kairomones, being involved as chemical cues in the host selection process. Other chemicals such as ethanol present in the bark of moribund hosts may also act as behaviour-modifying compounds. While chemical cues play a prime role in host selection by scolytids, visual cues are also involved. Unfortunately, very little information is available on the host selection process for conifer-feeding beetles other than scolytids.

The research described in this dissertation was undertaken in order to obtain information regarding host selection by *M. scutellatus* and other conifer-feeding beetles, notably to determine the importance of chemical and visual cues for the orientation of beetles to their hosts and of chemical and physical cues for the evaluation of host suitability for oviposition.

OBJECTIVES

Given 1) the ecological and economic importance of *M. scutellatus* and other conifer-feeding cerambycids, 2) the paucity of information about host selection behaviour by these beetles, 3) the importance of host selection behaviour as a component of beetle biology, and 4) the potential application of knowledge of this behaviour in pest management programmes, this research was undertaken to investigate certain aspects of host selection behaviour by conifer-feeding beetles. This included studies of host attraction of cerambycids and their associates, and evaluation of oviposition substrate by *M. scutellatus*.

A — Attraction

A.1 — Importance of visual cues (trap evaluation)

Hypothesis: Tree bole silhouette affects host finding by conifer-feeding beetles.

Since 1) certain scolytids respond to visual stimuli when approaching hosts, and 2) susceptible host material (i.e., host tree bole) offers a clear silhouette to approaching beetles, an experiment was designed to verify if **trap silhouette affects the attraction of conifer-feeding beetles and of their associates.**

A.2 — Importance of chemical cues

Hypothesis: Major host monoterpenes and ethanol attract conifer-feeding beetles.

Since 1) host selection behaviour of many scolytids is affected by monoterpenes and ethanol, 2) monoterpenes and ethanol are the major volatiles emanating from moribund and dead trees of the family Pinaceae, and 3) the major monoterpenes found in Canadian Pinaceae are α–pinene, β–pinene, camphene, limonene, 3–carene and myrcene, the effects of these chemicals on attraction of conifer-feeding beetles and their associates were verified.

Experiment 1 was designed to verify if **the above monoterpenes affect beetle attraction, if ethanol attracts beetles, and if ethanol affects attraction to the monoterpenes.** Experiment 2 was designed to **distinguish between effects due to the**

major monoterpene α-pinene and those due to the other monoterpenes. Experiment 3 verified if **attraction to the pure monoterpene blend differs from attraction to commercial turpentine** containing a complex mixture of terpenes.

B — Evaluation of oviposition substrate

B.1 — Importance of volatile chemicals

Hypothesis: Volatile bark chemicals affect oviposition by *M. scutellatus*.

Since 1) host volatiles probably play a role in the attraction of *M. scutellatus* to their hosts, and 2) females on host bark are likely exposed to these volatiles, experiments were designed to verify if **volatile compounds present in the bark of host and non-host trees affect oviposition by female *M. scutellatus*.**

B.2 — Importance of outer bark

Hypothesis: Properties of the outer bark affect oviposition by *M. scutellatus*.

Since 1) female lamiines must chew through the outer bark before ovipositing, 2) many cerambycids (excluding lamiines) preferentially lay under bark scales, 3) many cerambycids (including lamiines) are reported to lay more eggs near physical irregularities such as bases of branches, and 3) the texture of the outer bark of various host species is quite different, experiments were designed to verify if **female *M. scutellatus* preferentially lay in the outer bark or in the phloem** and if **the presence or absence of scales on the outer bark affects oviposition.**

LITERATURE REVIEW

A — The insects

A.1 — Beetles associated with conifers

Insects play a major role in the biodegradation of dying and dead standing trees and of recently felled timber. By attacking trees which have been or are to be harvested, they compete strongly with the forest products industry for the wood fibre.

Major wood-boring beetle families associated with conifers in Canada include the Buprestidae, Melandryidae, Cerambycidae, Scolytidae, and Curculionidae (Baker 1972; Furniss and Carolin 1977). Species in several other families breed in decaying logs and stumps (e.g., Lucanidae, Elateridae, Eucnemidae, Oedemeridae). Anobiids generally attack seasoned wood, though certain species of *Ernobius* attack conifer cones. A few bostrichids (*Stephanopachys* species) attack the wood of dead conifers. Non-boring beetles associated with conifers include certain Scarabaeidae (e.g., *Dichelonyx* species feeding on needles as adults and probably roots as larvae, certain *Phyllophaga* adults feeding on foliage, *Phyllophaga* and *Serica* species feeding on roots, others such as *Polyphylla decemlineata* (Say) feeding on needles and roots). A few chrysomelids feed on needles. Major predators of wood-boring beetles are in the families Cleridae and Trogositidae.

There are 350 to 380 species of Cerambycidae in Canada (Campbell 1979). As pointed out by Campbell (1979, p.382), "because most of the taxa of the family are well known and because the species are economically important, cerambycids are ideally suited for detailed life history studies, studies on nutrition and intracellular symbionts of wood feeding insects, dispersal mechanisms, distribution patterns, host specificity, effects of temperature and humidity on developmental rates, or many other interesting approaches". The family comprises seven subfamilies, namely the Parandrinae, Prioninae, Spondylinae, Aseminae, Lepturinae, Cerambycinae, and Lamiinae (Linsley 1961). In Canada, most species associated with conifers are in the subfamilies Lepturinae, Cerambycinae, Aseminae, and Lamiinae. Cerambycids are generally cambium and wood feeders.

A.2 — *Monochamus* species in Canada

Sawyer beetles (*Monochamus* spp.) are large cerambycids belonging to the subfamily Lamiinae, tribe Monochamini (Dillon and Dillon 1941; Linsley and Chemsak 1984). While about 150 *Monochamus* species have been described world-wide (Hellrigl 1971), only eight species occur in North America (Linsley and Chemsak 1984). These are *M. scutellatus*, *M. obtusus* Casey, *M. marmorator* Kirby, *M. mutator* LeConte, *M. carolinensis* (Olivier), *M. clamator* (LeConte), *M. titillator* (Fabricius), and *M. notatus* (Drury). All species probably occur in Canada, with *M. obtusus* and *M. titillator* barely extending their ranges into southern British Columbia and southern Ontario, respectively. All North American species feed on conifers both as larvae and as adults. The whitespotted sawyer, *M. scutellatus*, is both the most prevalent and most widespread of Canadian species, and includes the subspecies *M. s. scutellatus* (Say) and *M. s. oregonensis* (LeConte) (Raske 1973a; Linsley and Chemsak 1984). *M. s. scutellatus* has been recorded across most of Canada and northern U.S.A., from Labrador south to North Carolina west through Minnesota and to central British Columbia, and north to Alaska. *M. s. oregonensis* occurs in western North America from the Rocky Mountains to the Pacific coast from Alaska south to northern California.

General discussions of the biology of *M. s. scutellatus* include those of Richmond and Lejeune (1945), Belyea (1952), Rose (1957), Wilson (1962), Soper and Olson (1963), Raske (1972, 1973b, 1975), and Cerezke (1975). Hosts include most species of the Pinaceae occurring in its range, including *Pinus* spp., *Picea* spp., *Abies balsamea* (L.) Mill., *Larix laricina* (DuRoi) K. Koch, and *Pseudotsuga menziesii* (Mirb.) Franco. Adults generally emerge from infested logs between mid-June and mid-August. They feed on the thin bark of twigs and small branches of healthy hosts for three to ten days. After this maturation feeding, adults are usually found on the boles of moribund or recently killed trees, where mating and oviposition eventually occurs. Females chew 3 to 6 mm long elliptical egg niches in the bark, into which the eggs are laid (usually one per niche), using the ovipositor to wedge the eggs into the phloem. The oviposition period can last four to six weeks; oviposition has never been recorded in Canada after the first week of September. Eggs hatch after 12 days, and larvae

bore to the cambium. The first and second stadia last two to three weeks each, and the first and second instars feed in the cambial region, scoring the wood surface with tunnels packed with frass and wood shavings. By early September, most larvae are in the third stadium, and they tunnel deep into the wood where they overwinter. Feeding both in the wood and in the cambial region continues the following summer, and moulting to the fourth instar occurs at that time. In the fall of the second year or in the following spring, larvae chew pupal chambers in the sapwood close to the bark. Pupation occurs early in the spring, and adults emerge by chewing a circular hole out through the bark. While a two year life cycle is most common, it can also be completed in one year in the south of the insect's range and can last four years in the north.

A.3 — Economic importance of *Monochamus* species

M. scutellatus is the most economically important softwood borer in Canada. Damage done by larvae of *Monochamus* species and of other borers can take many forms, including:

1. passive or active introduction of decay fungi into the wood,
2. direct loss of wood volume for pulpwood,
3. decrease in lumber volume and lumber quality,
4. potential loss of export markets,
5. restrictions of uses to which infested timber can be put,

1. Holes and galleries made by wood-boring insects can act as infection courts for decay and stain fungi. Decay can often be seen extending from sawyer beetle galleries into the heartwood (Basham and Belyea 1960). Although a direct causal relationship has not been proven, the rate and extent of radial penetration of sap rot in balsam fir is related to the intensity of *Monochamus* attack (Basham and Belyea 1960; Basham et al. 1974).

2. During the first summer after felling, direct volume losses of up to 1.5% can be caused by borers in Jack pine and black spruce pulpwood (Prentice and Campbell 1959). After two summers, pulpwood volume losses of up to 5 to 10 percent could be due to *Monochamus* borers (Wilson 1961a).

3. Wood borers can be responsible for lumber volume and quality losses. In jack pine and spruce damaged by wind, *M. scutellatus* caused most of the lumber degrade and volume

loss during the first two years after blowdown in northern Ontario; value loss was about 10% after one year and 16% after two years (Gardiner 1975). Over two summers, red and white pine killed by fire suffered a 17 to 59% loss in lumber value because of borers and staining (Prebble and Gardiner 1958). Lumber value losses of 30% could be expected for *Monochamus* attacks of three or more entrance holes per square foot (32 per square metre) of lodgepole pine log surface area (Safranyik and Raske 1970). Sawyer beetle and ambrosia beetle damage can reduce the value of white pine lumber by 35% (Becker and Abbott 1960).

4. The presence of wood borers in exported wood adversely affects international trade. Shipments of infested wood can be refused entry, be destroyed or fumigated at the exporter's expense, and can result in the loss of future sales. Sawyer beetles are the most commonly encountered borers found in Canadian lumber exports.

5. The presence of insect borings limits the uses to which wood products can be put. For example, poles used in transmission lines must be free of insect borer holes greater than 1.5 mm in diameter (Canadian Standards Association 1982).

In areas with high sawyer populations, adult feeding on twigs and branches can result in reduced tree growth or in tree death (Benoit 1978). In addition, *Monochamus* species are the principal vectors of the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner and Bührer) Nickle (Mamiya and Enda 1972; Holdeman 1980; Wingfield and Blanchette 1983), which causes pine wilt disease in several species of *Pinus* and certain other conifers (Kobayashi 1978; Dropkin et al. 1981). This nematode is now known to occur throughout most of Canada. Sweden has already imposed restrictions on the importation of all wood products from North America, and other countries are considering various import restrictions because of the presence of the nematode.

A.4 — Traps for forest beetles

Insect traps are necessary for several aspects of insect control and research, such as detection and surveys, monitoring of insect numbers and activity, mass trapping, and field evaluations of semiochemicals. While many types of insect traps have been designed (see Southwood [1978] for an extensive discussion of trap types), those which have been used for

forest Coleoptera can be separated into four classes: 1) flight interception traps, 2) silhouette interception or barrier traps, 3) sticky traps, and 4) Norwegian drainpipe traps and bucket traps. Other traps such as pitfall traps (Hertel 1970; Thomas and Hertel 1979; Tilles et al. 1986), light traps (Stewart and Lam 1970; Solomon et al. 1972), trough water traps (Svihra 1972), bucket traps (Galford 1980), shelter traps (Garth and Shanks 1978; Thomas and Hertel 1979), and trap trees (Johann 1986; Borden et al. 1983, 1987a) have also been used occasionally to trap special groups of beetles.

A.4.1 — Flight interception traps

These are often called **window traps**, since they consist of vertical panes of clear glass or acrylic plastic. Beetles flying into and hitting a pane close their wings and drop to a collection container. Since capture depends on this 'dropping' behaviour, flight interception traps are fairly specific for beetles, capturing few other insects. Traps consisting of a single pane of glass above a collection trough were first used to trap scolytids (Chapman and Kinghorn 1955, 1958; Dyer 1962; Dyer and Chapman 1965; Chapman 1966; Nijholt and Chapman 1968; Moeck 1970, 1971; Bauer and Vité 1975; Billings et al. 1976; Payne et al. 1978a, 1978b; Rose et al. 1981), and were subsequently used for studies of other groups such as cerambycids, clerids and trogositids (Billings and Cameron 1984) and carabids (van Huizen 1977). Juillet (1963) showed that unbaited interception traps can capture as many or more beetles as certain types of unbaited Malaise, rotary, or sticky traps.

The major modification of the basic window trap design involves the use of four panes attached to a central axis, resulting in a 'baffle' or 'vane' trap (Hines and Heikkenen 1977); two perpendicular intercepting panes can be used with the same result. These were used to trap scolytids, cerambycids, weevils, and buprestids (Hines and Heikkenen 1977), buprestids, cerambycids, clerids and scolytids (Montgomery and Wargo 1983), and these and other forest beetles (Wilkening et al. 1981; Younan and Hain 1982).

While other 'clear' traps have been used (e.g., Lindgren et al. 1983; Niemeyer 1985), the traps involved were complex, with many curved or angular surfaces; the resulting light refraction and reflection no doubt made these traps visible to insects, and they cannot be considered as flight interception traps.

A.4.2—Silhouette interception traps

Like flight interception traps, these traps capture beetles because the insects drop when they hit an object and are unable to land properly. Unlike the interception traps, the silhouette traps are clearly visible to approaching insects, and most likely capture only insects attempting to land on them.

Lindgren multiple funnel traps were designed by Lindgren (1983) and used to trap scolytids (Lindgren et al. 1983; Niemeyer 1985; McLean et al. 1987; Borden et al. 1987a, 1987b). They are available commercially (Phero Tech Inc., Vancouver, British Columbia, Canada V5L 3K3), and are being used commercially with success in scolytid mass trapping programmes in lumber mill yards in British Columbia (Lindgren, personnal communication, Phero Tech Inc.).

Bark beetle slot traps (*Schlitzfalle*) (Theyson GmbH, D–3320 Salzgitter 1, F.R.G.) have been variously referred to as slot traps (Niemeyer et al. 1983), flat funnel slot traps (Vité 1984), and lamina traps (Niemeyer 1985). Slot traps of different colours and sizes have been compared by Niemeyer (1985) for trapping of *Ips typographus* L., and have been used to trap scolytids (Dubbel et al. 1985; McLean et al. 1987) and clerids and trogositids (Kohnle and Vité 1984).

Bounce-column traps were first described by Clements and Williams (1981) and used by Fatzinger (1985) and Siegfried (1987) to trap various scolytids and other borers, including weevils and cerambycids. These consist of air-conditioning duct or stovepipes held upright at the centre of plastic wading pools containing water and detergent; insects hitting the duct fall and drown in the pool.

Traps similar to flight interception traps but using coloured instead of transparent panes (Hilker 1984) act as silhouette interception traps.

A.4.3 — Sticky traps

Many types of objects can be coated with a suitable sticky substance to serve as a trap. Sticky chemicals usually used are Stikem Special™ (Seabright Enterprises, Emeryville, California, USA 94608) and Tree Tanglefoot™ or Tangle-Trap™ (Tanglefoot Company, Grand Rapids, Michigan, USA 49504).

Forest Coleoptera have been captured with sticky vanes (Browne 1978; McLean and Borden 1979; Ikeda et al. 1980; Lindgren and Borden 1983; Payne et al. 1984; Boutz et al. 1985), metal screen (hardware cloth) cylinders (Moeck 1971; Byrne et al. 1974; McLean and Borden 1975, 1977; Browne 1978; Borden et al. 1980; Lanne et al. 1987; Schlyter et al. 1987b; Schroeder and Eidmann 1987), cylinders and platforms (Solomon et al. 1976), and various flat surfaces such as flat hardware cloth, cards, boards or bark (Wickman 1965, 1969; Bedard and Browne 1969; Werner 1972a; Gardiner 1975; Billings et al. 1976; Nijholt and Schönherr 1976; Payne et al. 1978a, 1978b; Moeck et al. 1981; Younan and Hain 1982; Montgomery and Wargo 1983).

A.4.4 — Norwegian drainpipe traps, bucket traps

These consist of drainpipes (Bakke and Sæther 1978) or buckets (Moser and Browne 1978) within which scolytid pheromone dispensers are placed; attracted beetles land and enter into the traps through 2-5 mm holes drilled all along and around the pipes or buckets, and fall into a collection container. Norwegian drainpipe traps (bark-beetle-trap, 1979 model) are available commercially (Borregaard Industries Limited, 1701 Sarpsborg, Norway). Commercial and other models have been used to trap many species of scolytids (Niemeyer and Watzek 1977; Bakke and Sæther 1978; Klimetzek and Vité 1978; Borden et al. 1980; Moeck 1980; Lie and Bakke 1981; Rose et al. 1981; Regnander and Solbreck 1981; Bakke 1983; Bakke et al. 1983; Lindgren et al. 1983; Bakke 1985; Austarå et al. 1986; Eidmann et al. 1987; Schlyter et al. 1987a, 1987b).

B — Host selection

B.1 — Terminology

The expression "host selection" denotes the series of behavioural events leading an insect to feed or oviposit on a host. Miller and Strickler (1984) have suggested the scheme shown in Figure 1 to represent the various possible steps leading to host utilisation. It views the process as a chain of events, consistent with classical views as seen with Thorsteinson

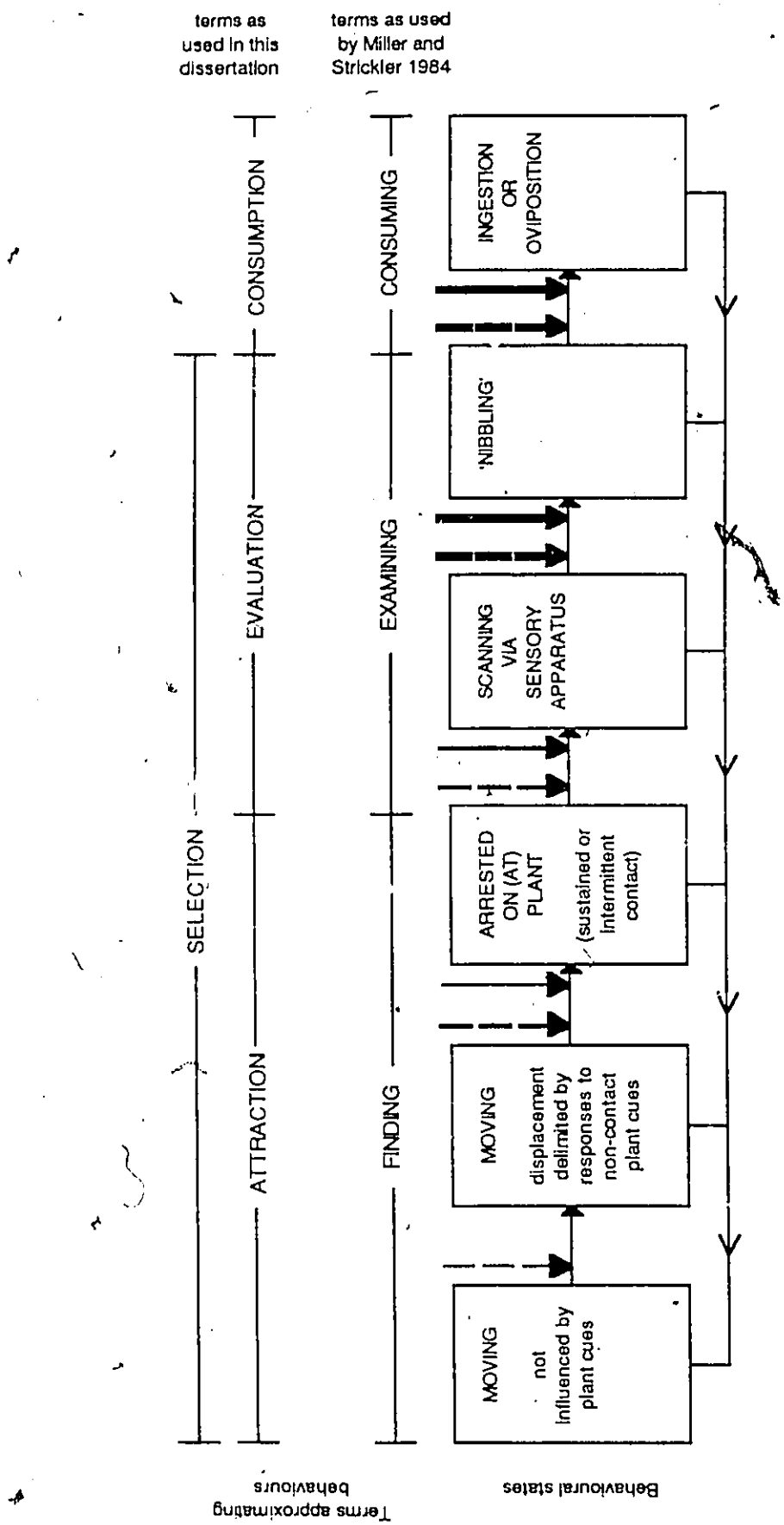


Figure 1. Behavioural events which lead a generalised insect to feed or oviposit on a host plant. Broken and solid downward arrows indicate non-contact and contact sensory cues, respectively. Modified from Miller and Strickler 1984.

(1960) and Kennedy (1965). Host finding and examining are considered as two steps leading to consumption (ingestion or oviposition). Host finding would include the initial movement of the insect not influenced by plant cues, movement affected by non-contact plant cues, and arrestment on a plant.

While terms such as host selection or attraction may "...connote mechanisms inaccurately..." (Miller and Strickler 1984), their widespread use and heuristic value make their continued existence likely. If they are well defined and the limitations of their mechanistic significance (or lack of significance) is understood, they can be useful terms. Thus, in this dissertation, **host selection** is considered as the series of behavioural responses occurring after dispersal and culminating in consumption of the host (Figure 1). **Attraction** involves both the **orientation** in response to non-contact cues and the **arrestment** on the host in response to either or both contact and non-contact cues. The **evaluation** of the substrate after arrestment culminates in **consumption** (feeding or oviposition). The term 'evaluation' is used rather than Miller and Strickler's term 'examining' both in order to avoid the use of a participle as a noun and, more importantly, because the behaviour culminates in a choice being made (consume or not), a fact better reflected by the word evaluation.

B.2 — Semiochemicals from the Pinaceae

If compounds are to act as kairomones eliciting attraction, these must be sufficiently volatile to be released from the host and disperse in the air. As seen below, compounds in the conifers acting as attractant kairomones have all been found to be terpenes or products of fermentation such as ethanol.

Essential oils (or volatile oils) include the volatile hydrocarbons present in the foliage, bark or wood of conifers. The steam volatiles (easily separated by steam distillation from less volatile compounds) include primarily monoterpenes as well as sesquiterpenes and some diterpenes; nonterpenoid esters, alcohols and aromatic ethers can also be found in the steam volatiles (von Rudloff 1969). Terpenoids have been extensively studied, both because of their prevalence in plants and their economic importance (see, e.g., Derfer and Derfer 1983; Banthorpe and Charlwood 1980). The monoterpenes and other terpenoid chemicals in the bark

and foliage of conifers act as effective deterrents against feeding by beetles and other herbivores (Hanover 1975; Cates and Alexander 1982).

Extensive analyses of leaf oils of North American conifers led von Rudloff (1969, p.132) to state that "qualitative differences may lead to correlations at higher taxonomic levels, whereas quantitative differences may be characteristic of individual species". Since most wood-boring cerambycids and other borers are oligophagous, attacking most tree species of their host family found in their geographic range, it appears likely that the qualitative composition of the terpene attractants would be more important than the precise quantitative composition.

Table 1 presents the monoterpene content of several North American species of Pinaceae. The six most prevalent compounds in these and other species of Pinaceae include α–pinene, β–pinene, camphene, 3–carene, limonene, and myrcene (Figure 2) (Guenther 1949; Zavarin and Snajberk 1965; Drew and Pylant 1966; Zavarin 1968; Hunt and von Rudloff 1974; von Rudloff 1975; Wroblewska et al. 1977; Wilkinson 1980).

Since Graham (1968) demonstrated the production of ethanol in conifer bark tissue as a result of anaerobic fermentation, several other authors have reported the production of fermentation products in moribund or dead conifers, with ethanol generally being the most abundant compound (Moeck 1970; Oda 1974; Ikeda and Oda 1980; Ikeda et al. 1980).

B.3 — Host attraction of conifer-feeding beetles

Host attraction of conifer-feeding beetles has been studied most extensively in the Scolytidae. Following a dispersal flight, host selection involves orientation to a host tree (or random landing), arrestment and landing on the host, and inhibition of further dispersal to permit activities such as mating and oviposition (Borden 1977). Primary attraction refers to the attraction of beetles to an unattacked host, usually in response to host volatiles; in species producing sex or aggregation pheromones, secondary attraction refers to the attraction of beetles to a host in response to the complex of beetle-produced pheromones and host compounds (Borden 1974, 1982).

TABLE 1. PERCENT CONTENT OF MAJOR MONOTERPENES IN SELECTED CANADIAN SPECIES OF PINACEAE. [a]

Species and Tissue	Monoterpenes								
	camphene	3–carene	limonene	myrcene	β–phellandrene	α–pinene	β–pinene	terpinolene	"others"
Abies spp.									
A. amabilis									
blister [f]	0.5	38.0	1.0	1.0	26.5	15.5	16.5	+	1.0
A. balsamea									
blister [f]	+	4.0	28.5	0.5	19.0	17.0	31.0	+	0
chips [b]	1.8	(8.2)	2.3	(8.2)	(0.7)	62.8	22.9	0	1.1
A. grandis									
phloem, S [c]	1.2	0.3	0.2	4.5	+	48.1	42.0	0.2	3.6
phloem, M [c]	1.5	3.1	1.1	9.3	0.6	45.0	33.9	0.6	4.9
phloem, I.14 [c]	0.3	8.8	3.0	22.5	1.7	26.7	23.7	1.5	12.2
phloem, I.28 [c]	2.6	18.9	5.9	18.0	5.8	18.7	21.2	1.3	7.8
blister [f]	0.5	34.5	5.0	0.5	26.0	13.0	18.5	0	2.0
A. lasiocarpa									
blister [f]	+	6.5	11.5	1.0	43.0	9.0	28.5	0.5	0
Larix laricina									
chips [b]	1.2	(15.5)	3.9	(15.5)	(4.4)	25.3	47.0	1.2	1.5
Picea spp.									
P. glauca									
chips [b]	1.0	(3.6)	19.7	(3.6)	(3.9)	42.2	29.6	0.3	1.0
P. mariana									
chips [b]	+	(1.8)	1.8	(1.8)	(1.8)	51.8	42.7	+	0
P. sitchensis									
chips [b]	0.7	(4.0)	10.8	(4.0)	(42.4)	17.5	10.8	4.0	10.0
Pinus spp.									
P. banksiana									
chips [b]	2.0	(1.1)	2.9	(1.1)	(1.6)	63.3	28.6	+	0.5
P. contorta									
chips [b]	0.5	(21.7)	0	(21.7)	(63.0)	4.9	2.2	1.7	3.2
P. monticola									
chips [b]	2.8	(0.6)	6.5	(0.6)	0	76.3	8.8	+	5.1
P. ponderosa									
chips [b]	1.7	(43.6)	14.5	(43.6)	(1.7)	12.3	19.8	2.3	4.1
P. resinosa									
wood [e]	1	4	–	1	–	72	18		6
chips [b]	2.2	(5.4)	1.1	(5.4)	(1.1)	80.4	9.8	+	0
P. strobus									
chips [b]	3.2	(1.0)	1.0	(1.0)	(0.6)	73.9	19.8	0.6	0
resin [d]	3.8	9.4	4.3	14.1	6.5	26.6	32.9	2.4	0
Pseudotsuga menziesii									
P. m. menziesii									
chips [b]	3.1	(1.9)	8.2	(1.9)	(1.9)	75.5	5.4	1.9	1.9
blister [f]	0.5	10.0	5.0	1.0	1.5	31.0	36.0	5.5	0.5
P. m. glauca									
blister [f]	1.5	1.0	10.5	1.0	2.5	76.0	6.5	1.0	0

TABLE 1. *CONCLUDED.*

[a] Percent of total monoterpene hydrocarbons. + = trace detected. – = presence or absence not reported.

[b] Drew and Pylant 1966. Pulpwood chips (no bark), pulp mill digestion procedure ('sulfate turpentine'). Values for 3–carene and myrcene are total combined values for both compounds; β–phellandrene = β–phellandrene + *cis*–β–ocimene. Percentages are transformed from original data which were percentages of total turpentine (including 'heavy unidentified components', sesquiterpenes, oxygenated terpenes). 'Others' include 'light hydrocarbons', α–terpinene, α–phellandrene, γ–terpinene, α–ocimene, *trans*–β–ocimene, and p–cymene.

[c] Raffa and Berryman 1982. Phloem monoterpenes. U=uninjured phloem; M=14 days after mechanical injury; I.14=14 days after fungal inoculation; I.28=28 days after fungal inoculation. 'Others' include tricyclene, sabinene, unidentified monoterpenes.

[d] Wilkinson 1980. Cortical oleoresin. Mean of 1568 trees. Expressed as % of total monoterpene hydrocarbons.

[e] Wroblewska et al. 1977. Wood turpentine, mean of healthy control wood. 'Others' include unidentified compounds and high-boiling components.

[f] Zavarin and Snajberk 1965. Blister balsam. 'Others' include santene, tricyclene, sabinene, α–phellandrene.

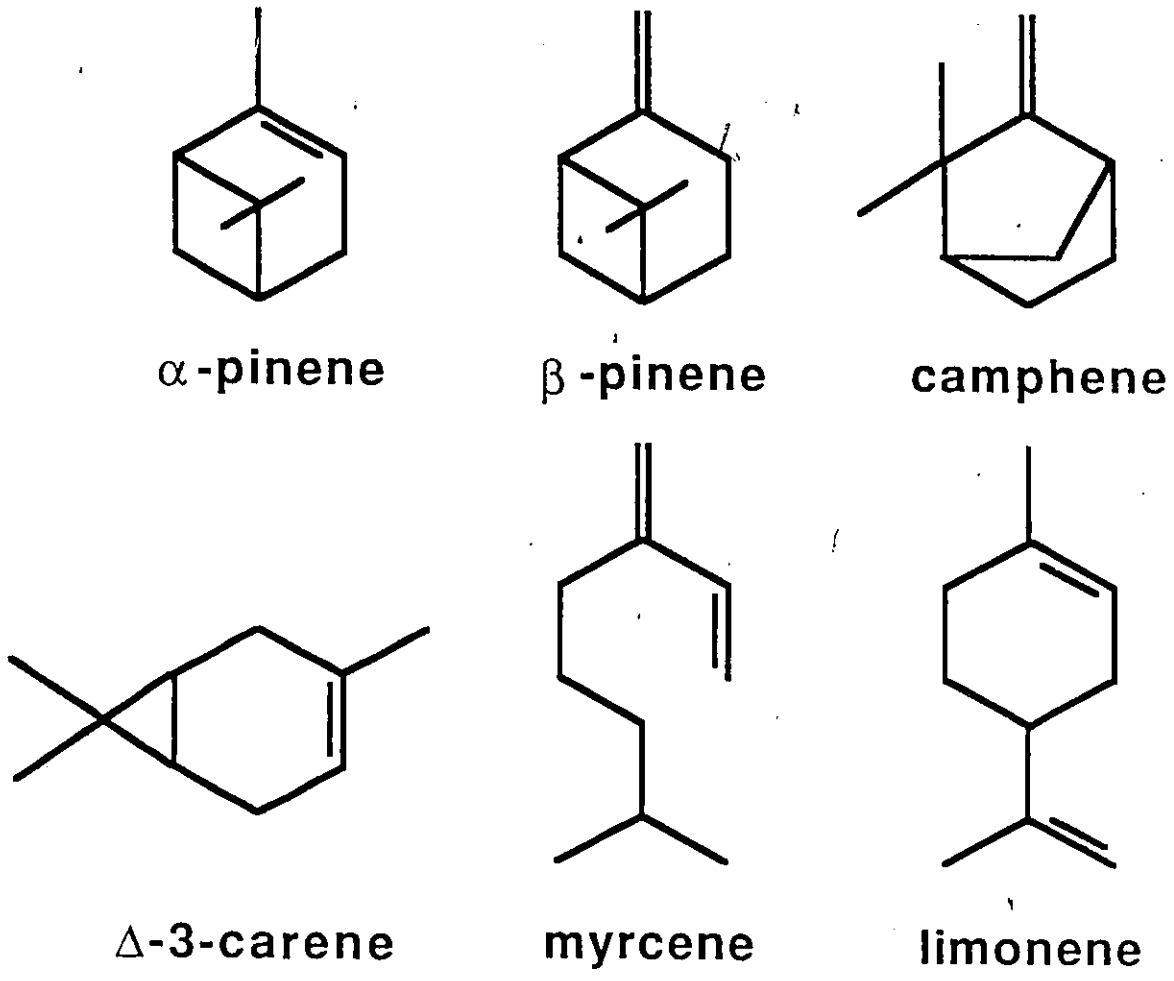


Figure 2. Structures of the common monoterpenes present in trees of the family Pinaceae.

B.3.1 — Chemical cues

Extensive studies with species of Scolytidae associated with conifers have shown that while many do not orient to host-produced chemicals, others are attracted to susceptible host material and to host resin or phloem (see Moeck et al. 1981; Wood 1972, 1982). Pure conifer terpenes have been found to attract bark and ambrosia beetles, including *Hylastes ater* Paykull (attracted to α–pinene in the laboratory) (Perttunen 1957), *Ips grandicollis* (Eichhoff) (various terpenes in the field) (Werner 1972a), *Tomicus (Blastophagus) minor* (Hartig) (α–terpineol and cis– and trans–carveol in the laboratory) (Kangas et al. 1970), *Tomicus (Blastophagus) piniperda* (L.) (various terpenes in the laboratory and in the field) (Perttunen et al. 1970; Byers et al. 1985; Schroeder and Eidmann 1987), and other scolytids (Rudinsky 1966; Chararas 1979). Ethanol, produced by fermentation in moribund trees (Graham 1968), may act as an attractant for conifer-feeding species such as *Gnathotrichus sulcatus* (LeConte) (Cade et al. 1970; Moeck 1971), *Trypodendron lineatum* (Olivier) (Graham 1968; Moeck 1970, 1971; Nijholt and Schönherr 1976), *Xyleborus saxeseni* Ratzeburg (Moeck 1971), and *Xyloterus (Trypodendron) domesticus* L. (Kerck 1972; Nijholt and Schönherr 1976). Ethanol may synergise attraction to host terpenes such as α–pinene, as seen with *T. lineatum* (Bauer and Vité 1975; Nijholt and Schönherr 1976), *Hylastes nigrinus* (Mannerheim) and *Pseudohylesinus nebulosus* (LeConte) (Nijholt and Schönherr 1976), or to pine turpentine, as seen with *Dendroctonus terebrans* (Olivier) (Fatzinger 1985). Monoterpenes, including α–pinene, myrcene and camphene, as well as ethanol have been shown to synergise attraction to pheromones in several species of Scolytidae (see Borden 1982; Wood 1982).

Monoterpenes and ethanol may also play a role in the orientation of beetles in families other than Scolytidae. Among the weevils, *Hylobius pales* (Herbst) was attracted to the host terpenes (+)–α–pinene and α–phellandrene in olfactometer tests (Thomas and Hertel 1969) and to various monoterpenes released with ethanol in the field (Siegfried 1987). *Hylobius abietis* (L.) was attracted synergistically to monoterpenes and ethanol in trapping experiments (Tilles et al. 1986). *Pissodes strobi* (Peck) was reported to be attracted to monoterpenes (Wilkinson 1972). In non-controlled experiments, turpentine appeared to attract many species of Cerambycidae, Scolytidae, Curculionidae, and Cleridae (Gardiner 1957) and species of

Buprestidae, Cleridae, and Trogositidae (Wickman 1969). Sawyers (*Monochamus* spp.) and pine reproduction weevils were attracted to turpentine in the field, and attraction was synergised by ethanol (Fatzinger 1985). Becker (1962) showed that monoterpenes attract many beetles in the laboratory, including the cerambycid *Hylotrupes bajulus* (L.) which is attracted to α–pinene (Becker 1942, 1944). Perttunen (1957) also reported attraction of *H. bajulus* to α–pinene and other terpenes. Upwind flights in laboratory olfactometers indicated responses of the clerid *Thanasimus dubius* (Fabricius) to α– and β–pinene (Mizell et al. 1984). The cerambycid *Monochamus alternatus* Hope was attracted to a mixture of monoterpenes and to monoterpenes and ethanol (Ikeda et al. 1980, 1981). Among the many sensilla present on the antennal flagella of *M. scutellatus* and *M. notatus* (Dyer and Seabrook 1975), the sensilla basiconica were found to respond electrophysiologically to at least six monoterpenes (Dyer and Seabrook 1978b). Ethanol may possibly be involved in attraction of cerambycids and other beetles, as indicated by trapping with fermented baits (Champlain and Knull 1932; Galford 1980). Certain species of Cerambycidae, Cleridae and Scolytidae were attracted to traps baited with ethanol placed in an oak forest (Montgomery and Wargo 1983); other water-soluble chemicals including acetone, acetaldehyde, and methanol did not affect trap catches.

B.3.2 — Visual cues

Silhouette has been reported as being important for the orientation of scolytids such as *X. domesticus* (Kerck 1972) and *T. lineatum* (Vité and Bakke 1979; Borden et al. 1982). Results of Niemeyer (1985) indicate that black barrier traps probably elicit landing behaviour for *I. typographus*, since increasing trap size did not increase catch. Niemeyer (1985) reported that responses of *Ips* spp. to white and black traps varied depending on the background (open vs. forested) and on the close proximity of traps of similar and other colours, indicating the possible importance of background contrast.

Scolytids in the genera *Dendroctonus* and *Trypodendron* (Groberman and Borden 1981, 1982) and *Ips* (Schönherr 1971) respond in the laboratory to light of different wavelengths. Laboratory trapping has shown that *Pityogenes chalcographus* L. and *I. typographus* respond to different rates of UV and visible light reflectance from white silhouette traps (Hilker 1984). Dubbel et al. (1985) have shown that *I. typographus* and *T. lineatum* are

captured in equal numbers in pheromone-baited clear, black, green, grey and redbrown barrier traps, and in lower numbers in white traps; the capture of other Coleoptera was not affected by trap colour. In the open, baited black flight barrier traps captured more *I. typographus* than hyaline-white traps (Niemeyer 1985). Colour of multiple funnel traps has been shown not to affect catches of Scolytidae (Lindgren et al. 1983). *Dendroctonus ponderosae* Hopkins and *Ips montanus* (Eichhoff) prefer dark coloured traps (Schönherr 1976), and are attracted more to light of short wavelengths (Schönherr 1971).

Gardiner (1957) noted that beetles, notably cerambycids, landed on convenient landing surfaces rather than directly on pans containing turpentine bait, and that trapping was facilitated by placing baits close to tree trunks or walls, indicating probable visual orientation when landing.

B.4 — Pheromones

Because responses to pheromones can interact with or affect host selection behaviour, these are mentioned briefly. For conifer-feeding beetles, only among the Scolytidae have aggregation pheromones eliciting attraction to host material been well documented (see Borden 1982; Wood 1982).

Among the Cerambycidae, evidence indicates that both air-borne pheromones and pheromones detected by direct antennal contact exist. Some Callichromini (Cerambycinae) may use pheromones to attract mates from a distance (Duffy 1953; Linsley 1959). Males of *Xylotrechus pyrrhoderus* Bates attract females, and similar attraction is seen when using hexane extracts of males (Iwabuchi 1982); the major pheromone components have been identified (Sakai et al. 1984) and found to induce both electrophysiological activity (Iwabuchi et al. 1985) and attraction of females (Iwabuchi et al. 1986). Female *Xylotrechus chinensis* Chevrolat detect and fly to conspecific males (Iwabuchi et al. 1987); pheromone components were identified by Kuwahara et al. (1987) and Iwabuchi et al. (1987). Galford (1977) did not find any evidence supporting the existence of attractant pheromones for *Enaphalodes rufulus* (Haldeman) or *Megacyllene robiniae* (Forster). While pheromones acting at a distance probably occur in relatively few cerambycids, pheromones used to identify conspecifics or to

mark the substrate are probably more prevalent, and are likely detected by the antennal contact (Linsley 1959). Male *M. robiniae* recognise twigs which have been exposed to females and persistently search and remain on these substrates (Galford 1977). *H. bajulus* males identify females by antennal contact, and attempt to copulate with pieces of female elytra (Doppelreiter 1979). Male *Acalolepta luxuriosa* Bates attempted to copulate with a model treated with female extracts (Kuboki et al. 1985). *Monochamus sartor* Fabricius males appear to recognise females by antennal contact (Hellrigl 1971). Personal and published observations indicate that similar sexual recognition may occur in other *Monochamus* spp. (Hellrigl 1971; Hughes 1979, 1981). Evans and Higgs (1975) have identified many monooxygenated compounds in the frass of *H. bajulus*, including (–)–verbenone and p–cymen–8–ol, the latter compounds eliciting oviposition on treated substrates (Higgs and Evans 1978), indicating that these compounds may act as pheromones.

B.5 — Evaluation of oviposition sites by cerambycids

Oviposition behaviour of the Cerambycidae has been reviewed by Trägårdh (1930) and Butovitsch (1939). Butovitsch (1939) recognised two groups based on site preparation. While female Lamiinae use the mandibles (and occasionally the ovipositor) to cut an egg niche, members of all other subfamilies simply lay on available sites, most commonly under bark scales or in cracks in the bark. Trägårdh (1930) suggests that the oviposition behaviour is related to the distinctive features of the lamiine head — head vertical, lower part of head tapering gradually downwards, frons concave, antennae inserted at the top of the frons on the antennal prominences, strong mandibles. Since the publication of these two papers, descriptions of the oviposition behaviour of various cerambycids support the proposed distinction between the Lamiinae and other subfamilies. In eastern Canada, Gardiner (1969) noted that all nine species of Lamiinae which were observed ovipositing chew a slit for the egg. In the Cerambycinae, all nine observed species laid under bark scales or directly on the exposed bark surface; all of the three species of Aseminae laid under bark scales. The 11 observed species of Lepturinae oviposited directly on rotten wood (one species), in small checks in decaying wood (five species) or under bark scales (five species).

Female Lamiinae generally cannot be induced to lay on non-host material. For example, *Monochamus* species lay only in suitable hosts (personal observation). Oviposition niches are often left empty, possibly because of unsuitability of the substrate. Females in other subfamilies can oviposit on non-host material in experimental situations: conifer-feeding *Criocephalus* species (Cerambycinae) lay on *Quercus* in cages (Chararas 1979), while *Xylotrechus undulatus* (Say) (Cerambycinae) (personal observation), *Semanotus litigiosus* (Cerambycinae) (Wickman 1968) and *Gaurotes abdominalis* (Lepturinae) (Gardiner 1969) oviposit under filter papers or elsewhere in rearing cages.

Chewing an egg niche could serve three purposes: 1) Provide a site for the egg protected from physical and biotic influences. Similar protection is provided by laying under bark scales or in bark and wood crevices. 2) Provide immediate access to the food for the larvae at hatching. Larvae of species which lay on the bark must bore to the cambium, during which time they may be subjected to physical stress or predators. 3) Permit the evaluation of the oviposition substrate and selection of an adequate site. Although the identity of the host may largely be determined during host attraction (long-range orientation and arrestment), the chewing of a niche permits both the further identification of the host and of the exact condition of the substrate. Substrate evaluation could be mediated by contact chemoreceptors and mechanoreceptors on the mouthparts and/or ovipositor. A major distinguishing feature of the Lamiinae is the pointed terminal segment of the maxillary palpi; members of other subfamilies have the terminal segment obtuse or truncate (Linsley 1961). Female *M. scutellatus* can be seen to palpate egg niches as they are chewed, and acute maxillary palpi would be of advantage in substrate evaluation, provided of course they are equipped with appropriate sensilla. Since lamiines deposit their eggs in the cambial region, receptors on the ovipositor could also be involved in evaluating substrate suitability.

B.6 — Host selection scheme for *M. scutellatus*

The scheme of events leading to oviposition by *M. scutellatus* outlined in Figure 3 is proposed. A similar scheme would probably be applicable to other species of Lamiinae. Behaviour would involve the following steps:

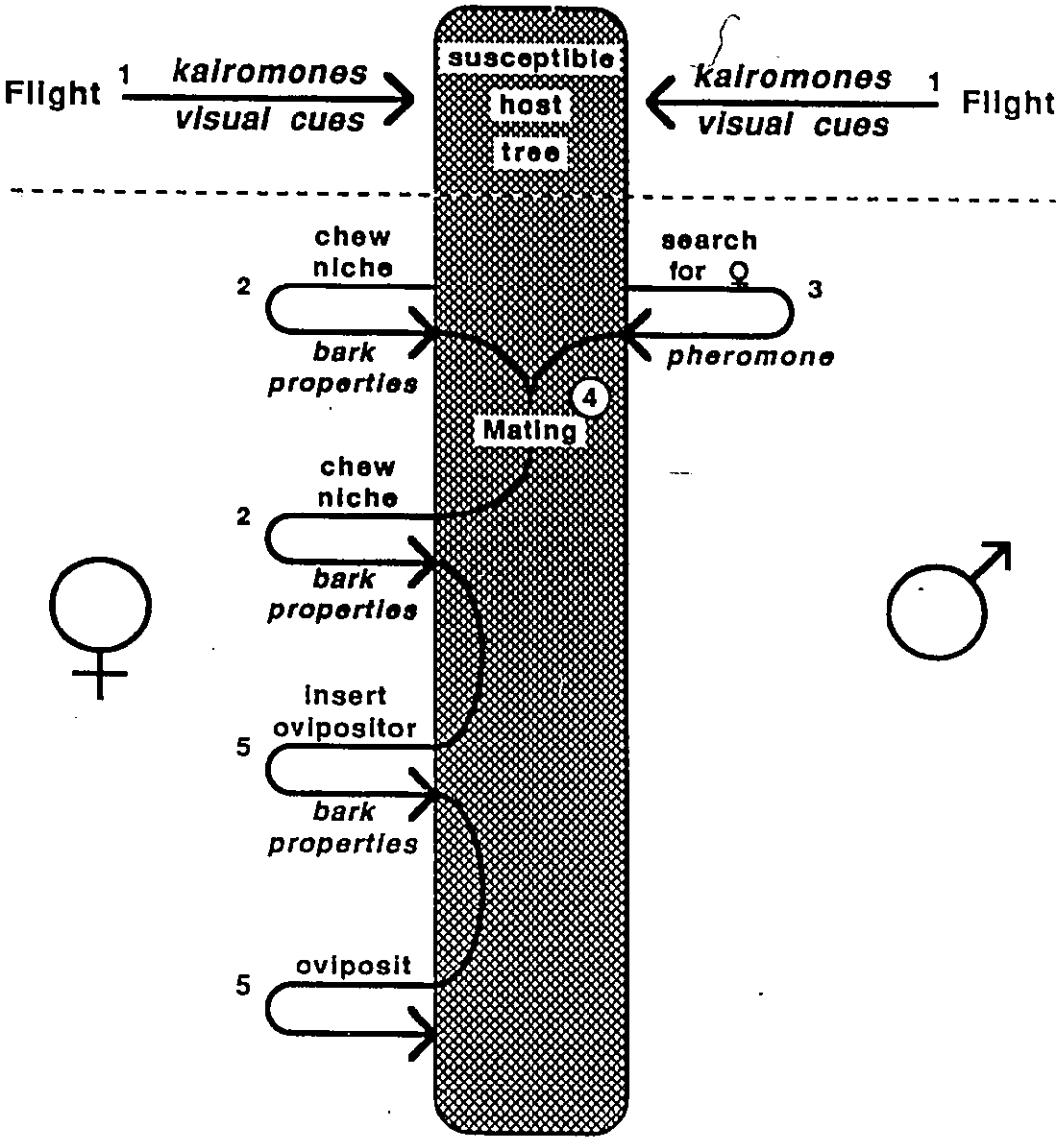


Figure 3. Proposed scheme of events leading to oviposition by Monochamus scutellatus. Events above dotted line involve attraction to the host, while those below involve mating and oviposition. See text for explanation of numbers.

1. Males and females are attracted by tree volatiles from hosts on which beetles mate and oviposit. *M. scutellatus* males and females can be attracted to and oviposit on bolts of *A. balsamea* or *P. mariana* as early as a few hours after tree felling (Wilson 1961b). Logs can remain attractive and serve as oviposition substrates for nine to twelve months after tree death (Parmalee 1941). It is not clear whether changes in quantity or quality of volatiles accounts for changes in a tree's acceptability as a host.

2. Mature female *M. s. scutellatus* and *M. s. oregonensis* may chew egg niches in host bark both before and after mating; eggs are usually laid in only 30% of all niches (Rose 1957). Cues evoking substrate acceptance (ensuring that females remain on the bole) or inciting oviposition could include chemical and physical properties of the bark or phloem, such as terpenes and their oxygenation products, fermentation products, moisture content, resin pressure, and bark thickness, hardness or texture. Higgs and Evans (1978) have shown that the frass of *H. bajulus* contains (–)–verbenone and p–cymen–8–ol, and that adults preferentially oviposit on wood treated with these substances. However, it has not been determined whether these chemicals also occur in the wood as a result of microbial or other oxidation of terpenes, in which case the compounds could act as kairomones rather than (or in addition to) as aggregation pheromone as suggested by Higgs and Evans.

3. Males probably identify the sex of conspecifics by antennal contact. *M. scutellatus* females are generally seen on boles earlier in the day than males (Hughes 1979). Marking of the bark by females would ensure that arriving males would remain on the boles, leading to aggregation and ensuring mating of females with dominant males.

4. Mating behaviour of *M. scutellatus* has been well described by Hughes (1979, 1981). Antennal contact is apparently used by males to distinguish sexes. While males quickly mount females, contact between males leads to aggressive behaviour, including stridulation.

5. After mating, the female chews new niches and, if the substrate is suitable, the ovipositor is inserted into the niche and an egg is laid. Further evaluations of the subsrate could occur at this time.

METHODS

A — Attraction

Field Site

Field trapping experiments were carried out on the grounds of the Petawawa National Forestry Institute (P.N.F.I.) near Chalk River, Ontario, Canada. The forests in the area are part of the Central Ottawa District of the Great Lakes - Saint Lawrence Forest Region (Rowe 1972), and are locally dominated by natural stands of eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Aiton), and jack pine (*Pinus banksiana* Lambert), and plantations of red pine and larch (*Larix* spp.) and spruce (*Picea* spp.) hybrids. No major insect or disease problems were observed in the area.

A.1 — Importance of visual cues (trap evaluation)

All traps were baited, using similar chemicals (monoterpenes and ethanol) and bait dispensers. The monoterpenes and ethanol had been shown to attract many species of conifer-feeding beetles in preliminary trials. Ethanol baits consisted of two 11 ml specimen vials each containing 10 ml of 95% ethanol; vials were capped with inverted vial caps with four 2 mm holes cut into the sides of each cap with a cork borer. Two similarly capped vials were used as dispensers for 10 ml of the monoterpene mix (65% (±)–α–pinene, 20% (–)–β–pinene, 5% (±)–limonene, 5% (+)–camphene and 5% myrcene; all terpenes purchased from Aldrich Chemical Co., Milwaukeee, Wisconsin). A lamp wick (10 x 70 mm) was placed in each of the monoterpene vials to provide a higher and more constant rate of vaporisation over the trapping period (see Appendix 1). Thus, every trap was baited with four vials.

Three types of traps were tested: sticky stovepipe traps, Lindgren multiple funnel traps, and flight interception traps (Figure 4).

Sticky stovepipe traps (pipe traps). These traps offered a clear, black vertical silhouette to approaching insects. Each trap consisted of two metal stovepipes (each 75 cm length, 16 cm diameter) painted black (Flat Black, Pittsburgh Paints 54-198). These were

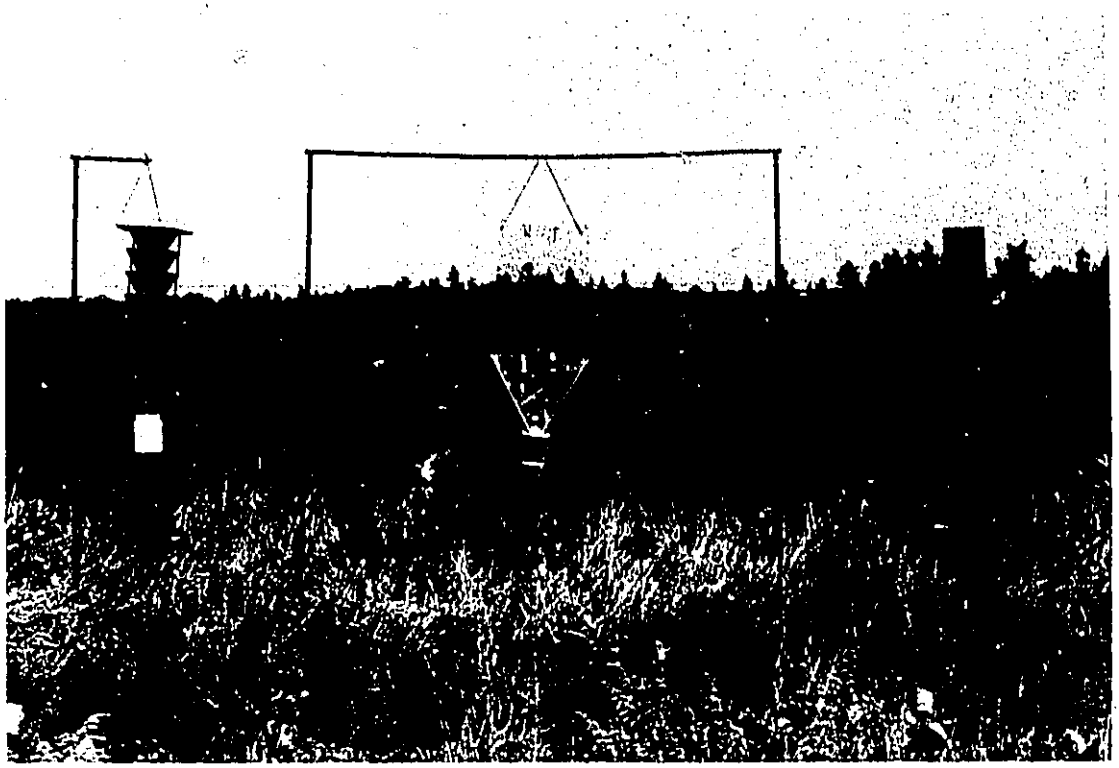


Figure 4. Three trap designs used for trapping beetles. Lindgren multiple funnel trap (left), flight interception trap (centre), and sticky stovepipe trap (right). Supports for the funnel trap and the interception trap are those used in open sites.

assembled and were held upright using a 110 cm steel rod stuck in the ground and passing through two eyebolts bolted inside the bottom pipe. An aluminium plate (30 cm diameter with 2 cm high lip), also painted black, was impaled on the steel rod below the trap, in order to retain insects which fell from the pipes. A thin layer of hot Stikem Special™ (Stikem) was applied to the top 70 cm of the top pipe with a scraper, and a thread of Stikem was placed inside the lip of the aluminium plate. The total trapping surface of the trap (i.e., sticky pipe surface, from 0.8 to 1.5 m above the ground) was 0.35 m^2. Bait vials were suspended at the top of the traps within the top pipe, with the vial caps protruding above the trap top.

Cerambycids and other large insects were collected from the traps with forceps and placed in collection vials. Every three or four weeks, the Stikem and all captured insects were removed from the traps with a scraper and placed in metal canisters, and a fresh layer of Stikem was applied to the top pipe. The vials and canisters containing the collected insects were refrigerated until the insects were cleaned. A series of solvents was used to clean the insects: 1) warm mineral spirits (repeated as necessary to remove the Stikem from the insects), 2) ethyl acetate, 3) acetone, 4) ethanol (95%), and 5) ethanol (80%). The cleaned insects were pinned or stored in 75% ethanol.

Lindgren multiple funnel traps (funnel traps). Funnel traps (Phero Tech Inc., 1140 Clark Dr., Vancouver, British Columbia V5L 3K3) consisted of eight partly-stacked black funnels above a plastic collection bottle (Lindgren 1983). These offered an irregular vertical silhouette to approaching insects. In open fields, the traps were hung from copper pipe (1.3 cm diameter) supports (Figure 4), while in the forest, the traps were suspended from nylon ropes hung between adjacent trees. In both cases, the traps were suspended so that the upper end of the top funnel was 1.5 m above the ground. The total trapping surface for each trap (considered as a cylinder extending from the top of the top funnel to the top of the bottom funnel) was 0.35 m^2.

The four bait vials were held by wires at the bottom end of each of the four middle funnels. To collect the insects, the labelled collection bottles were removed and covered to return to the laboratory, and a clean bottle was screwed into place at the bottom of the trap.

Flight interception traps (interception traps). The interception traps were designed so as to offer few visual cues to approaching insects. The traps were built from 3 mm thick sheets of clear acrylic thermoplastic (Acrylite®). Two acrylic panes (each 50 x 50 cm) were kerfed halfway along the middle and slipped together perpendicularly one to another. An inverted acrylic pyramid, consisting of four truncated triangular acrylic sheets glued together, served as a funnel leading into a plastic container to capture the insects which hit the panes and dropped. The 1 litre collection container had a snap-top lid which had been cut at the centre to fit over the bottom of the funnel to which it was bolted. A snugly-fitting black vinyl funnel was placed at the top inside the container to prevent insects from flying or walking out. The acrylic funnel and the two perpendicular panes were held together by wires. In open fields, the traps were hung from a copper pipe (1.3 cm diameter) frame (Figure 4), while in the forest, the traps were hung from nylon ropes strung between adjacent trees. In both cases, traps were suspended so that their top was 1.5 m above the ground. The trapping surface was 1.00 m^2 if considered as the total surface of the panes, or 0.79 m^2 if considered as a cylinder 50 cm in diameter and 50 cm high.

One ethanol and one monoterpene vial were held by wires at the top of the panes such that the caps protruded above the top, and one ethanol and one monoterpene vial were attached to the bottom of the panes so that the caps were about 2 cm below the panes. When collecting the insects, the labelled containers were removed and covered for return to the laboratory, and a clean container was attached to the bolted lid.

The three treatments (trap types) were replicated in 12 blocks, using a randomised block design. Vegetation cover alternated with each block, with odd-numbered blocks being set up in open fields (clear-cuts or young plantations with little vegetation taller than 60 cm) and even-numbered blocks placed within forested sites. Each trap in a block was 20 m from the two other traps in that block. All traps were at least 30 m from the forest-field boundary.

Trapping was done from June 19 to August 8, 1985. Traps were serviced weekly. Trapped insects were collected, and the relative positions of the three traps in each block were changed, moving the entire traps. Vials containing baits, each numbered and previously

weighed in the laboratory, were placed on the traps, and the vials containing bait chemicals from the previous week were brought back to the laboratory for weighing and determination of quantity of chemicals released during the trapping period. Insects were cleaned, preserved in ethanol or pinned, identified to species or family, and counted.

The number of insects captured per treatment in each block was pooled over all trapping periods in order to minimise trap position effects. Since data did not meet the criteria necessary to justify parametric testing, non-parametric tests were done to evaluate results. Analyses were done for species with 20 or more individuals captured (for species in most families), or with three or more individuals captured (for species in the families Buprestidae, Elateridae, Cleridae, Cerambycidae, and Scolytidae). Friedman tests corrected for ties (Zar 1984, equation 13.38) were carried out to verify effects of trap design. In cases where trap design was found to affect capture (for α=0.05), Newman-Keuls tests were done to verify significance (P<0.05) of the differences between the rank sums of each of the three trap designs, using standard error (SE) values corrected for ties (Zar 1984, section 13.9), and standard $Q_{0.05}$ table values. Non-parametric Mann-Whitney tests corrected for ties (Zar 1984, section 9.9) were done in order to verify effects of forest cover on trap captures, and the significance probabilities were noted. See Appendix 2 for equations used for analyses in this and other experiments.

A.2—Importance of chemical cues

Trapping was done using sticky stovepipe traps and Lindgren multiple funnel traps. Candidate monoterpenes were selected to obtain a blend similar to the terpenes occurring in most eastern Canadian members of the family Pinaceae (Table 1). Monoterpenes selected were (±)–α–pinene (97% pure), (–)–β–pinene (98%), (±)–camphene (95%), (±)–limonene (95%) and myrcene (89%) (Aldrich Chemical Co., Milwaukee, Wisconsin) and (+)–3–carene (90%) (ICN Biomedicals Inc., Plainview, New York).

Experiment 1: Effects of monoterpenes and ethanol. Trapping was done with pipe traps. Four treatments (chemical attractants) were compared using: 1) unbaited control traps, 2) traps baited with 95% ethanol, 3) traps baited with a monoterpene blend, and 4) traps baited with the monoterpenes and with ethanol.

Ethanol baits consisted of two 20 ml scintillation vials each containing 20 ml of 95% ethanol; vials were capped with inverted specimen vial caps with four 2 mm holes cut into the sides of each cap with a cork borer. Two similarly capped vials were used as dispensers for the monoterpene mix (65% α–pinene, 20% β–pinene, 5% limonene, 5% myrcene and 5% camphene), except that a 10x75 mm lamp wick was placed inside each vial. For traps baited with both monoterpenes and ethanol, two monoterpene vials and two ethanol vials were used.

The four treatments were replicated in four blocks in a randomised block design, with two blocks in the forest and two in open fields. The four traps in a given block were placed at the corners of a square measuring 20 m per side. Traps were placed at least 30 m from the forest-field boundary.

Trapping was done from June 12 to August 5, 1986. Traps were serviced biweekly (12 to 15 day intervals). This involved randomly changing the positions of the four treatments in each block, moving the entire traps to their new positions. Fresh bait vials were attached to the top of the traps, and the vials containing bait chemicals from the previous trapping period were brought back to the laboratory for weighing. Large insects were collected from the traps with forceps. After four weeks and at the end of the experiment, the Stikem and all captured insects were removed from the traps; a fresh layer of Stikem was applied after the fourth week. Captured insects were cleaned as described on page 26. Insects were identified to species (conifer-feeding beetles and their associates) or family (other Coleoptera), and counted.

The number of insects captured per treatment in each block was pooled over all trapping periods in order to minimise trap position effects. Non-parametric tests were done to evaluate results. Data were analysed by Friedman tests corrected for ties (Zar 1984, equation 13.38), verifying significance for $\alpha=0.10$, $\alpha=0.05$ and $\alpha=0.01$. Significance of the differences between the rank sums of the four treatments was verified using Scheffé multiple contrasts for $\alpha=0.10$, $\alpha=0.05$ and $\alpha=0.01$ (using a standard error term corrected for ties [Zar 1984, equation 13.48]) and Newman-Keuls tests for $\alpha=0.05$ (using a standard error term corrected for ties [Zar 1984, section 13.9]).

Experiment 2: Effects of α-pinene, minor monoterpenes, and ethanol. To distinguish between the attraction due to α–pinene and that due to other (minor)

monoterpenes, an experiement was carried out with eight treatments: 1) unbaited control, 2) 95% ethanol, 3) minor monoterpenes (β-pinene, 3–carene, limonene, myrcene, and camphene), 4) ethanol and minor monoterpenes, 5) α-pinene, 6) α-pinene and minor monoterpenes, 7) ethanol and α-pinene, 8) ethanol, α-pinene, and minor monoterpenes. The minor monoterpene blend consisted of 45% β–pinene, 15% 3–carene, 15% limonene, 15% myrcene, and 10% camphene.

Ethanol baits consisted of two 11 ml specimen vials each containing 10 ml of 95% ethanol; each vial was capped with a specimen vial cap with one 3 mm hole cut into the top with a cork borer. Two 4 ml vials with a 7 mm hole in each of the caps were used as dispensers for the α–pinene (4 ml per vial). Minor monoterpene baits consisted of 4 ml of the monoterpene blend in one 4 ml vial with a pierced cap (7 mm hole). Traps baited with the ternary treatment (treatment 8) were therefore baited with two ethanol vials, two α-pinene vials and one minor monoterpene vial.

The experiment was carried out in open fields. A randomised block design was used, with the eight treatments replicated in ten blocks, using pipe traps in five of the blocks and funnel traps in the other five blocks. The eight traps in a given block were placed in two parallel lines with 20 m between the lines and 20 m between traps in a line. Traps were placed at least 40 m from the forest-field boundary.

The experiment ran from June 15 to August 16, 1984. Traps were serviced weekly (5 to 11 day intervals). The positions of the eight treatments in each block were randomly changed, moving the entire traps to their new positions in the block. Bait vials were replaced weekly; on July 29, August 9, and August 16, the volumes of chemical baits remaining from the previous trapping period were measured to determine rates of vaporisation. All insects were collected weekly from the funnel traps. Large insects were collected weekly from the pipe traps; after four weeks, the Stikem and captured insects from the pipe traps were removed with a scraper and placed in metal canisters, and a fresh layer of Stikem was applied. All insects were similarly removed at the end of the experiment. The collected insects were refrigerated until cleaning. After cleaning, the insects were preserved in 75% ethanol or pinned, identified to species (conifer-feeding beetles and their associates), and counted.

The number of insects captured per treatment was pooled within each block over all trapping periods. Data were analysed as in Experiment 1.

Experiment 3: Effects of commercial turpentine and of a monoterpene blend. A small-scale study was done to compare attraction to commercial turpentine with attraction to the monoterpene blend used in Experiment 1. Trapping was done with pipe traps using: 1) traps baited with 95% ethanol and the monoterpene blend, and 2) traps baited with 95% ethanol and commercial turpentine (Record Chemical Company Inc., Montréal, Québec). Bait dispensers and trapping procedure were as in Experiment 1. The two treatments were replicated in four blocks. Traps in a block were 20 m apart, and were at least 60 m from traps in adjacent blocks. Trapping was carried out over three trapping periods, from July 7 to August 5, 1986. Since trap position effects were unlikely in this two-treatment test, data from each trapping period were treated as a replicate for each of the four blocks, giving a total of 12 replicates. Data were analysed by Wilcoxon signed ranks tests for paired-sample experiments (Zar 1984, section 10.4).

B—Evaluation of oviposition substrate

Bioassay chamber and testing procedures

Chamber. Most observations relating to oviposition by cerambycids have involved observing insects on bolts in the wild, or confining beetles in cages where beetles had access to one or a few bolts of one or a few tree species. While such setups permit general comparisons of acceptability of the bolts for oviposition, each bolt may in fact offer oviposition sites of different qualities. For example, bark thickness and texture may vary, depending on the presence of knots, sub-cortical wounds, etc. A bioassay chamber was therefore developed which 1) permitted careful control or monitoring of the properties of test substrates, 2) provided for the exposure of the insects to volatile chemicals, and 3) provided a uniform arena within which beetles could be offered substrates for oviposition.

The chamber is shown in Figures 5, 6, and 7. The top board, 30 x 30 x 1.9 cm, had a 20 cm diameter hole cut in its centre. The board was bolted to wood spacers (1.5 cm high) and bottom board (30 x 30 x 0.6 cm). A 40 x 40 cm nylon screen (2 mm mesh) was placed between the top board and spacers; holes (2.5 cm diameter) were cut in the screen to provide access to the test substrates. Test substrates were held in Stender preparation dishes (2.5 cm high, 5 cm diameter) (Figure 8). A white translucent vinyl cylinder (20 cm diameter, 25 cm high) was placed in the hole in the top board, and was shut at the top with a flat piece (30 x 30 cm) of aluminium screen (3 mm mesh). All wood elements of the chamber were painted flat black.

Procedure. The following steps were followed when setting up a chamber for a test. A data sheet was prepared, showing the nature of the test substrates, position of the substrates, and other relevant information (Figure 9). A clean sheet of white paper (21.6 x 27.9 cm) was placed on the bottom board, and the preparation dishes with the test substrates were placed on the paper; dishes were marked on their side to indicate the orientation of the dishes in the chamber. The wood spacers, nylon screen and top board were put into place and bolted together, taking care to stretch the screen taut and ensuring that the substrates were below the holes in the screen. The vinyl cylinder was put into place. A test began by placing an insect on the nylon screen in the centre of the cylinder and putting the aluminium screen on top to prevent escape, and ended when the insect was removed. The chamber was dismantled, and the aluminium screen, vinyl cylinder, and nylon screen were washed in soapy water and rinsed thoroughly with tap water, and allowed to dry.

After a test, substrates were examined carefully and oviposition niches and other superficial signs of activity were drawn onto the data sheets; in some cases, photographs of the dishes were taken (Figure 10). Thickness of the outer bark and phloem of each plug were measured at two points, using a microscope with a grid ocular. The plugs were cut into 1 to 2 mm wide strips to find eggs. In some cases, plugs were soaked in water for 24 hr or more to make the cutting of the strips easier.

All tests were done under natural light, and temperature and humidity were monitored with a hygrothermograph.

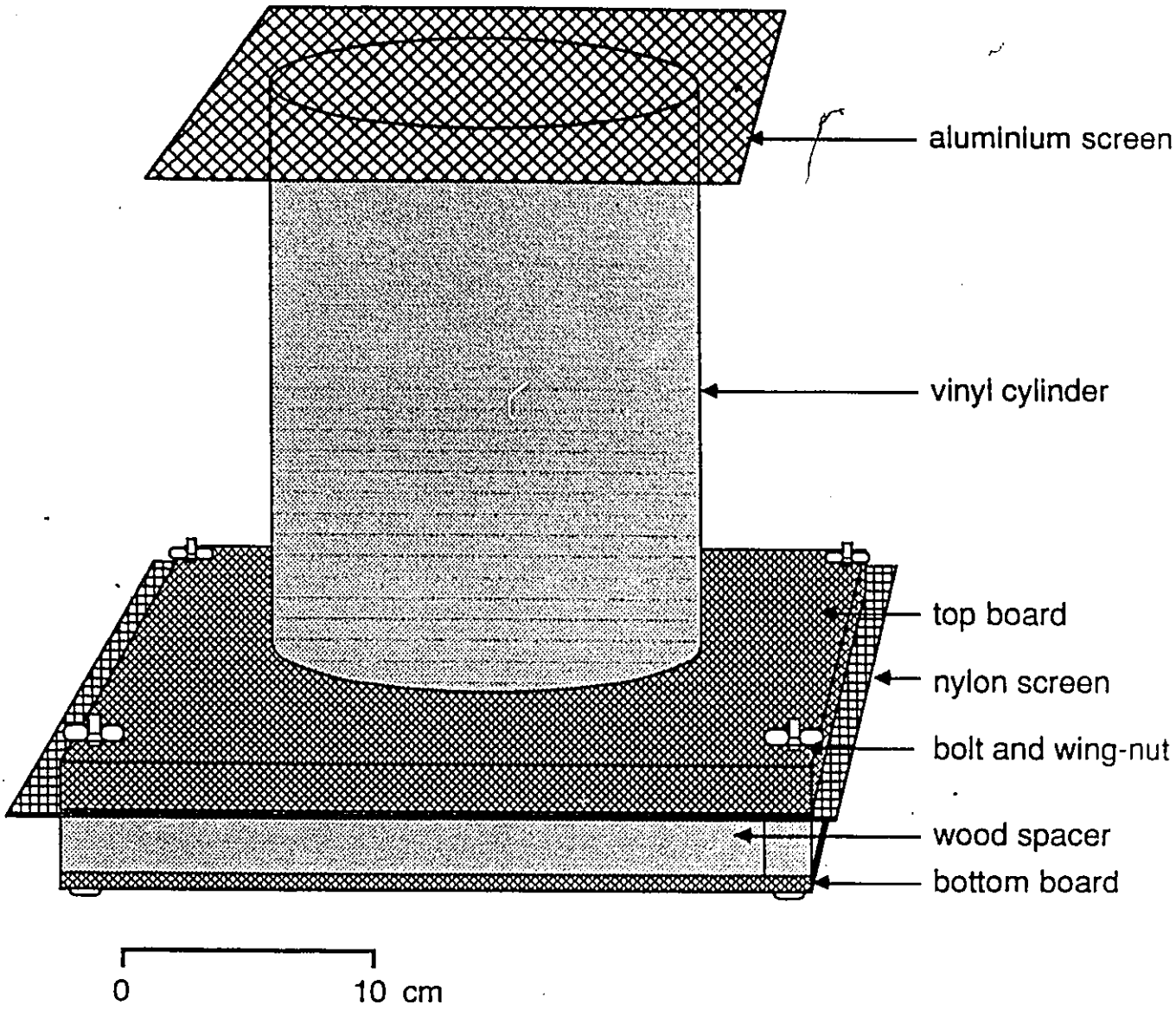


Figure 5. Side view of oviposition bioassay chamber.

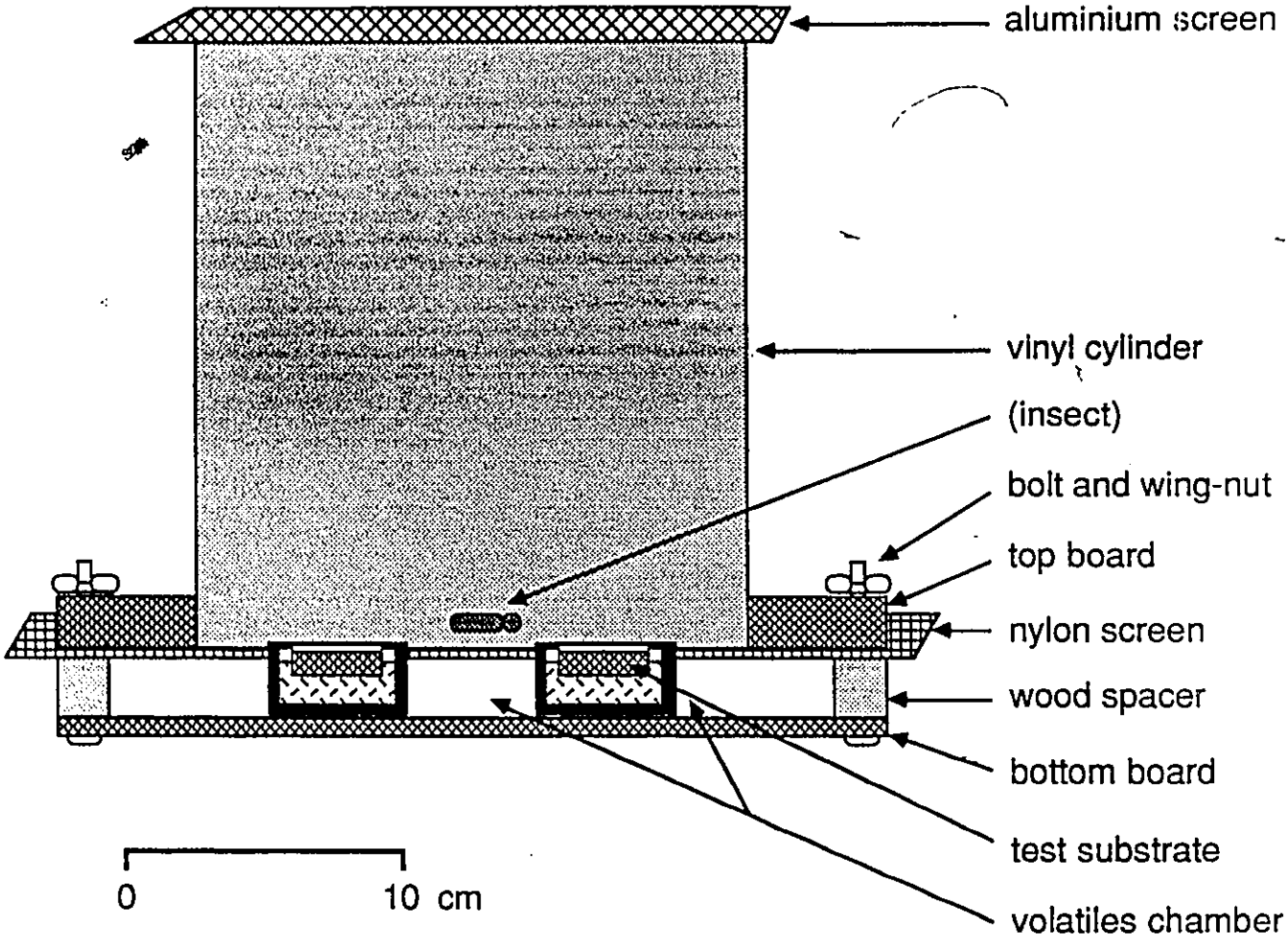


Figure 6. Cross section of oviposition bioassay chamber.

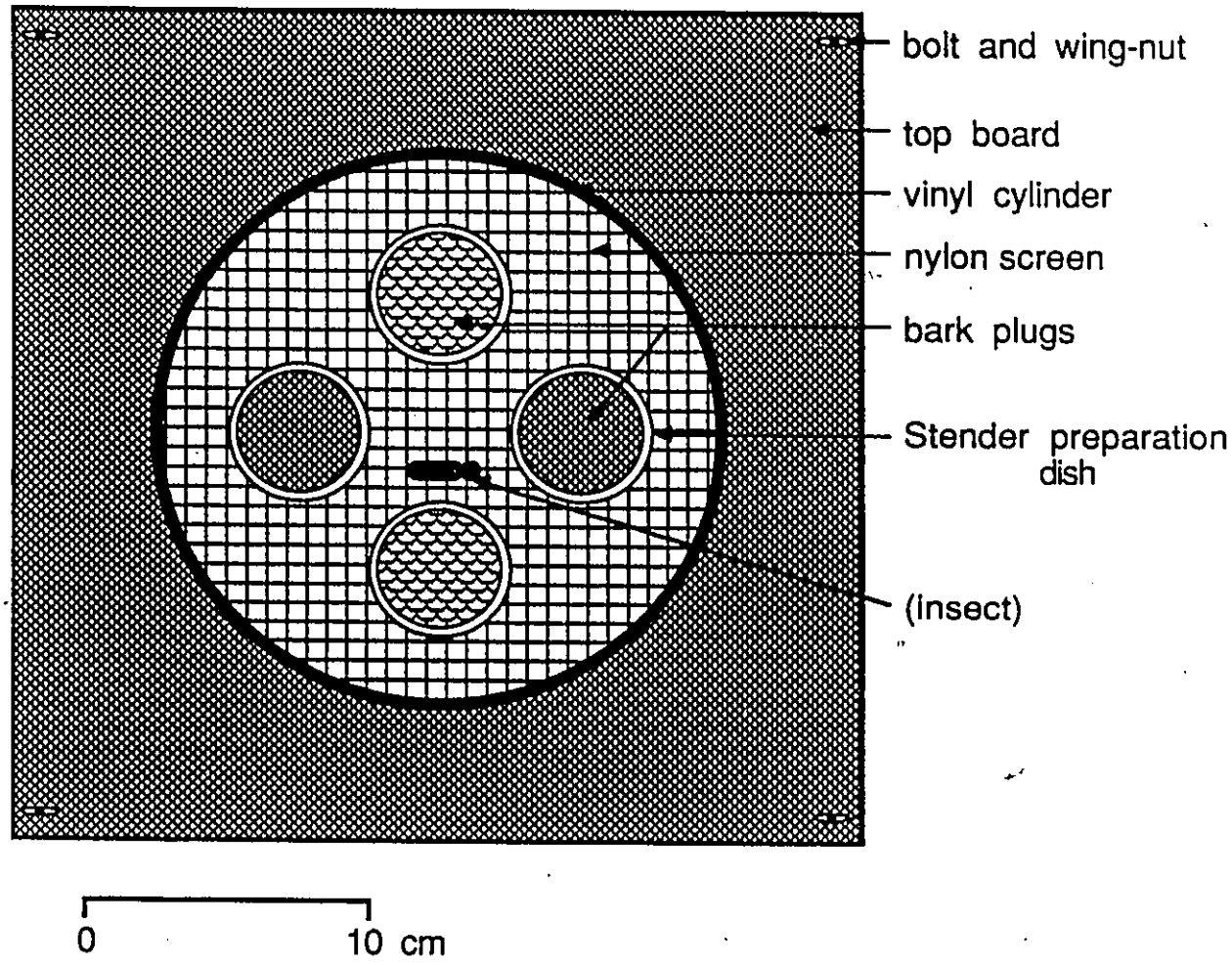


Figure 7. Top view of oviposition bioassay chamber (top aluminium screen removed).

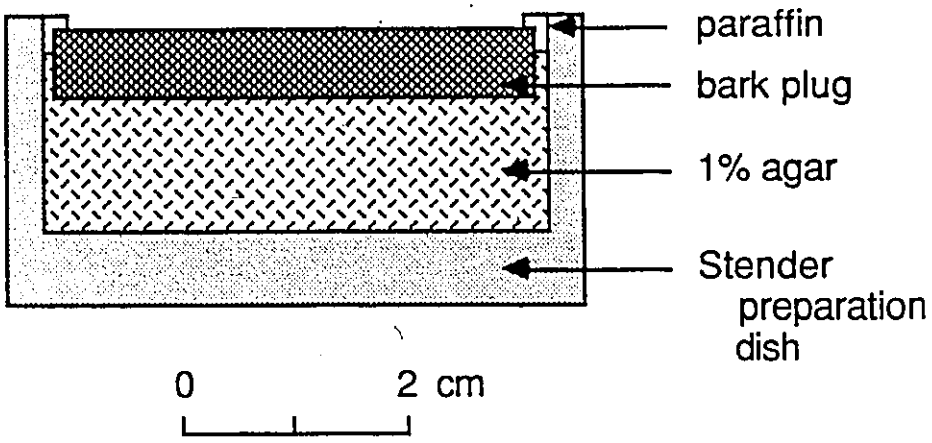


Figure 8. Cross section of preparation dish and test substrate (bark plug) used in oviposition bioassay chamber.

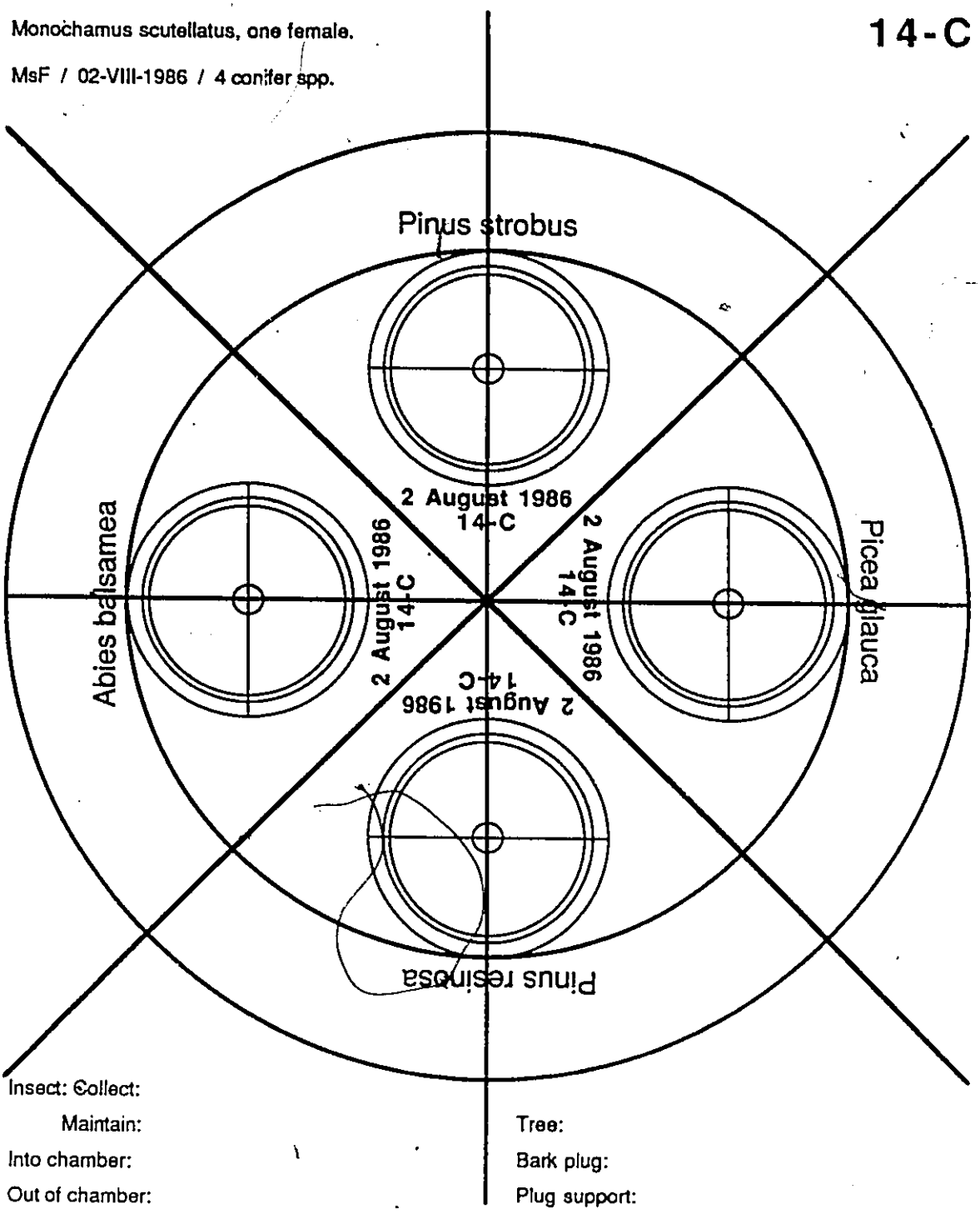


Figure 9. Data sheet showing positions of four preparation dishes with test substrates. Outer circle corresponds to outer edge of test arena. (75% of actual size)

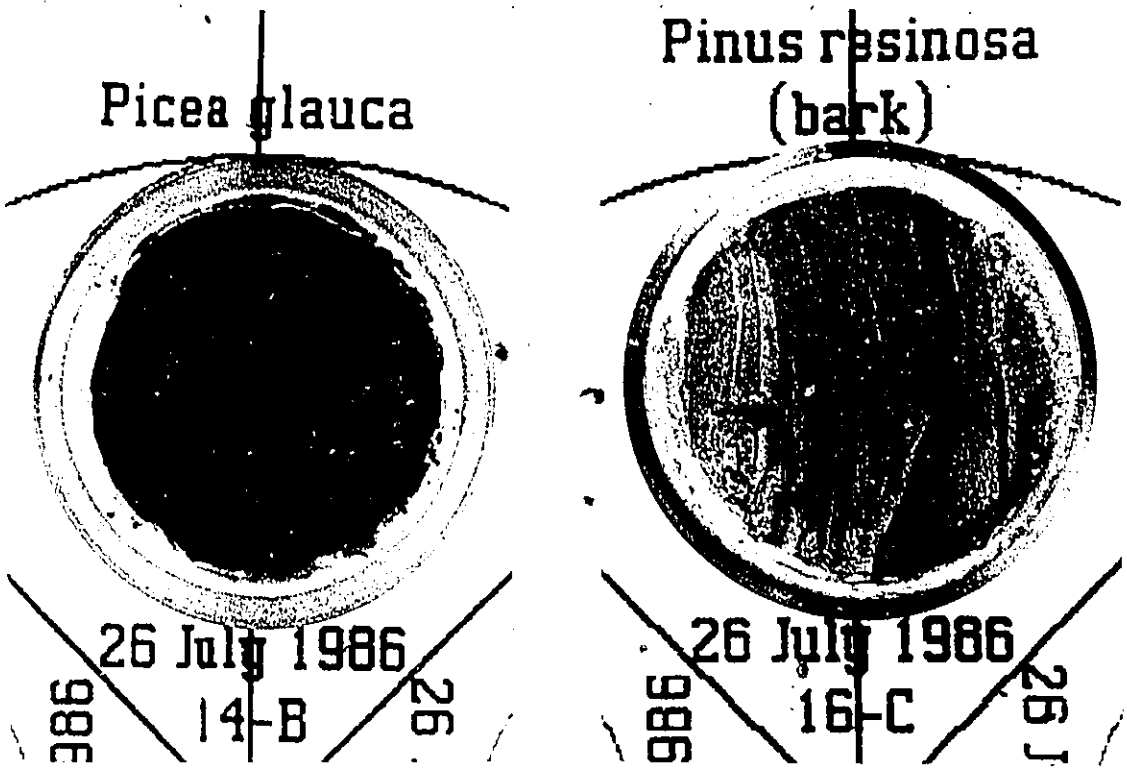


Figure 10. Photos of two test substrates taken at the end of a test, showing oviposition slits. Chambers were disassembled before taking photos.

Test substrates. As mentioned above, test substrates were offered in Stender preparation dishes (Figure 8). Substrates consisted of plugs of bark (4.2 cm diameter) cut with a 4.5 cm hole saw. The centre bit had been removed from the saw, and the saw was held in an electric drill using bolts and washer (Figure 14). The use of a drill guide permitted cutting of smooth holes. Holes were drilled into the xylem. A knife and chisel were used to lift the outer bark and phloem; with care, it was relatively easy to separate the plug from the xylem in the cambial region. The support medium was prepared and poured into the preparation dishes, to about 5 mm from the top, and allowed to cool slightly. Plugs were placed flat onto the medium and were pressed gently down to ensure removal of air bubbles below the plugs. A thread of molten paraffin was placed at the outer edge of the plug with a dropper; the end of the dropper was kept in the hot paraffin when not in use, preventing the congealing of the paraffin inside.

Various media were tested for use as support for the plugs. These included: 2.5% agar, 1% agar, 0.5% agar, 0.5% agar + 10% α–cellulose. The 1% agar proved to be the most convenient medium. It was sufficiently solid to prevent the formation of free water droplets on its surface. At the same time, it set slowly enough that it was possible to press the plugs onto the freshly congealed surface and obtain uniform adhesion of the agar on the bottom of the plugs. Beetles oviposited on suitable plugs regardless of the nature of the medium. Therefore, 1% agar solutions were used in all but the preliminary experiments.

Test trees. Because of their prevalence at the P.N.F.I. and in much of the eastern part of the range of *M. scutellatus*, tree species included in the tests were red pine, *Pinus resinosa* Aiton, white pine, *Pinus strobus* L., balsam fir, *Abies balsamea* (L.) Miller, white spruce, *Picea glauca* (Moench) Voss (Pinaceae), aspen, *Populus tremuloides* Michaux, largetooth aspen, *Populus grandidentata* Michaux (Salicaceae), white birch, *Betula papyrifera* Marshall (Betulaceae), and red maple, *Acer rubrum* L. (Aceraceae).

Healthy trees of these species were felled at the P.N.F.I., and logs about 1 m in length were cut; paraffin was applied to the ends of the logs to retard drying and checking. Logs were left outside for 7 to 10 days and were then placed in plastic bags and stored at 4° C.

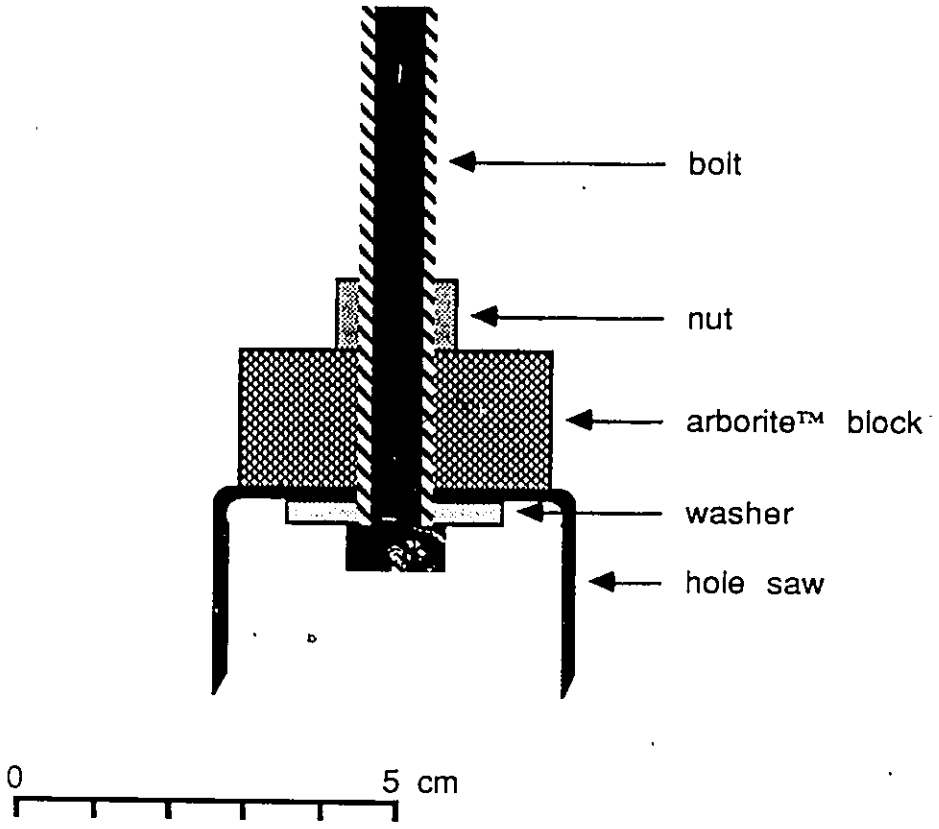


Figure 11. Hole saw drill bit, as modified to cut bark plugs for oviposition tests.

Test insects. Insects used in tests included *M. scutellatus* and *M. notatus*. Adults were captured at the P.N.F.I. Adults were collected into 1 litre containers, from piles of recently felled white pine, white spruce, red pine, and balsam fir. They were kept in cages (30 x 30 x 60 cm), with about 12 adults per cage, and were maintained at 20° C under natural light. Every day, fresh 50 cm boughs of red pine, white pine, white spruce, and balsam fir were placed in each of the cages as food for the adults, and were mist sprayed with distilled water.

B.1 — Preliminary experiments

In order to verify the suitability of the chambers and of the test protocol, and to make general observations of the activity of the beetles in the chambers, a few experiments were carried out with female *M. scutellatus*. Details of procedures are shown in Table 8.

An experiment was carried out using female *M. notatus*, in order to compare the number of eggs laid on bark plugs of four different host species. Data were analysed by Friedman test and Newman-Keuls test.

B.2 — Evaluation of conifer hosts

Chambers were prepared, offering four substrates in each chamber, consisting of bark plugs of *P. resinosa*, *P. strobus*, *A. balsamea*, and *P. glauca*. The experiment was replicated ten times, using ten different females. Each replicate ran from 13:00 EST to 11:00 EST of the next day. Data were analysed with a Friedman test, and significance of the differences between the ranks of the four tree species were verified by a Newman-Keuls test.

B.3 — Effects of volatiles

Bark chips were prepared by cutting pieces of bark from the same logs as those used for the plugs, and grinding the bark into chips using a blade grinder. Plastic weighing boats were filled with the chips (30 g of conifer chips or 60 g of aspen chips) and were placed in the chamber on the bottom board (below the nylon screen), with one boat in the centre and four between the four preparation dishes. The chambers, including chips, were assembled 30 minutes before the beginning of a test. Each experiment was replicated five times. The

following list outlines the tests involved; details of the experiments are shown in Tables 11, 12, and 13.

A) Choice of four hardwood species in each chamber; verify if presence of host volatiles can induce oviposition on non-host species (Table 11).

Test 1. *P. tremuloides* vs. *P. grandidentata* vs. *B. papyrifera* vs. *A. rubrum*, without bark volatiles.

Test 2. *P. tremuloides* vs. *P. grandidentata* vs. *B. papyrifera* vs. *A. rubrum*, with red pine volatiles.

Test 3. *P. tremuloides* vs. *P. grandidentata* vs. *B. papyrifera* vs. *A. rubrum*, with white spruce volatiles.

B) Choice of two hardwood and two conifer species; verify if presence of host (red pine) or non-host (aspen) volatiles affects choice of substrate (Table 12).

Test 4. *P. resinosa* vs. *P. glauca* vs. *P. tremuloides* vs. *A. rubrum*, without bark volatiles.

Test 5. *P. resinosa* vs. *P. glauca* vs. *P. tremuloides* vs. *A. rubrum*, with red pine volatiles.

Test 6 *P. resinosa* vs. *P. glauca* vs. *P. tremuloides* vs. *A. rubrum*, with aspen volatiles.

C) Choice of one host and one non-host species; outer bark and phloem of each plug were separated with a scalpel; test substrates were prepared by placing host outer bark on non-host phloem, or non-host outer bark on host phloem (Table 13).

Test 7. *P. resinosa* outer bark on *A. rubrum* phloem vs. *A. rubrum* outer bark on *P. resinosa* phloem.

Test 8. *P. glauca* outer bark on *A. rubrum* phloem vs. *A. rubrum* outer bark on *P. glauca* phloem.

Data for each of the 8 tests were analysed by Friedman tests and Newman-Keuls tests. In order to analyse effects of volatiles for tests 4 to 6, data for these tests were combined and analysed by a non-parametric two-factor Kruskal-Wallis test (Zar 1984, section 13.4),

considering the four substrate species as one factor and the three types of bark volatiles (no bark, red pine bark, aspen bark) as the second factor. In experiments 7 and 8, each chamber contained two dishes with each of the two treatments (test substrates); non-parametric Scheffé-type contrasts were done to verify differences between the two treatments.

B.4 — Importance of outer bark

One experiment involved offering four substrates for oviposition, namely red pine outer bark, red pine phloem, white spruce outer bark, and white spruce phloem. Outer bark and phloem were separated with a scalpel just before preparing the substrate dishes. A second experiment was run at the same time to compare the responses to whole bark of red pine and of white spruce (Table 14).

One other experiment was carried out using red pine bark with many bark scales (rough) and bark without scales (smooth). Plugs were cut from adjacent portions of the same tree. In a given replicate, two smooth and two rough substrates were offered for oviposition (Table 15).

Data were analysed by Friedman tests and Newman-Keuls tests and by Scheffé-type contrasts.

RESULTS

A — Attraction

A.1 — Importance of visual cues (trap evaluation)

More than 6000 beetles in 33 families were captured during the experiment (Table 2), with pipe traps capturing 75% of all beetles, interception traps 15%, and funnel traps 11%. Dominant families were the Scolytidae (accounting for 14.5% of all beetles captured), Elateridae (14.4%), Lampyridae (12.1%), Cerambycidae (12.0%), Cleridae (10.5%), Curculionidae (9.3%), Staphylinidae (4.0%), and Buprestidae (3.4%), with other families accounting for 19.8% of captures.

Species captured in significantly greater numbers in interception traps included *Serica atracapila* Kirby (Scarabaeidae), *Agriotes stabilis* (LeConte) (Elateridae), *Trichodes nutalli* (Kirby) (Cleridae), and *Isomira quadriastriata* Couper (Alleculidae).

For species of Buprestidae which feed on conifers, catches were 10 insects in interception traps, 27 in funnel traps, and 153 in pipe traps. For conifer-feeding Cerambycidae, catches were 53 in interception traps, 108 in funnel traps, and 551 in pipe traps. Catches of Clerid predators of conifer-feeding beetles were 62 in interception traps, 135 in funnel traps, and 371 in pipe traps.

Forest cover had a clear effect on trap captures for many species. Species of Buprestidae and most Elateridae were captured by traps in open fields in greater numbers than by traps set under the forest canopy, while melandryids were captured mostly in forested sites. Responses by species of Cleridae, Cerambycidae, Scolytidae, and Curculionidae varied (see Table 2). Of particular interest is the presence of *P. strobi* in large numbers in forested sites, even though most weevil attacks occurred in the open fields where many spruce seedlings had leaders damaged by the weevils.

Rates of vaporisation of the chemical baits were calculated for two trapping periods, from July 11 to July 18 and July 18 to July 25. Rates during these trapping periods are listed in Table 3 and Figure 12. Lowest rates were observed for funnel traps, and highest rates for

TABLE 2. TOTAL NUMBER OF BEETLES CAPTURED IN TRAPS, CLASSIFIED BY TRAP DESIGN AND FOREST COVER, CHALK RIVER, ONTARIO, 19 JUNE TO 8 AUGUST 1985.

Family and Species [a]	Total Number	Trap Design [b]			Cover [c]	
		Flight Intercept	Multiple Funnel	Sticky Pipe	Open	Forested
CARABIDAE						
Total Carabidae	117	63	20	34	98	19
HISTERIDAE						
Total Histeridae	41	5	4	32	19	22
LEIODIDAE						
Anisotoma sp.	25	4	13	8	21 *	4 *
SILPHIDAE						
Nicrophorus defodiens Mannerheim	27	1 a	2 a	24 b	3 **	24 **
Other Silphidae	20	8	1	11	10	10
Total Silphidae	47	9	3	35	13	34
STAPHYLINIDAE						
Total Staphylinidae	248	12	2	234	49	199
SCARABAEIDAE						
Serica atracapilla Kirby	54	45 b	3 a	6 a	7 **	47 **
Other Scarabaeidae	56	20	5	31	35	21
Total Scarabaeidae	110	65	8	37	42	68
BUPRESTIDAE						
Chalcophora virginiensis (Drury)	27	2	7	18	25	2
Chalcophora liberta (Germar)	9	1	4	4	9 ***	0 ***
Dicerca tenebrosa (Kirby)	38	2	5	31	27	11
Dicerca dumolini (Gory & Laporte)	2	0	0	2	1	1
Dicerca callosa callosa Casey	3	0	0	3	3	0
Dicerca tenebrica (Kirby)	14	0 a	2 ab	12 b	14 ***	0 ***
Buprestis salisburyensis (Herbst)	1	1	0	0	1	0
Buprestis maculipennis Gory	1	1	0	0	1	0
Buprestis maculativentris Say	13	0	6	7	11	2
Buprestis nuttali (Kirby)	1	0	0	1	1	0
Melanophila fulvoguttata (Harris)	13	0	0	13	13	0
Melanophila aeneola Melsheimer	1	0	0	1	0	1
Chrysobothris neopusilla Fisher	1	0	0	1	0	1
Chrysobothris adelpha Gemminger & Harold	1	0	0	1	1	0
Chrysobothris femorata (Olivier)	2	0	0	2	1	1

TABLE 2. *CONTINUED...*

Family and Species [a]	Total Number	Trap Design [b] Flight Intercept	Multiple Funnel	Sticky Pipe	Cover [c] Open	Forested
Chrysobothris cribraria Mannerheim	8	0 a	1 a	7 b	7	1
Chrysobothris verdigripennis Frost	14	1 a	2 a	11 b	13 ***	1 ***
Chrysobothris dentipes (Germar)	26	1 a	0 a	25 b	23 **	3 **
Chrysobothris scabripennis Castelnau & Gory	1	0	0	1	1	0
Chrysobothris trinervia (Kirby)	28	1 a	2 a	25 b	24 *	4 *
Chrysobothris sexsignata (Say)	6	0 a	0 a	6 a	2	4
Agrilus vittaticollis (Randall)	1	0	0	1	1	0
Total Buprestidae	211	10	29	172	179	32
ELATERIDAE						
Lacon brevicornis (LeConte)	10	1	3	6	8	2
Lacon obtecus (Say)	6	0	3	3	5	1
Limonius aurifer LeConte	6	4	0	2	0	6
Limonius aeger LeConte	5	3	1	1	0 **	5 **
Athous brightwelli (Kirby)	4	2	1	1	0 **	4 **
Athous rufifrons (Randall)	6	3	2	1	1 *	5 *
Denticollis denticornis (Kirby)	5	4	0	1	3	2
Ctenicera spinosa (LeConte)	1	0	1	0	1	0
Ctenicera hamata (Say)	3	1	0	2	0 *	3 *
Ctenicera propola propola (LeConte)	7	2	0	5	5	2
Ctenicera triundulata (Randall)	48	11	10	27	30	18
Ctenicera mediana (Germar)	50	16	9	25	43 **	7 **
Ctenicera inflata (Say)	1	0	1	0	1	0
Ctenicera hieroglypha (Say)	8	1	4	3	6 *	2 *
Ctenicera pulchra (LeConte)	5	4	0	1	5 *	0 *
Hemicrepidius memnonius (Herbst)	5	4	1	0	3	2
Hemicrepidius brevicollis (Candeze)	1	1	0	0	0	1
Dalopius cognatus Brown	3	2	1	0	3 *	0 *
Sericus brunneus (Linnaeus)	5	5	0	0	4	1
Agriotes stabilis (LeConte)	166	114 b	15 a	37 ab	131 ***	35 ***
Agriotes collaris (LeConte)	2	2	0	0	1	1
Agriotes limosus (LeConte)	17	8	3	6	15 **	2 **
Ampedus pullus Germar	64	0 a	1 a	63 b	51	13
Ampedus sanguinipennis (Say)	6	2	0	4	5	1
Ampedus apicatus (Say)	6	0	3	3	5	1
Ampedus evansi Brown	13	1	5	7	9 *	4 *
Ampedus mixtus (Herbst)	1	1	0	0	1	0
Ampedus luctuosus (LeConte)	5	2	3	0	4	1

TABLE 2. *CONTINUED...*

Family and Species [a]	Total Number	Trap Design [b] Flight Intercept	Multiple Funnel	Sticky Pipe	Cover [c] Open	Forested
Ampedus melsheimeri (Leng)	8	2	6	0	1 *	7 *
Ampedus rubricollis (Herbst)	1	1	0	0	1	0
Melanotus castanipes (Paykull)	285	41 a	82 a	162 b	117 *	168 *
Melanotus similis (Kirby)	24	15 b	9 b	0 a	17	7
Cardiophorus convexulus LeConte	6	4	2	0	6 **	0 **
Other Elateridae	111	0	0	111	63	48
Total Elateridae	894	257	166	471	545	349
LAMPYRIDAE						
Ellychnia corrusca (Linnaeus)	468	9 a	6 a	453 b	133 *	335 *
Lucidoda atra (Fabricius)	242	4 a	6 a	232 b	227 ***	15 ***
Pyractonema angulata (Say)	22	0 a	1 a	21 b	12	10
Photuris pennsylvanica (DeGeer)	19	2	0	17	16	3
Total Lampyridae	751	15	13	723	388	363
CANTHARIDAE						
Cantharis rotundicollis Say	84	4 a	1 a	79 b	34	50
Other Cantharidae	112	6	0	106	75	37
Total Cantharidae	196	10	1	185	109	87
LYCIDAE						
Total Lycidae	34	2	2	30	13	21
CLERIDAE						
Phyllobaenus humeralis difficilis (LeConte)	1	0	0	1	1	0
Thanasimus dubius (Fabricius)	338	49 a	101 b	188 b	37 ***	301 ***
Thanasimus undulatus (Say)	85	10 a	22 a	53 b	2 ***	83 ***
Thanasimus undulatus nubilus Klug	13	1	2	10	1	12
Enoclerus nigripes rufiventris (Spinola)	33	1 a	2 a	30 b	10	23
Enoclerus nigrifrons gerhardi Wolcott	77	0 a	2 a	75 b	77 ***	0 ***
Trichodes nuttalli (Kirby)	83	78 b	4 a	1 a	83 ***	0 ***
Phlogistosternus dislocatus (Say)	21	1 a	6 ab	14 b	3 *	18 *
Total Cleridae	651	140	139	372	214	437
COCCINELLIDAE						
Total Coccinellidae	57	3	3	51	39	18

TABLE 2. *CONTINUED...*

Family and Species [a]	Total Number	Trap Design [b] Flight Intercept	Multiple Funnel	Sticky Pipe	Cover [c] Open	Forested
CEPHALOIDAE						
Cephaloon lepturides Newman	30	27	2	1	27 *	3 *
ALLECULIDAE						
Isomira quadristriata Couper	68	55 b	7 a	6 a	21	47
Hymenorus niger Melsheimer	31	14 b	17 b	0 a	29 **	2 **
Other Alleculidae	7	2	4	1	7	0
Total Alleculidae	106	71	28	7	57	49
MELANDRYIDAE						
Serropalpus sp.	133	18	13	102	9 ***	124 ***
Other Melandryidae	10	1	6	3	6	4
Total Melandryidae	143	19	19	105	15	128
MORDELLIDAE						
Tomoxia inclusa LeConte	66	3 a	12 a	51 b	53 **	13 **
CERAMBYCIDAE						
Tragosoma depsarius (Linnaeus)	1	0	0	1	1	0
Asemum striatus (Linnaeus)	140	8 a	29 a	103 b	26 **	114 **
Tetropium cinnamopterum cinnamopterum Kirby	33	3	3	27	0 ***	33 ***
Leptura sp.?	1	0	0	1	0	1
Leptura sp.?	1	0	0	1	0	1
Evodinus monticola monticola (Randall)	1	0	1	0	0	1
Anthophylax attenuatus (Haldeman)	1	0	1	0	0	1
Rhagium inquisitor (Linnaeus)	33	1 a	6 a	26 b	18	15
Acmaeops proteus proteus (Kirby)	238	16 a	9 a	213 b	92	146
Pygoleptura nigrella nigrella (Say)	7	1	1	5	4	3
Typocerus sparsus LeConte	2	2	0	0	2	0
Trachysida aspera brevifrons (Howden)	3	1	0	2	1	2
Stictoleptura canadensis canadensis (Olivier)	1	0	1	0	1	0
Trigonarthris proxima (Say)	4	0	0	4	2	2
Cosmosalia chrysocoma (Kirby)	4	2	0	2	4	0
Pronocera collaris collaris (Kirby)	1	0	0	1	1	0
Phymatodes dimidiatus (Kirby)	1	0	0	1	0	1
Xylotrechus sagittatus sagittatus (Germar)	5	2	0	3	0 **	5 **
Xylotrechus undulatus (Say)	135	13 a	41 a	81 b	43	92
Neoclytus muricatulus muricatulus (Kirby)	4	0	0	4	4	0

TABLE 2. *CONTINUED...*

Family and Species [a]	Total Number	Trap Design [b] Flight Intercept	Multiple Funnel	Sticky Pipe	Cover [c] Open	Forested
Clytus ruricola (Olivier)	20	0 a	0 a	20 b	2	18
Cyrtophorus verrucosus (Olivier)	2	0	0	2	1	1
Monochamus scutellatus scutellatus (Say)	85	2 a	15 a	68 b	48	37
Monochamus notatus (Drury)	5	0	1	4	1	4
Pogonocherus penicillatus LeConte	5	0	0	5	4	1
Saperda obliqua Say	1	0	0	1	1	0
Saperda lateralis Fabricius	1	0	0	1	0	1
Hyperplatys aspersa (Say)	1	1	0	0	1	0
Amniscus sexguttata (Say)	1	1	0	0	1	0
Neacanthocinus pusillus (Kirby)	5	1	1	3	0 *	5 *
Total Cerambycidae	742	54	109	579	258	484
SCOLYTIDAE						
Scolytus piceae (Swaine)	4	0	0	4	3	1
Hylurgops pinifex (Fitch)	44	1 a	2 a	41 b	3 **	41 **
Hylastes porculus Erichson	126	21 a	19 a	86 b	29 **	97 **
Dendroctonus valens LeConte	19	4	4	11	10	9
Polygraphus rufipennis (Kirby)	47	2 a	1 a	44 b	0 ***	47 ***
Trypodendron lineatum (Olivier)	16	1 a	0 a	15 b	2 *	14 *
Dryocetes autographus (Ratzeburg)	385	33 a	41 a	311 b	303	82
Dryocetes affaber (Mannerheim)	25	1 a	0 a	24 b	18	7
Xyleborus dispar (Fabricius)	1	1	0	0	1	0
Pityogenes hopkinsi Swaine	5	0	0	5	0 *	5 *
Orthotomicus caelatus (Eichhoff)	189	2 a	1 a	186 b	67	122
Ips pini (Say)	22	3 a	3 a	16 a	4	18
Ips calligraphus (Germar)	1	0	0	1	0	1
Ips grandicollis (Eichhoff)	14	0 a	0 a	14 b	5	9
Total Scolytidae	898	69	71	758	445	453
CURCULIONIDAE						
Hylobius pales (Herbst)	64	10 a	4 a	50 b	33	31
Pissodes strobi (Peck)	489	46 a	7 a	436 b	145	344
Other Curculionidae	26	1	0	25	18	8
Total Curculionidae	579	57	11	511	196	383
OTHER COLEOPTERA	259	20	6	233	113	146
TOTAL COLEOPTERA	6205	915	661	4629	2893	3312

TABLE 2. *CONCLUDED.*

[a] Species with a total of 20 or more individuals captured (most families); all species are listed for families Buprestidae, Elateridae, Cleridae, Cerambycidae, and Scolytidae.

[b] For each species, if Friedman test (corrected for ties) showed trap design effects (α=0.05), treatments followed by the same letter are not significantly different (P>0.05), non-parametric Newman-Keuls test corrected for ties. Three treatments with 12 replicate blocks.

[c] For each species, treatments followed by asterisks are significantly different (* for P<0.10, ** for P<0.05, *** for P<0.01), Mann-Whitney test corrected for ties. Two treatments with 18 replicates.

TABLE 3. RATES OF VAPORISATION (G·DAY^{-1}·TRAP^{-1}) OF ETHANOL AND MONOTERPENE BAITS, AS DETERMINED GRAVIMETRICALLY FOR THE TRAPPING PERIODS 11 JULY TO 18 JULY 1985 AND 18 JULY TO 25 JULY 1985. [a]

	TRAP TYPES								
	Flight Interception			Multiple Funnel			Sticky Stovepipe		
	Open	Forest	All	Open	Forest	All	Open	Forest	All
Ethanol:									
Mean=	1.799	1.397	1.598	1.635	1.249	1.442	2.353	1.615	1.984
S.D.=	0.238	0.242	0.312	0.337	0.190	0.332	0.173	0.338	0.459
95% C.I.=	0.151	0.154	0.132	0.214	0.121	0.140	0.110	0.215	0.194
n=	12	12	24	12	12	24	12	12	24
Monoterpenes:									
Mean=	1.282	0.907	1.095	1.169	0.803	0.986	1.427	1.046	1.237
S.D.=	0.184	0.240	0.284	0.221	0.162	0.266	0.110	0.311	0.300
95% C.I.=	0.117	0.153	0.120	0.140	0.103	0.112	0.070	0.198	0.127
n=	12	12	24	12	12	24	12	12	24

[a] Means, standard deviations (S.D.), 95% confidence intervals (95% C.I.), and sample sizes (n) for traps in open sites, forested sites, and both open and forested sites.

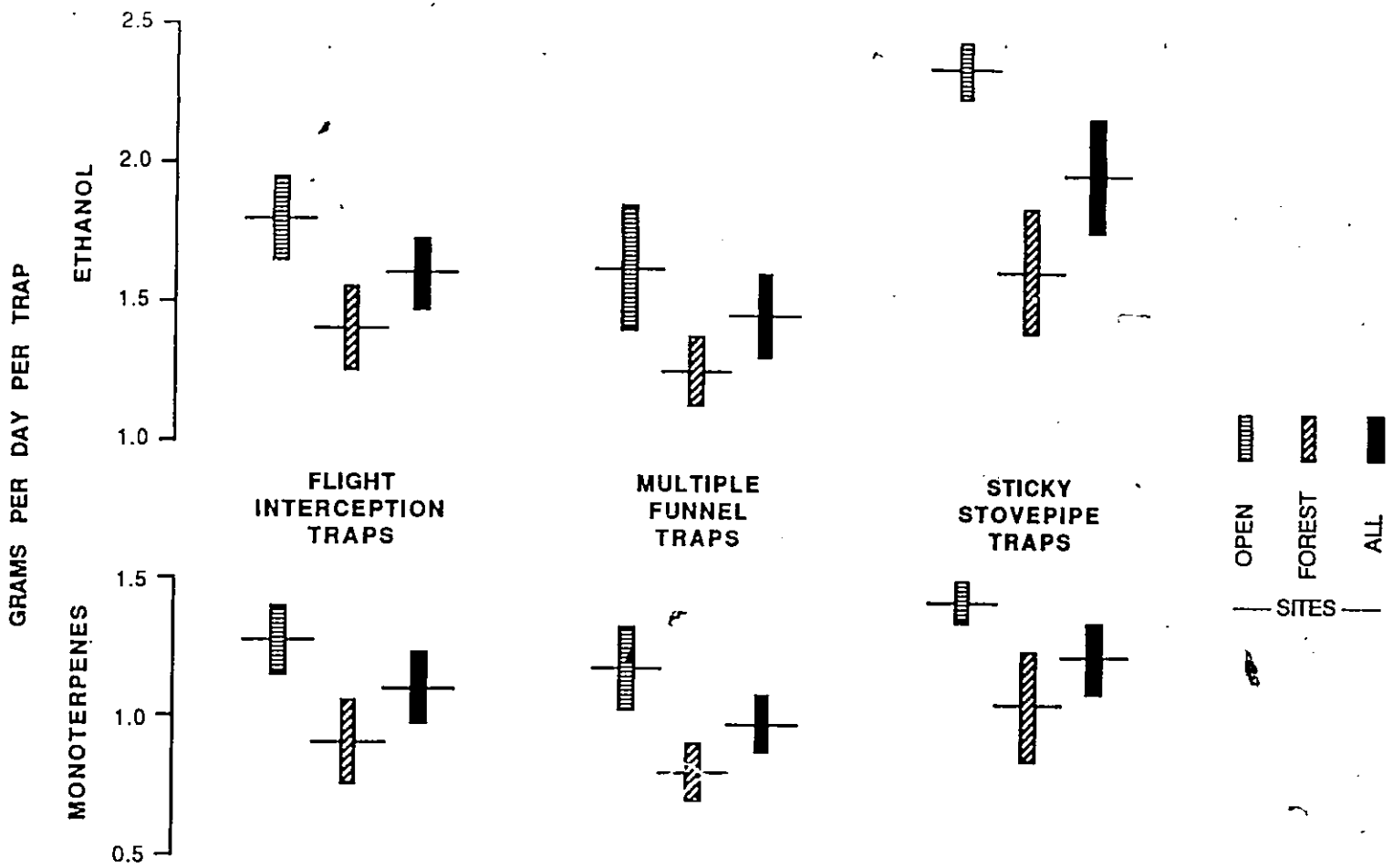


Figure 12. Rates of vaporisation of ethanol and monoterpene baits for flight interception traps, multiple funnel traps, and sticky stovepipe traps, as determined gravimetrically for the trapping periods 11 July to 18 July and 18 July to 25 July 1985. For each trap type and chemical bait combination, results show means and 95 % confidence intervals of rates for traps in open sites (n = 12), forested sites (n = 12), and the combination of both open and forested sites (n = 24).

pipe traps (25% higher than funnel trap rate for monoterpenes, 38% higher than funnel trap rate for ethanol).

A.2 — Importance of chemical cues

Rates of vaporisation of the chemical baits for all three experiments are given in Table 4. In Experiment 2, given the elution rates for the α–pinene and the minor monoterpenes, and the composition of the minor monoterpene blend, terpenes were released from traps baited with both α–pinene and minor monoterpenes at a mean rate of 0.59 $g \cdot day^{-1} \cdot trap^{-1}$ and in a ratio of about 73% α–pinene, 12% β–pinene, 4% each of carene, limonene and myrcene, and 3% camphene.

Experiments 1 and 2. Results are shown in Table 5 (Experiment 1) and Table 6 (Experiment 2). Species of Buprestidae generally did not respond to the chemicals tested. While the low number of *Buprestis maculativentris* Say captured in Experiment 1 did not yield significant results, data for Experiment 2 indicate treatment effects. However, the ranks of neither ethanol-baited traps (lowest rank) or traps baited with α-pinene and ethanol (highest rank) were significantly different from control traps. For the Melandryid *Serropalpus* sp., traps baited with the complete monoterpene blend (α–pinene and minor monoterpenes) and ethanol ranked highest in both experiments, with these compounds possibly acting synergistically as indicated by the Scheffé contrasts in Experiment 1.

Four species of Cerambycidae showed definite responses to the treatments. In Experiment 2, *Asemum striatum* (L.) was found to be attracted by α–pinene, with minor monoterpenes exerting no apparent effect on attraction; while Scheffé contrasts indicate a possible synergism between the α–pinene and ethanol ($P<0.05$ for treatments with both compounds vs other treatments), an examination of rank sums and Newman-Keuls test results show that the attraction is probably due simply to the presence of α–pinene ($P<0.01$ for the contrast between treatments with α–pinene vs treatments without). Both experiments indicated significant treatment effects for *Acmaeops proteus proteus* (Kirby), due largely to the presence of monoterpenes (Experiment 1); rank sums and Newman-Keuls test indicate that the α–pinene may account for much of the attraction to the monoterpenes (Experiment 2). *Xylotrechus*

TABLE 4. RATES OF VAPORISATION ($G \cdot DAY^{-1} \cdot TRAP^{-1}$) OF BAITS FOR THREE EXPERIMENTS EVALUATING CHEMICAL ATTRACTANTS, CHALK RIVER, ONTARIO. [a]

Experiment	Terpenes				Ethanol		
	Type	Mean	S.D.	n	Mean	S.D.	n
1 [b] 12 June - 5 Aug. 1986	blend	0.94	0.46	31	1.84	0.48	32
2 [c] 15 June - 16 Aug. 1984	α–pinene	0.43	0.09	30	1.82	0.37	30
	minor terpenes	0.16	0.05	30			
3 [b] 7 July - 5 Aug. 1986	blend	1.59	0.61	8	2.57	0.53	16
	turpentine	1.36	0.49	8			

[a] Mean, standard deviation (S.D.) and sample size (n),

[b] Dispensers (per trap): terpenes, two 20 ml vials with wicks; ethanol, two 20 ml vials. Traps: sticky stovepipe traps.

[c] Dispensers (per trap): α–pinene, two 7 ml vials; minor terpenes, one 7 ml vial; ethanol, two 11 ml vials. Traps: sticky stovepipe traps and multiple funnel traps.

TABLE 5. RESULTS OF FIELD TRAPPING EXPERIMENT USING BAITED STICKY STOVEPIPE TRAPS TO DETERMINE THE EFFECTS OF MONOTERPENES AND ETHANOL ON BEETLE ATTRACTION, CHALK RIVER, ONTARIO, 12 JUNE TO 5 AUGUST 1986 (EXPERIMENT 1)

Family and Species [a]		Total number (#) and rank total (R) per treatment [b] Ø	E	T	TE	Friedman's Chi-square [c]	Contrasts [d] (T+TE) vs Ø	(T+TE) vs (Ø+E)	TE vs (Ø+E)	TE vs (Ø+E+T)
CARABIDAE	#	13	20	17	17					
SCARABAEIDAE	#	13	6	18	9					
BUPRESTIDAE										
Chalcophora liberta	#	0	1	2	2	4.71	n.s.	n.s.	n.s.	n.s.
	R	7.5	9.5	11.5	11.5					
Dicerca tenebrosa	#	6	3	4	9	5.00	n.s.	n.s.	n.s.	n.s.
	R	11.5	7	8.5	13					
Dicerca callosa	#	2	0	2	2	2.20	n.s.	n.s.	n.s.	n.s.
	R	10.5	8	10.5	11					
Buprestis maculativentris	#	2	1	3	4	1.40	n.s.	n.s.	n.s.	n.s.
	R	10.5	8.5	10	11					
Melanophila fulvoguttata	#	0	0	5	6	6.25	n.s.	n.s.	n.s.	n.s.
	R	7.5	7.5	12.5	12.5					
Chrysobothris rugosiceps	#	0	2	0	3	5.82	n.s.	n.s.	n.s.	n.s.
	R	8	11.5	8	12.5					
Chrysobothris dentipes	#	2	1	8	2	5.40	n.s.	n.s.	n.s.	n.s.
	R	9.5	8	13	9.5					
Chrysobothris scabripennis	#	0	1	5	1	3.00	n.s.	n.s.	n.s.	n.s.
	R	8.5	10	11.5	10					
Chrysobothris sexsignata	#	1	1	2	2	0.33	n.s.	n.s.	n.s.	n.s.
	R	9.5	9.5	10.5	10.5					
Other Buprestidae	#	2	7	9	5					
ELATERIDAE	#	65	90	78	94					
LAMPYRIDAE	#	57	45	43	93					
CANTHARIDAE	#	10	15	20	10					
CLERIDAE										
Thanasimus dubius	#	2	7	37	98	11.68***	0.05	0.01	0.01	0.10
	R	5a	7a	12ab	16b					
Thanasimus undulatus	#	0	1	11	9	7.50*	n.s	0.10	n.s.	n.s.
	R	7a	8a	14a	11a					
Thanasimus undulatus nubilus	#	3	5	1	3	5.40	n.s.	n.s.	n.s.	n.s.
	R	9.5	13	8	9.5					
Enoclerus nigrifrons gerhardi	#	2	4	17	19	8.82**	0.10	0.05	n.s.	n.s.
	R	6a	7a	14a	13a					
Trichodes nuttalli	#	1	1	1	2	0.60	n.s.	n.s.	n.s.	n.s.
	R	9.5	9.5	10	11					
Phlogistosternus dislocatus	#	0	3	0	6	6.00	n.s.	n.s.	n.s.	n.s.
	R	8	11	8	13					
Other Cleridae	#	2	1	0	1					
ALLECULIDAE	#	50	21	10	25					

TABLE 5. *CONCLUDED.*

Family and Species [a]		Total number (#) and rank total (R) per treatment [b] Ø	E	T	TE	Friedman's Chi-square [c]	Contrasts [d] (T+TE) vs Ø	(T+TE) vs (Ø+E)	TE vs (Ø+E)	TE vs (Ø+E+T)
MELANDRYIDAE										
Serropalpus sp.	#	1	11	80	124	8.04**	n.s.	n.s.	0.05	0.10
	R	7a	8ab	10.5ab	14.5b					
Other Melandryidae	#	0	0	2	0					
MORDELLIDAE	#	10	16	17	16					
CERAMBYCIDAE										
Asemum striatum	#	0	4	6	10	3.88	n.s.	n.s.	n.s.	n.s.
	R	7	9.5	11.5	12					
Tetropium cinnamopterum	#	0	0	1	4	3.00	n.s.	n.s.	n.s.	n.s.
	R	9	9	10.5	11.5					
Acmaeops proteus	#	2	5	12	18	9.53**	0.05	0.05	0.10	n.s.
	R	5a	8a	13b	14b					
Pygoleptura nigrella	#	3	0	2	0	7.36*	n.s.	n.s.	n.s.	n.s. [f]
	R	13.5a	7.5a	11.5a	7.5a					
Xylotrechus undulatus	#	0	3	27	34	10.54***	0.05	0.01	0.10	n.s. [e]
	R	4.5a	7.5ab	14b	14b					
Monochamus scutellatus	#	0	0	8	33	8.77**	n.s.	0.05	0.10	n.s.
	R	7a	7a	12a	14a					
Hyperplatys aspersa	#	3	2	1	0	3.00	n.s.	n.s.	n.s.	n.s.
	R	11.5	10.5	9.5	8.5					
Other Cerambycidae	#	4	10	9	15					
CURCULIONIDAE										
Pissodes strobi	#	1	2	27	21	9.00**	0.10	0.05	n.s.	n.s.
	R	6a	7a	13.5a	13.5a					
Other Curculionidae	#	1	5	0	7					
SCOLYTIDAE										
Dryocetes autographus	#	1	2	1	53	11.00***	n.s.	n.s.	0.05	0.01
	R	7.5a	9a	7.5a	16b					
Orthotomicus caelatus	#	0	0	0	6	9.00**	n.s.	n.s.	0.05	0.05
	R	8.5a	8.5a	8.5a	14.5a					
Other Scolytidae	#	1	2	2	14					
OTHER COLEOPTERA	#	57	40	43	50					

[a] Species of wood-boring or predatory families with a total of 5 or more individuals captured.

[b] Treatments: Ø = blank control, E = ethanol, T = monoterpene blend, TE = monoterpene blend and ethanol. Four treatments replicated in four blocks. Rank totals in a row followed by the same letter are not significantly different ($P>0.05$), non-parametric Newman-Keuls test corrected for ties.

[c] Corrected for ties. * for $P<0.10$, ** for $P<0.05$, *** for $P<0.01$.

[d] Non-parametric Scheffé-type contrasts. Significance probability is less than value indicated, or is not significant (n.s.).

[e] $P<0.10$ for T vs (Ø + E).

[f] $P<0.10$ for (Ø + T) vs (E + TE), $P<0.10$ for Ø vs (E + TE).

TABLE 6. RESULTS OF FIELD TRAPPING EXPERIMENT USING BAITED STICKY STOVEPIPE TRAPS AND MULTIPLE FUNNEL TRAPS TO DETERMINE THE EFFECTS OF α–PINENE AND MINOR MONOTERPENES ON BEETLE ATTRACTION, CHALK RIVER, ONTARIO, 15 JUNE TO 16 AUGUST 1984 (EXPERIMENT 2).

Family and Species [a]		Total number (#) and rank total (R) per treatment [b]								Friedman's Chi-square [c]	Contrasts [d]
		Ø	E	M	ME	A	AM	AE	AME		
BUPRESTIDAE											
Chalcophora virginiensis	#	7	12	9	5	7	9	9	9	4.82	
	R	42	51.5	49	34.5	44	46.5	46	46.5		
Dicerca tenebrosa	#	21	20	9	18	22	25	22	27	10.46	
	R	49.5	44.5	33.5	43.5	41.5	48.5	39.5	59.5		
Dicerca callosa	#	1	1	2	2	5	1	1	2	10.49	
	R	42	42	42.5	46	58	41.5	42	46		
Dicerca tenebrica	#	6	4	3	6	2	4	5	2	4.53	
	R	49	45	41.5	51.5	40	48	46.5	38.5		
Buprestis maculativentris	#	17	7	14	26	17	25	26	18	15.32**	
	R	46ab	28.5a	37ab	50ab	39ab	53.5ab	61.5b	44.5ab		
Melanophila fulvoguttata	#	2	5	1	2	6	6	4	13	13.04*	
	R	40a	45.5a	38.5a	42a	48a	49a	42a	55a		
Chrysobothris floricola	#	8	4	9	8	11	11	7	8	6.05	
	R	46.5	37.5	47	43	48.5	50.5	43	44		
Chrysobothris rugosiceps	#	8	14	10	9	6	9	12	17	10.34	
	R	41	50.5	46	42	38.5	43.5	43	55.5		
Chrysobothris femorata	#	2	5	10	7	4	1	7	4	8.67	
	R	38	46	53.5	47.5	43	36.5	49.5	46		
Chrysobothris dentipes	#	2	2	6	6	6	3	6	14	10.46	
	R	38.5	38.5	45.5	46	48	42	45	56.5		
Chrysobothris scabripennis	#	4	2	0	1	2	1	1	1	2.33	
	R	47.5	46.5	41.5	44.5	45.5	45.5	44.5	44.5		
Chrysobothris sexsignata	#	1	4	0	4	5	3	5	5	8.40	
	R	40	47	38	48	49	43	44	51		
Other Buprestidae	#	12	18	7	6	10	16	15	11		
CLERIDAE											
Phyllobaenus humeralis difficilis	#	3	3	1	4	2	1	0	3	5.99	
	R	47.5	47.5	41	49.5	45	43	39	47.5		
Thanasimus dubius	#	0	0	1	1	3	9	13	10	19.67***	A(4vs4)**, AE(2vs6)*
	R	37.5a	37.5a	40ab	40ab	47ab	48ab	57b	53ab		
Thanasimus undulatus nubilus	#	0	2	3	2	0	4	3	2	9.34	
	R	38.5	45	48	44	38.5	52	49	45		

TABLE 6. *CONTINUED...*

Family and Species [a]		Total number (#) and rank total (R) per treatment [b]								Friedman's Chi-square [c]	Contrasts [d]
		Ø	E	M	ME	A	AM	AE	AME		
Enoclerus nigripes rufiventris	#	6	13	10	15	18	19	26	12	18.51***	A(4vs4)**
	R	33.5a	43ab	35a	38.5ab	51ab	49ab	60b	50ab		
Enoclerus nigrifrons gerhardi	#	1	8	4	9	15	17	21	21	17.25**	A(4vs4)**
	R	33a	40ab	35ab	43ab	50.5ab	51ab	51ab	56.5b		
Trichodes nutalli	#	8	3	4	5	2	7	3	5	6.62	
	R	52	40.5	44	46	37	51.5	41	48		
Other Cleridae	#	5	4	0	4	3	3	1	2		
MELANDRYIDAE											
Dircaea quadrimaculata	#	8	5	6	3	2	2	3	2	11.91	
	R	58	48	49	44	39.5	39	43.5	39		
Serropalpus sp.	#	0	5	4	12	6	16	21	18	15.19**	
	R	32a	41.5ab	39.5ab	41.5ab	45.5ab	55ab	49ab	56b		
Other Melandryidae	#	2	3	2	2	2	3	1	1		
CERAMBYCIDAE											
Asemum striatum	#	3	2	2	0	16	12	22	14	32.79***	A(4vs4)***, AE(2vs6)**
	R	36.5a	34a	34a	32a	58b	46.5ab	66b	53ab		
Rhagium inquisitor	#	9	3	7	5	12	3	8	27	6.66	
	R	43	41.5	44	43	50	39.5	49	50		
Acmaeops proteus	#	1	7	4	7	4	13	24	6	19.84***	
	R	32.5a	44ab	40.5ab	46ab	41.5ab	52ab	63b	40.5ab		
Pygoleptura nigrella	#	2	0	5	2	3	5	2	1	9.91	
	R	43.5	35.5	51.5	43.5	47.5	55.5	43.5	39.5		
Stictoleptura canadensis	#	1	3	0	5	1	2	1	1	9.37	
	R	42.5	50.5	38.5	54.5	42.5	46.5	42.5	42.5		
Trigonarthris proxima	#	2	2	3	4	1	2	1	1	6.40	
	R	45	45	49	53	41	45	41	41		
Xylotrechus undulatus	#	0	0	7	8	15	25	14	23	26.78***	A(4vs4)**, AM(2vs6)**, AorM(6vs2)**
	R	27.5a	27.5a	41.5ab	44.5ab	54.5ab	60b	43ab	61.5b		
Neoclytus muricatulus	#	1	3	3	2	5	2	4	1	5.66	
	R	41	44.5	44.5	45	50.5	42.5	48.5	43.5		
Monochamus scutellatus	#	4	7	9	14	20	12	18	21	25.93***	AE(2vs6)***, A(4vs4)*, AorM(6vs2)*
	R	32a	32a	40.5ab	45ab	46.5ab	41.5ab	60b	62.5b		
Other Cerambycidae	#	1	5	4	6	6	4	1	5		

TABLE 6. *CONCLUDED.*

Family and Species [a]		Total number (#) and rank total (R) per treatment [b] Ø	E	M	ME	A	AM	AE	AME	Friedman's Chi-square [c]	Contrasts [d]
CURCULIONIDAE											
Pissodes strobi	#	0	5	1	1	4	2	4	7	14.72**	
	R	37.5a	51.5ab	40.5ab	41ab	43ab	41.5ab	46.5ab	58.5b		
Hylobius pales	#	4	1	3	10	9	8	22	32	29.72***	AE(2vs6)***, A(4vs4)**
	R	36.5a	32.5a	34a	40.5a	45.5ab	41.5a	64b	65.5b		
Other Curculionidae	#	8	4	8	15	5	4	6	3		
SCOLYTIDAE											
Hylastes porculus	#	1	2	3	3	4	5	1	2	4.28	
	R	40.5	44.5	44	46.5	52	45.5	41.5	45.5		
Dryocetes autographus	#	11	18	4	76	16	6	83	79	51.16***	AE(2vs6)***, ME(2vs6)***,
	R	30a	37.5a	27a	65b	38a	24a	69.5b	69b		E(4vs4)***
Orthotomicus caelatus	#	7	17	4	4	13	3	10	5	9.73	
	R	47.5	41.5	41	40	43	41.5	58.5	47		
Ips grandicollis	#	0	0	5	4	7	2	4	3	16.24**	
	R	37a	37a	42.5ab	45ab	61b	43.5ab	49.5ab	44.5ab		
Other Scolytidae	#	2	7	4	13	5	4	8	2		

[a] Species with a total of 12 or more individuals captured.

[b] Treatments: Ø = blank control, E = ethanol, M = minor monoterpenes, ME = minor monoterpenes and ethanol, A = α–pinene, AM = α–pinene and minor monoterpenes, AE = α–pinene and ethanol, AME = α–pinene, minor monoterpenes and ethanol. Eight treatments replicated in ten blocks. Rank totals in a row followed by the same letter are not significantly different ($P>0.05$), non-parametric Newman-Keuls test corrected for ties.

[c] Corrected for ties. * for $P<0.10$, ** for $P<0.05$, *** for $P<0.01$.

[d] Non-parametric Scheffé-type contrasts. * for $P<0.10$, ** for $P<0.05$, *** for $P<0.01$. Letters indicate treatment effects contrasted, numbers indicate number of treatments involved in contrast: A(4vs4) = [A+AM+AE+AME]vs[Ø+E+M+ME], E(4vs4) = [E+ME+AE+AME]vs[Ø+M+A+AM], AE(2vs6) = [AE+AME]vs[Ø+E+M+ME+A+AM], ME(2vs6) = [ME+AME]vs[Ø+E+M+A+AM+AE], AM(2vs6) = [AM+AME]vs[Ø+E+M+ME+A+AE], AorM(6vs2) = [M+ME+A+AM+AE+AME]vs[Ø+E].

undulatus (Say) was attracted to monoterpenes in both experiments; in Experiment 2, maximum attraction was obtained with traps baited with both α–pinene and the minor monoterpenes, and contrasts indicate a possible effect of the minor monoterpenes on attraction. Ethanol and α–pinene acted synergistically to attract *M. scutellatus*, with the minor monoterpenes having little effect on this attraction (Experiment 2); in the absence of ethanol, α–pinene and other monoterpenes may possibly exert moderate attraction.

P. strobi responded to the treatments in both experiments, with attraction being due to the monoterpenes (Experiment 1). In Experiment 2, *H. pales* was clearly attracted to traps baited with both α–pinene and ethanol which acted synergistically.

Among the Scolytids, results of Experiment 1 indicated probable attraction of *Orthotomicus caelatus* (Eichhoff) to the combination of monoterpenes and ethanol, but no treatment effects were detected in Experiment 2. *I. grandicollis* was found to respond to monoterpenes in Experiment 2. The clearest response was that of *Dryocetes autographus* (Ratzeburg). In Experiment 1, almost all *D. autographus* were captured in traps baited with the combination of monoterpenes and ethanol. Experiment 2 demonstrated further that while α–pinene, minor monoterpenes, and ethanol alone did not attract this beetle, the combinations of α–pinene and ethanol and minor monoterpenes and ethanol were very attractive ($P<0.01$ for each of the relevant contrasts).

Definite treatment effects were detected for three species of clerid predators. Experiment 1 showed that *T. dubius* responded optimally to traps baited with both monoterpenes and ethanol, as indicated both by contrasts and Newman-Keuls test. Experiment 2 showed further that α–pinene probably accounts for most of the monoterpene effects, the minor monoterpenes having no apparent effect on attraction. Both *Enoclerus nigripes rufiventris* (Spinola) and *Enoclerus nigrifrons gerhardi* Wolcott were attracted by α–pinene.

Experiment 3. None of the species of wood borers or borer predators showed significantly greater attraction to either the pure monoterpene blend and ethanol or to commercial turpentine and ethanol (Table 7). Although results indicate that attraction to a monoterpene blend and ethanol does not differ significantly from attraction to chemically complex turpentine and ethanol, the small sample size used in the experiment should preclude

TABLE 7. RESULTS OF FIELD TRAPPING EXPERIMENT USING STICKY STOVEPIPE TRAPS BAITED WITH TURPENTINE AND ETHANOL OR WITH MONOTERPENE BLEND AND ETHANOL, CHALK RIVER, ONTARIO, 7 JULY TO 5 AUGUST 1986 (EXPERIMENT 3).

Family and Species [a]	Turpentine and Ethanol Number	T [b]	Monoterpene Blend and Ethanol Number	T [b]	n [b]	P [b]
BUPRESTIDAE						
Buprestis maculativentris	12	15	8	6	6	$P=0.50$
Chrysobothris dentipes	9	22	3	6	7	$0.20<P<0.50$
CLERIDAE						
Thanasimus dubius	41	10	34	0	4	$P=0.20$
Enoclerus nigrifrons gerhardi	10	2	11	4	3	– [c]
Trichodes nutalli	9	13	2	2	5	$P=0.20$
MELANDRYIDAE						
Serropalpus sp.	47	20.5	35	7.5	7	$0.20<P<0.50$
CERAMBYCIDAE						
Acmaeops proteus	10	8	6	2	4	$P=0.50$
Xylotrechus undulatus	11	29	4	7	8	$0.10<P<0.20$
Monochamus scutellatus	10	10	4	0	4	$P=0.20$
CURCULIONIDAE						
Hylobius pales	42	31	27	14	9	$0.20<P<0.50$
Pissodes strobi	4	5	7	10	5	$P\geq0.50$
SCOLYTIDAE						
Hylastes porculus	5	6.5	6	8.5	5	$P\geq0.50$
Dendroctonus valens	6	7.5	4	2.5	4	$P\geq0.50$
Trypodendron lineatum	1	0	11	1	1	–
Dryocetes autographus	58	9	71	12	6	$P\geq0.50$
Dryocetes affaber	7	3	5	0	2	–
Ips pini	21	13	11	2	5	$P=0.20$

[a] Species with 10 or more individuals captured.

[b] Wilcoxon paired-sample test Ts, n (number of non-zero differences), and P (significance probability). Two treatments replicated 12 times.

[c] Wilcoxon n too low to determine significance probability.

making definite conclusions. This is certainly the case with *T. dubius* and *M. scutellatus*, with Wilcoxon T values of zero for the monoterpene blend and ethanol (Table 7).

B—Evaluation of oviposition substrates

B.1 — Preliminary experiments

The nature of the support media appeared to have little effect on oviposition, eggs being laid on host material regardless of the medium (Table 8). For the test involving agar and α–cellulose, plugs adhered evenly to the filter paper and medium; when paper was not used, the plugs did not adhere closely to the medium, with a clear space being visible below the plugs by the end of a test. Plugs adhered well to the medium when agar was used alone.

The number of eggs laid per plug of red pine ranged from 2 to 9; as many as 16 eggs were laid by a female in a chamber in 24 hr. Eggs were laid at various depths, ranging from eggs laid right in the woody outer bark of red pine, to eggs laid in the spongy phloem. Beetles were most active from 15:00 to 21:00 EST, chewing egg niches and ovipositing almost exclusively during that period. At other times, females moved very little, resting mostly on the top screen.

Results for *M. notatus* are shown in Table 9. Eggs were laid in the agar, usually flat on the bottom surface of the bark plug, but in some cases with the egg standing on end entirely within the agar. Occasionally, the eggs were in the phloem or at the boundary between phloem and outer bark. *M. notatus* oviposited mostly in the white spruce and red pine, followed by white pine and balsam fir.

B.2 — Evaluation of conifer hosts

Results are shown in Table 10. Most eggs were laid in white spruce, followed by red pine, white pine, and balsam fir. No eggs were laid in balsam fir, although that species is a host of *M. scutellatus*.

TABLE 8. RESULTS OF PRELIMINARY EXPERIMENTS WITH *MONOCHAMUS SCUTELLATUS* IN OVIPOSITION BIOASSAY CHAMBERS, USING VARIOUS SUBSTRATES AND SUBSTRATE SUPPORT MEDIA

Test	Replicate [a]	Month.Day.Hour Begin	Month.Day.Hour End	Substrate support medium	Substrate [b] (bark plug)	Thickness (mm) O.B.[c]	Thickness (mm) Phloem	# of eggs
1	1	06.16.2300	06.17.2200	1% agar	*P. resinosa*	1.4	1.2	9
				1% agar	*P. resinosa*	1.4	1.3	7
	2	06.16.2330	06.17.2330	1% agar	*P. resinosa*	1.8	1.1	2
				1% agar	*P. resinosa*	1.7	1.8	4
2	1	06.18.1500	06.19.0800	agar+cellulose, with paper [d]	*P. resinosa*	1.2	1.0	3
				agar+cellulose, no paper [d]	*P. resinosa*	1.3	0.8	4
	2	06.18.1500	06.19.1000	agar+cellulose, with paper [d]	*P. resinosa*	1.2	1.0	6
				agar+cellulose, no paper [d]	*P. resinosa*	1.3	0.8	3
3	1	06.19.1530	06.20.0800	2.5% agar	*P. resinosa*	1.3	1.1	4
				2.5% agar	*P. tremuloides*	2.4	0.9	0
	2	06.19.1630	06.20.0930	2.5% agar	*P. resinosa*	1.3	1.1	8
				2.5% agar	*P. tremuloides*	2.4	0.9	0
4	1	06.20.1545	06.21.1530	2.5% agar	*P. resinosa*	1.0	1.5	2
				2.5% agar	*A. balsamea*	2.2	0.8	0
	2	06.20.1545	06.21.1530	2.5% agar	*P. resinosa*	1.0	1.5	5
				2.5% agar	*A. balsamea*	2.2	0.8	0
5	1	06.21.1100	06.23.1100	1% agar	*P. resinosa*	1.3	1.3	7
				1% agar	*P. resinosa*	1.5	1.1	8

[a] Replicates of a test done using different females. Each chamber (replicate) with two substrates (bark plugs).

[b] Tree species: *Pinus resinosa, Populus tremuloides, Abies balsamea.*

[c] O.B. = outer bark.

[d] 0.5% agar + 10% α–cellulose, with or without filter paper between medium and bark plug.

TABLE 9. NUMBER OF EGGS LAID BY *MONOCHAMUS NOTATUS* IN OVIPOSITION BIOASSAY CHAMBERS. CHOICE OF FOUR CONIFER SPECIES. [a]

	Pinus strobus			*Pinus resinosa*			*Picea glauca*			*Abies balsamea*		
Replicate	O.B.	Phl.	eggs	O.B.	Phl.	eggs	O.B.	Phl.	eggs	O.B.	Phl.	eggs
1	1.2	3.9	3	0.8	3.5	1	0.8	3.3	4	1.5	1.1	1
2	1.2	3.0	2	2.1	2.5	4	1.4	2.2	3	1.6	2.1	0
3	0.9	2.1	2	1.5	1.1	7	1.2	2.3	3	1.8	1.3	0
4	1.3	2.7	1	1.0	1.5	2	0.9	2.7	6	2.0	1.0	1
Total	4.6	11.7	8	5.4	8.6	14	4.3	10.5	16	6.9	5.5	2
Mean	1.15	2.93	2.0	1.35	2.15	3.5	1.08	2.63	4.0	1.73	1.38	0.5
S.D.	0.173	0.750	0.817	0.580	1.076	2.646	0.275	0.499	1.414	0.222	0.499	0.577
Rank total [b]			8.5 b			12.5 c			14.0 c			5.0 a

Friedman $\chi^2 = 7.82$ ($P<0.05$) [c]

[a] Four replicates using four different females. Each chamber (replicate) with four substrates (tree species). O.B. = outer bark thickness (mm); Phl. = phloem thickness (mm).

[b] Ranks followed by the same letter are not significantly different ($P>0.05$), Newman-Keuls test corrected for ties.

[c] Friedman test corrected for ties.

TABLE 10. NUMBER OF EGGS LAID BY *MONOCHAMUS SCUTELLATUS* IN OVIPOSITION BIOASSAY CHAMBERS. CHOICE OF FOUR CONIFER SPECIES. [a]

	Pinus strobus			*Pinus resinosa*			*Picea glauca*			*Abies balsamea*		
Replicate	O.B.	Phl.	eggs	O.B.	Phl.	eggs	O.B.	Phl.	eggs	O.B.	Phl.	eggs
1	0.8	1.9	2	1.0	2.1	2	1.4	2.7	5	1.4	1.6	0
2	1.3	2.1	0	1.1	2.1	3	0.9	2.1	4	1.1	0.9	0
3	1.2	2.5	0	1.4	2.9	5	1.3	2.5	7	2.1	1.8	0
4	1.6	3.0	0	0.9	1.8	0	0.9	2.2	8	1.9	2.2	0
5	0.9	2.1	0	1.1	2.1	0	0.9	1.9	3	2.2	2.2	0
6	1.1	1.9	0	1.6	3.0	0	1.4	2.4	3	1.5	1.3	0
7	1.2	2.9	0	1.3	2.2	0	1.1	2.3	2	1.4	1.3	0
8	0.9	2.2	5	1.8	2.9	1	1.0	2.1	0	1.9	1.5	0
9	1.1	2.3	0	1.3	2.3	2	1.2	2.1	2	2.3	1.6	0
10	1.4	2.9	0	1.7	3.1	7	1.0	2.5	4	1.5	1.3	0
Total	11.5	23.8	7	13.2	24.5	20	11.1	22.8	38	17.3	15.7	0
Mean	1.15	2.38	0.7	1.32	2.45	2.0	1.11	2.28	3.8	1.73	1.57	0
S.D.	0.246	0.421	1.636	0.305	0.472	2.404	0.203	0.244	2.394	0.403	0.411	0
Rank total [b]			20.5 a			27.0 ab			36.0 b			16.5 a

Friedman $\chi^2 = 17.88$ ($P<0.001$) [c]

[a] Ten replicates using ten different females. Each chamber (replicate) with four substrates (tree species). O.B. = outer bark thickness (mm); Phl. = phloem thickness (mm).

[b] Ranks followed by the same letter are not significantly different ($P>0.05$), Newman-Keuls test corrected for ties.

[c] Friedman test corrected for ties.

B.3 — Effects of volatiles

No eggs were laid in non-hosts, even in the presence of host volatiles (Table 11). When beetles were given a choice between host and non-host bark, eggs were laid in host bark, regardless of the presence of host or non-host volatiles ($0.75>P>0.50$ for effects of volatiles, two-factor Kruskal-Wallis test) (Table 12). Table 13 shows that the presence of phloem of another species did not affect the response to outer bark, eggs being laid only in the outer bark of hosts.

B.4 — Importance of outer bark

Beetles laid both in the outer bark and in the phloem, showing no preference for either type of substrate (Table 14). The presence of scales on the bark of red pine did not affect oviposition (Table 15).

TABLE 11. EFFECTS OF BARK VOLATILES ON OVIPOSITION BY *MONOCHAMUS SCUTELLATUS*. TESTS 1 TO 3. CHOICE OF FOUR HARDWOOD TREE SPECIES.

Test	No. of replicates [a]	Bark volatiles [b]	Substrate [c]	Total number of eggs	Rank total	Friedman χ^2
1	5	none	*P. tremuloides*	0	12.5	0
			P. grandidentata	0	12.5	
			B. papyrifera	0	12.5	
			A. rubrum	0	12.5	
2	5	*P. resinosa* 30 g	*P. tremuloides*	0	12.5	0
			P. grandidentata	0	12.5	
			B. papyrifera	0	12.5	
			A. rubrum	0	12.5	
3	5	*P. glauca* 30 g	*P. tremuloides*	0	12.5	0
			P. grandidentata	0	12.5	
			B. papyrifera	0	12.5	
			A. rubrum	0	12.5	

[a] Replicates of a test done using different females. Each chamber (replicate) with four substrates (tree species).

[b] Tree species (*Pinus resinosa* or *Picea glauca*) and fresh weight of bark chips placed in chamber before start of test.

[c] Tree species: *Populus tremuloides*, *Populus grandidentata*, *Betula papyrifera*, *Acer rubrum*.

TABLE 1-2. EFFECTS OF BARK VOLATILES ON OVIPOSITION BY *MONOCHAMUS SCUTELLATUS*. TESTS 4 TO 6. CHOICE OF TWO HARDWOOD AND TWO CONIFER TREE SPECIES.

Test	No. of replicates [a]	Bark volatiles [b]	Substrate [c]	Total number of eggs	Rank total [d]	Friedman χ^2 [e]
4	5	none	*P. resinosa*	14	16.0 ab	14.58
			P. glauca	20	19.0 b	(P<0.005)
			P. tremuloides	0	7.5 a	
			A. rubrum	0	7.5 a	
5	5	*P. resinosa* 30 g	*P. resinosa*	6	13.0 ab	10.03
			P. glauca	20	18.0 b	(P<0.025)
			P. tremuloides	0	9.5 a	
			A. rubrum	0	9.5 a	
6	5	*P. tremuloides* 60 g	*P. resinosa*	7	15.0 a	9.56
			P. glauca	18	17.0 a	(P<0.025)
			P. tremuloides	0	9.0 a	
			A. rubrum	0	9.0 a	

[a] Replicates of a test done using different females. Each chamber (replicate) with four substrates (tree species).

[b] Tree species (*Pinus resinosa* or *Populus tremuloides*) and fresh weight of bark chips placed in chamber before start of test.

[c] Tree species: *Pinus resinosa, Picea glauca, Populus tremuloides, Acer rubrum.*

[d] Rank totals in a test followed by the same letter are not significantly different (P>0.05), Newman-Keuls test corrected for ties.

[e] Corrected for ties.

Non-parametric two-factor Kruskal-Wallis test (three experiments combined; factor A = substrate species, factor B = species of bark volatiles):

substrate effects: H = 80.87 (P<0.001)
volatiles effects: H = 1.12 (0.75<P<0.50)
interaction effects: H = 1.58 (0.975<P<0.95).

TABLE 13. EFFECTS OF BARK VOLATILES ON OVIPOSITION BY *MONOCHAMUS SCUTELLAUS*. TESTS 7 AND 8. CHOICE OF LAYERED OUTER BARK AND PHLOEM.

Test	No. of replicates [a]	Substrate [b]	Total number of eggs	Rank total [c]	Friedman χ^2 [d]	Treatment contrasts [e]
7	5	*P. resinosa* on *A. rubrum* 1	21	16.0 a	9.92	*P. resinosa* on *A. rubrum*
		P. resinosa on *A. rubrum* 2	15	17.0 a	(P<0.025)	vs
		A. rubrum on *P. resinosa* 1	0	8.5 a		*A. rubrum* on *P. resinosa*
		A. rubrum on *P. resinosa* 2	0	8.5 a		P<0.05
8	5	*P. glauca* on *A. rubrum*	31	18.5 b	13.91	*P. glauca* on *A. rubrum*
		P. glauca on *A. rubrum*	14	16.5 b	(P<0.005)	vs
		A. rubrum on *P. glauca*	0	7.5 a		*A. rubrum* on *P. glauca*
		A. rubrum on *P. glauca*	0	7.5 a		P<0.001

[a] Replicates of a test done using different females. Each chamber (replicate) with four substrates.

[b] Test 7: *Pinus resinosa* outer bark on *Acer rubrum* phloem (two per chamber) and *Acer rubrum* outer bark on *Pinus resinosa* phloem (two per chamber).
Test 8: *Picea glauca* outer bark on *Acer rubrum* phloem (two per chamber) and *Acer rubrum* outer bark on *Picea glauca* phloem (two per chamber).

[c] Rank totals in a test followed by the same letter are not significantly different (P>0.05), Newman-Keuls test corrected for ties.

[d] Corrected for ties.

[e] Scheffé-type contrasts, corrected for ties.

TABLE 14. RESULTS OF EXPERIMENTS TO DETERMINE IF *MONOCHAMUS SCUTELLATUS* PREFERENTIALLY OVIPOSITS IN HOST PHLOEM OR OUTER BARK.

Test	No. of replicates [a]	Substrate [b]	Total number of eggs	Rank total [c]	Friedman χ^2 [d]	Treatment contrasts [e]
1	5	*P. resinosa* outer bark	8	11.5 a	5.62	Outer bark
		P. resinosa phloem	5	8.0 a	(P<0.25)	vs
		P. glauca outer bark	18	15.0 a		phloem
		P. glauca phloem	28	15.5 a		P>0.10
2	5	*P. resinosa* 1	9	10.5 ab	9.14	*P. resinosa*
		P. resinosa 2	2	7.0 a	(P<0.05)	vs
		P. glauca 1	22	17.5 b		*P. glauca*
		P. glauca 2	19	15.0 ab		P<0.05

[a] Replicates of a test done using different females. Each chamber (replicate) with four substrates.

[b] Species: *Pinus resinosa*, *Picea glauca*.

[c] Rank totals in a test followed by the same letter are not significantly different (P>0.05), Newman-Keuls test corrected for ties.

[d] Corrected for ties.

[e] Scheffé-type contrasts, corrected for ties.

TABLE 15. EFFECTS OF BARK TEXTURE (BARK SCALES) ON OVIPOSITION BY *MONOCHAMUS SCUTELLATUS* IN BIOASSAY CHAMBERS.

Test	No. of replicates [a]	Substrate [b]	Total number of eggs	Rank total [c]	Friedman χ^2 [d]	Treatment contrasts [e]
1	5	*P. resinosa*, rough 1	8	10.0 a	2.63	*P. resinosa*, rough
		P. resinosa, rough 2	10	13.0 a	(P<0.50)	vs
		P. resinosa, smooth 1	17	16.0 a		*P. resinosa*, smooth
		P. resinosa, smooth 2	11	11.0 a		P>0.10

[a] Replicates done using different females. Each chamber (replicate) with four substrates.

[b] Species: *Pinus resinosa*.

[c] Rank totals in a test followed by the same letter are not significantly different (P>0.05), Newman-Keuls test corrected for ties.

[d] Corrected for ties.

[e] Scheffé-type contrast, corrected for ties.

DISCUSSION

A — Attraction

Visual cues. Trap evaluation experiments showed that sticky stovepipe traps consistently captured more conifer-feeding beetles and their clerid predators than did other traps. Traps had been set up such that the trapping heights were similar for all three designs (0.8 to 1.5 m for pipe traps, 0.9 to 1.5 m for funnel traps, and 1.0 to 1.5 m for interception traps). The trap surface areas were identical for the pipe and funnel traps (0.35 m^2), and greater for the interception traps (1.0 m^2). All traps were omnidirectional, capturing insects flying to the traps from any direction. Rates for bait release were similar for the three trap designs (Table 3), the slightly lower rate obtained with funnel traps likely due to the lighter winds blowing across the vials which were placed at the lower ends of the funnels. The odour plume extending downwind from the traps were likely most 'tree-like' for the funnel traps, since bait vials were placed at different heights along the series of funnels (Lindgren 1983); for the pipe traps, chemicals were essentially released from a single source (top of trap), while for the interception traps, chemicals were released from two sources, one at the top and the other at the bottom of the panes. Given the overall similarities of the three trap designs, it appears that differences in the numbers of beetles captured were due to the traps' appearance, with most beetles associated with trees attempting to land on the pipe traps with the clear vertical silhouette. Further indirect support for this conclusion comes from the fact that beetles not normally associated with trees were captured in greatest numbers by interception traps.

Forest cover had a definite effect on trap captures, with many species being captured almost exclusively in traps either in open fields or within the forest. Differences in the number of beetles in traps either in open fields or under the forest canopy may be due to several factors: 1) Differences in the number of beetles present, related to the normal habitat of a given species. 2) Greater activity of the beetles in either the open or forested sites; increased flight leads to an increase in the chance of encountering a trap. 3) Differences in responsiveness to the baits or trap silhouette; for example, beetles may search for resting or overwintering sites in the forest,

and therefore not respond to baited traps. Major differences between the open and forested sites include the actual difference in habitat (difference in vegetation) and climatic differences. The proximity of traps to trees in the forest could be expected to affect both the dispersion of chemicals (due to weaker winds in the forest, as evidenced by the lower rates of vaporisation of baits in forested sites [Table 3]) and the visual orientation to traps, inasmuch as the background affects the visibility of the traps. Differences in temperature (and to a certain extent in relative humidity) between forested and open sites affect responses: 1) Beetles may not fly below a certain temperature threshold. 2) Temperature affects the rate of bait release; this would affect all three trap designs equally.

Chemical cues. Conifer-feeding beetles generally responded to monoterpenes, with or without ethanol, being captured in greater number in traps baited with terpenes. The monoterpene blend used was typical of many species of Pinaceae, but most beetles responded primarily to α–pinene. While most conifer-feeding beetles which were captured are associated with moribund trees, only in a few cases did ethanol have a definite affect on attraction. Rates of vaporisation of monoterpenes obtained in both the chemical bait experiments and the previous trap evaluation experiment were about 1 $g \cdot day^{-1} \cdot trap^{-1}$ (Tables 3 and 4), or about the same rate as would be obtained with 100 kg of fresh pine logs (Ikeda et al. 1980). No experiment was designed to verify the responses to dramatically different rates of bait release, but the positive responses of beetles to the rates of monoterpene release used indicate that beetles should be able to respond to an individual moribund tree.

Mechanisms of attraction. For many conifer-feeding beetles, orientation to the baited traps appears to be mediated by both chemical cues and visual cues. While the responses of insects observed in these experiments are being heuristically referred to as 'attraction', the true nature of the behavioural mechanisms involved is not known. The terpenes may be acting as arrestants, as was demonstrated with *Dendroctonus pseudotsugae* Hopkins exposed to phloem tissue of *Pseudotsuga menziesii* (Mirbel) Franco (Bennett and Borden 1971). Most of the species which were found to respond to the test chemicals also landed in greatest numbers on the pipe traps with clear vertical silhouettes. Thus, while insects

responding to the monoterpenes and ethanol may well be attracted from a distance, the chemicals also may be acting as arrestants for insects flying within sight of the traps.

The discussion which follows examines the responses by individual families and species.

Buprestidae. Except for *B. maculativentris* and *M. fulvoguttata*, no buprestid showed a preference for any of the chemical baits used; even for these species, a definite response was not indicated, with only Experiment 2 showing results significant at $P<0.10$. Trap evaluation demonstrated that all species were captured in lowest numbers by flight interception traps, with pipe traps clearly outperforming other traps for most species (the only exceptions were *B. salisburyensis* and *B. maculipennis*, represented by only one specimen each, captured in interception traps). Trap silhouette therefore appears to play a more important role in the orientation of these beetles than monoterpenes or ethanol. Montgomery and Wargo (1983) also failed to find any increase in trap catch for buprestids when ethanol was used as a bait in an oak forest. Evans (1966) showed that *Melanophila acuminata* (DeGeer) posseses an array of infra-red detectors permitting orientation to sources of heat, such as forest fires; while buprestids are known heliophiles, such specialised structures do not appear to be common among buprestids. Until contradictory evidence arises, tree silhouette must be assumed to be the major cue involved in attraction of buprestids. This of course implies that beetles land indiscriminately on both hosts and non-hosts, and that evaluations of the tree are carried out by the insects after landing. Buprestids were almost all captured in open sites, consistent with the habitat and warm temperature preferences of most buprestids (Wellso et al. 1976).

Cleridae. Monoterpenes appear important for the attraction of several species of Cleridae, including *T. dubius*, *T. undulatus*, *E. nigripes rufiventris*, and *E. nigrifrons gerhardi*. Alpha-pinene was responsible for most of the responses to the monoterpenes. Only in the case of *T. dubius* did ethanol have an effect, synergising attraction to the α–pinene. Mizell et al. (1984) found upwind flight of *T. dubius* in response to α–pinene and β–pinene in an olfactometer, but did not verify effects of ethanol. In the field, Billings and Cameron (1984) found no attraction of *T. dubius* (nor of *M. titillator* or *I. grandicollis*) to flight

interception traps baited with loblolly pine turpentine, but the rate of vaporisation of the turpentine in their study ranged from 25 to 40 mg·day^{-1}·trap^{-1}, or about 25 to 40 times less than the rates obtained in the chemical bait experiments (Table 4). No attraction of *T. dubius* was detected to turpentine released at 3.6 g·day^{-1}·trap^{-1} from flight interception traps (Billings 1985); the greatest response was for traps baited with both frontalin and turpentine (see the discussion in the next section). Montgomery and Wargo (1983) reported attraction of *Phlogistosternus dislocatus* (Say) to ethanol. Because few specimens were captured in this study, results for this species were not significant, but all of these beetles were captured in traps baited either with ethanol or with ethanol and monoterpenes (Table 5). Clerids were consistently captured in greatest number by pipe traps, except for *T. nutalli* which were almost all captured by interception traps in open sites (Table 2). This species is not a predator of tree-dwelling insects, attacking bees and wasps instead (Knull 1951). Its capture in flight interception traps is likely due to random interception of the beetles as they flew in the open fields, with the beetles avoiding the clearly visible pipe and funnel traps.

Cerambycidae. While Table 5 shows possible repulsion of *P. nigrella* in response to ethanol ($P<0.10$), the response was not detected in Table 6, where a greater number of beetles had responded.

Four species responded in sufficient numbers to show definite attraction to monoterpenes, namely *A. striatum*, *A. proteus*, *X. undulatus*, and *M. scutellatus*. Alpha-pinene accounted for most monoterpene effects, although minor monoterpenes probably affected attraction of *X. undulatus* and *M. scutellatus* (Table 6). Ethanol synergised attraction to monoterpenes for *M. scutellatus*. Results obtained with *M. scutellatus* are similar to those observed in Japan with *M. alternatus*. That species has been shown to be attracted to a blend of ten monoterpenes, with ethanol synergising attraction (Ikeda et al. 1980); among the monoterpenes, α–pinene proved the most attractive, with some activity being detected for β–pinene and β–phellandrene (Ikeda et al. 1981). In Florida, traps baited with turpentine and ethanol captured most sawyers (*M. carolinensis* and *M. titillator*), followed by traps with turpentine alone and with ethanol alone (Fatzinger 1985). As mentioned above, the fact that Billings and Cameron (1984) found no attraction of *M. titillator* to traps baited with loblolly

pine turpentine may be due to the low rate of bait release which they used. Billings (1985) found that turpentine (without ethanol) released from interception traps at a rate of 3.6 $g \cdot day^{-1} \cdot trap^{-1}$ did not increase trap catches compared to control traps. *M. titillator* has been found to be attracted to traps baited with the bark beetle pheromones verbenone, *exo*–brevicomin, *endo*–brevicomin, ipsenol, ipsdienol, and *cis*–verbenol (Billings and Cameron 1984); attraction to *Ips* pheromones (2% *cis*–verbenol, 2% ipsdienol, 2% ipsenol) was strongly synergised by the simultaneous release of turpentine (Billings 1985). The response of *M. scutellatus* to scolytid pheromones has not been determined, but since closely related species generally respond to similar semiochemicals, there is a strong possibility that similar responses could occur. In the studies of Billings and Cameron (1984) and Billings (1985), flight interception traps were used. The present studies indicate that both *T. dubius* and *M. scutellatus* respond to trap silhouette (Table 2), with few beetles being captured by flight interception traps. The failure of traps in capturing *T. dubius* and *M. titillator* even when high rates of monoterpene release were used (Billings 1985) may be due to the absence of visual cues which appear to be important for the orientation to monoterpenes. The positive responses of *T. dubius* and *M. titillator* to interception traps baited with scolytid pheromones reported by Billings and Cameron (1984) and Billings (1985) seem to indicate that the visual element is less important for the orientation to these odour sources. Evans and Higgs (1975) have shown that several oxygenated monoterpenes are present in the frass of *H. bajulus*, including verbenone. The release of such compounds in the frass of *Monochamus* adults has not been examined. Autoxidation of monoterpenes and microbial activity can result in the production of many oxygenated terpenes in trees (Borden et al. 1986, 1987b), including verbenone and verbenol by oxidation of α–pinene, and ipsdienol and ipsenol by oxidation of myrcene. More research is thus needed to determine if *Monochamus* species generally respond to oxygenated monoterpenes and if these terpenes are primarily released from the trees or from the guts of *Monochamus* or other insects on the trees.

Curculionidae. Both *P. strobi* and *H. pales* responded to test baits. While *H. pales* was shown to be attracted to α–pinene in laboratory olfactometers (Thomas and Hertel 1969), its field response to α–pinene and ethanol is considerably greater than that to α–pinene alone,

as indicated in Table 6. Siegfried (1987) found the greatest attraction of *H. pales* to traps baited with α–pinene and ethanol, as well as attraction to β–phellandrene, limonene and ethanol and to β–pinene and ethanol. Although the experiments clearly showed attraction of *P. strobi* to monoterpenes, previous reports had suggested contradictory effects of terpenes for this weevil, with Wilkinson (1972) reporting attraction to white pine oleoresin, while Anderson and Fisher (1960) reported repellency of α–pinene and other terpenes.

Both *P. strobi* and *H. pales* were captured in greatest numbers by pipe traps, indicating probable visual orientation. *P. strobi* was present in large numbers in forested sites, even though most weevil attacks occurred in the open fields where many spruce seedlings had leaders damaged by the weevils. Sylvicultural practices recommend planting saplings of species susceptible to *P. strobi* under forest cover to minimise attack; it is not clear if the weevils flying under the forest canopy were searching for food or for shelter.

Scolytidae. *I. grandicollis* responded to chemical bait treatments, with traps baited with α–pinene capturing significantly ($P<0.05$) more beetles than control traps. The most dramatic response was that of *D. autographus*. Beetles were attracted to traps baited with both monoterpenes and ethanol, with few beetles responding to traps baited with either monoterpenes or ethanol alone. Attraction to α–pinene and ethanol was equal to that to minor monoterpenes and ethanol; attraction to the ternary combination (α–pinene, minor monoterpenes, and ethanol) was not any greater (Table 6). All species were captured mostly in pipe traps. The poor performance of funnel traps was somewhat surprising, since pheromone-baited funnel traps can capture large numbers of scolytids (e.g., Niemeyer 1985; McLean et al. 1987; Borden et al. 1987a, 1987b). Consistent with the discussion above regarding the responses of *Thanasimus* and *Monochamus*, it appears that the diffuse silhouette of funnel traps may be sufficient to induce landing in response to pheromones, but that the clear silhouette of pipe traps is needed to induce landing in response to monoterpenes.

Other families. Considered at the family level, no responses to chemical baits were apparent for the Carabidae, Scarabaeidae, Elateridae, Lampyridae, Cantharidae, Alleculidae, or Mordellidae. Capture by interception traps appears in many cases to be due to random interception. Responses by species of Elateridae varied from that of *Agriotes stabilis*

(LeConte), which was captured primarily by interception traps, to those of *Melanotus castanipes* (Paykull) and *Ampedus pullus* Germar, which responded clearly to pipe traps. In groups such as species of Lampyridae which use tree trunks as rest or display sites, orientation to the traps is probably in response to visual cues only; pipe traps captured considerably more lampyrids than the other traps.

B — Evaluation of oviposition substrate

Previous studies of oviposition by cerambycids consisted of observations of beetles which were offered test logs (e.g., Walsh and Linit 1985). The experiments using the bioassay chamber and test protocol as described in this dissertation are the first example of a systematic study of the selection of oviposition substrates by cerambycids. Use of the chamber permitted efficient screening of oviposition substrates.

Most eggs were laid by both *M. scutellatus* and *M. notatus* on white spruce, followed by red pine, white pine, and balsam fir (Tables 9 and 10). Both beetles are known to attack a variety of *Pinus*, *Picea*, and *Abies* species (Linsley and Chemsak 1984). Since beetles used in these experiments were collected in the field, the nature of the hosts upon which they had fed as larvae is not known. Cerambycids have been shown to oviposit more on species on which they fed as larvae (in accordance with Hopkins' host selection principle) (Craighead 1921), and the similarity in the responses of both *Monochamus* species to the four conifer hosts may reflect the relative abundance of susceptible conifer species in the test area.

While *M. scutellatus* oviposited readily in white spruce and red pine, the presence in the chamber of bark volatiles of these species did not induce oviposition on non-hosts (Table 11), nor were oviposition slits cut into non-host bark. When plugs of both hosts and non-hosts were present in a chamber, most eggs were laid in white spruce, followed by red pine, with no eggs being laid in non-hosts; the presence of bark volatiles of red pine or aspen did not affect the response (Table 12). Placing host outer bark on non-host phloem or non-host outer bark on host phloem did not affect the expected response (oviposit on host outer bark only) (Table 13). When white spruce outer bark was used, the beetles frequently chewed all the way

through the outer bark, exposing themselves to the non-host phloem. Chewing did not extend into the non-host phloem, and all eggs were laid in the host outer bark. Results from the eight experiments involved indicate that bark volatiles had no effect on the selection of oviposition site. Contact cues are therefore probably more important in substrate evaluation.

The bark texture was shown to have no effect on oviposition by *M. scutellatus* (Table 15), even though cerambycids in subfamilies other than Lamiinae often lay under such scales (Butovitsvh 1939; Gardiner 1969). Females oviposited in equal numbers in phloem and outer bark (Table 14), despite obvious physical differences between the two tissues (texture, hardness, water content), indicating that chemical properties common to the two may be more important than their physical characteristics. Oviposition sites in the outer bark or in the phloem resembled sites chewed in thick bark and thin bark, respectively (Walsh and Linit 1985), with large egg niches being chewed in the outer bark and only a small nick being chewed in the phloem before inserting the ovipositor. Dyer and Seabrook (1978a) found no difference in the content of five volatile monoterpenes (α–pinene, β–pinene, camphene, myrcene, limonene) or in the moisture content of the bark of fresh logs of white pine (not susceptible to attack) and logs seasoned three to four weeks (susceptible to attack by *Monochamus*), indicating that these factors are probably not important for the evaluation of substrates.

It therefore appears likely that contact chemical cues play a prime role in the evaluation of substrates for oviposition. Contact chemical cues could be detected by the mouthparts while chewing oviposition slits, by the ovipositor while probing these slits, or by both mouthparts and the ovipositor. While the particular acute apex of the lamiine mandibular palpi indicate that these palpi may be involved in the equally particular habit of chewing egg niches, sensilla on lamiine palpi have not been studied. Baker (1978) has identified probable chemoreceptors on the mouthparts of *Neoclytus muricatulus* (Kirby) and *X. undulatus* (Cerambycinae) and *A. proteus* (Lepturinae). Sensilla on cerambycid ovipositors have been studied only with *H. bajulus*, where both chemoreceptors and mechanoreceptors are found (Mares and Robinson 1986).

Host selection by *M. scutellatus*

The experiments described in this dissertation have led to the identification of some of the stimuli involved in host selection by *M. scutellatus* (see scheme outlined in Figure 3). Flight to a susceptible host occurs in response to chemical cues (monoterpenes and ethanol) and visual cues (tree silhouette). Chemical cues are primarily α–pinene and ethanol acting synergistically, with other monoterpenes possibly playing a minor role. Once a beetle has landed on a host, volatile compounds probably no longer affect beetle behaviour. Substrate evaluation is done when chewing egg slits and probing with the ovipositor, with chemical properties common to both the outer bark and phloem inducing oviposition.

As discussed above, the importance of oxygenated monoterpenes for host finding needs further study. If a response by *M. scutellatus* similar to that of *M. titillator* was detected, the likely sources of the compounds would be 1) the frass of conspecifics, 2) the frass of other conifer-feeding beetles, notably scolytids which use many oxygenated monoterpenes as pheromones (see Francke and Vité 1983), or 3) the tree itself. If the compounds were present primarily in the frass of conspecifics, these compounds would be acting as aggregation pheromones. If they were found to be coming from other beetles or from the tree, they would be acting as kairomones. Because of their large size, *Monochamus* beetles can compete successfully against bark beetles (Coulson et al. 1985). A strong response to scolytid pheromones would permit rapid location of weak or dead conifers, inasmuch as these would have been identified by the scolytids as being suitable for progeny development. Regardless of the possible role for oxygenated monoterpenes, the present study has shown that, in conjunction with visual cues, monoterpenes and ethanol can serve to identify suitable host trees for *M. scutellatus*.

CONCLUSIONS

A — Attraction

A.1 — Importance of visual cues (trap evaluation)

The superior performance of sticky stovepipe traps indicates that trap silhouette affects the attraction of conifer-feeding beetles and their associates. It therefore appears likely that tree bole silhouette acts as a visual cue for the orientation of these beetles to their hosts.

A.2 — Importance of chemical cues

Monoterpenes attracted many species of beetles, including *A. striatum, A. proteus, X. undulatus, M. scutellatus* (Cerambycidae), *P. strobi, H. pales* (Curculionidae), *D. autographus, I. grandicollis* (Scolytidae), *T. dubius, E. nigripes rufiventris, E. nigrifrons gerhardi* (Cleridae). Ethanol alone did not attract beetles, but did synergise attraction to monoterpenes for *M. scutellatus, H. pales*, and *D. autographus*. Alpha-pinene elicited most of the responses observed, but other monoterpenes were also highly attractive for *D. autographus*. Responses of beetles to turpentine and ethanol appeared to be similar to the responses to pure monoterpenes and ethanol. Therefore, major host monoterpenes and ethanol attract many species of beetles.

B — Evaluation of oviposition substrate

B.1 — Importance of volatile chemicals

Volatiles present in the bark of hosts (red pine and white spruce) and non-hosts (aspen) did not affect oviposition by *M. scutellatus*, indicating that volatile bark chemicals are probably not involved in the evaluation of oviposition substrates.

B.2 — Importance of outer bark

M. scutellatus females oviposited equally in host phloem or outer bark and in bark covered by scales or not. Properties common to both the phloem and outer bark therefore elicit oviposition. Given the differences in physical characteristics between the outer bark and phloem, it appears likely that chemical cues play a prime role in substrate evaluation.

Host selection by *M. scutellatus* therefore appears to involve attraction in response to host monoterpenes (notably α–pinene) and ethanol and to tree silhouette. After landing, contact chemical cues are used to evaluate the substrate prior to oviposition.

Potential applications

Given their good performance, traps offering a clear silhouette should be used for trapping a large variety of conifer-feeding beetles. Design changes with the funnel traps, such as the use of more funnels resulting in a longer vertical silhouette, could possibly enhance their performance and provide a non-sticky alternative to the pipe traps. Considering results from the three chemical bait experiments, the use of commercial turpentine and ethanol as attractant baits could prove useful for sampling a wide variety of conifer forest Coleoptera.

Results from this research could be put to other uses. 1) Baited traps could be used to survey forest Coleoptera. 2) Baited traps could be used to monitor adult populations for bionomic and population studies. 3) Techniques developed in this work could be adapted to the study of host selection in other wood-boring beetles. 4) Identification of behaviour-modifying chemicals could lead to the development of pest management strategies involving a) the use of attractants to capture beetles in traps for local suppression of beetle populations, b) the use of trapping for population monitoring, permitting sounder decisions regarding application of pesticides or implementation of other control procedures, and c) the use of anti-attractant chemicals or of compounds inhibiting oviposition to prevent oviposition on susceptible trees and logs.

REFERENCES

Anderson, J.M., and K.C. Fisher. 1960. The response of the white-pine weevil to naturally occurring repellents. *Canadian Journal of Zoology* **38**: 547-564.

Austarå, Ø., A. Bakke, and F. Midtgaard. 1986. Response in *Ips typographus* to logging waste odours and synthetic pheromones. *Journal of Applied Entomology* **101**: 194-198.

Baker, G.T. 1978. Sense organs on the antennal flagellum and certain mouthparts of three cerambycids (Insecta, Coleoptera). M.Sc. Thesis, Department of Biology, Carleton University, Ottawa, Canada.

Baker, W.L. 1972. Eastern Forest Insects. *U.S.D.A. Forest Service Miscellaneous Publications* Number 1175. 642 pp.

Bakke, A. 1983. Host tree and bark beetle interaction during a mass outbreak of *Ips typographus* in Norway. *Zeitschrift für Angewandte Entomologie* **96**: 118-125.

Bakke, A. 1985. Deploying pheromone-baited traps for monitoring *Ips typographus* populations. *Zeitschrift für Angewandte Entomologie* **99**: 33-39.

Bakke, A., and T. Sæther. 1978. Granbarkbillen kan fanges i rørfeller. *Skogeieren* **65**(11): 10.

Bakke, A., T. Sæther, and T. Kvamme. 1983. Mass trapping of the spruce bark beetle *Ips typographus*. Pheromone and trap technology. *Meddelelser fra Norsk Institutt for Skogforskning* **38**(3): 1-35.

Banthorpe, D.V., and B.V. Charlwood. 1980. The terpenoids. Pp. 185-220 *in* E.A. Bell and B.V. Charlwood (eds.), Secondary Plant Products. Encyclopedia of Plant Physiology, New Series, Volume 8. Springer Verlag, Berlin.

Basham, J.T., and R.M. Belyea. 1960. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part III. The deterioration of dead trees. *Forest Science* **6**: 78-96.

Basham, J.T., D.E. Etheridge, J. Hudak, D. Lachance, L.P. Magasi, and M.A. Stillwell. 1974. The deterioration of balsam fir trees killed by girdling in eastern Canada. *Canadian Forestry Service Information Report* O-X-214. 48 pp. + appendix.

Bauor, J., and J.P. Vité. 1975. Host selection by *Trypodendron lineatum*. *Naturwissenschaften* **62**: 539.

Becker, G. 1942. Zur Sinnesphysiologie des Hausbockkäfers. *Naturwissenschaften* **30**: 253-256.

Becker, G. 1944. Sinnesphysiologische Untersuchungen über die Eiablage des Hausbockkäfers. *Zeitschrift für Vergleichende Physiologie* **30**: 253-299.

Becker, G. 1962. Nahrungsfindung und Chemotaxien bei holzbewohnenden Käfern. *Zeitschrift für Angewandte Entomologie* **50**: 88-93.

Becker, W.B., and H.G. Abbott. 1960. Lumber downgrading losses due to insect damage to small unseasoned pine logs. *Journal of Forestry* **58**: 46-47.

Bedard, W.D., and L.E. Browne. 1969. A delivery-trapping system for evaluating insect chemical attractants in nature. *Journal of Economic Entomology* **62**: 1202-1203.

Belyea, R.M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part I. Notes on the seasonal history and habits of insects breeding in severely weakened and dead trees. *Canadian Entomologist* **84**: 325-335.

Bennett, R.B., and J.H. Borden. 1971. Flight arrestment of tethered *Dendroctonus pseudotsugae* and *Trypodendron lineatum* (Coleoptera: Scolytidae) in response to olfactory stimuli. *Annals of the Entomological Society of America* **64**: 1273-1286.

Benoit, P. 1978. Principaux insectes des forêts du Québec en 1977. *Phytoprotection* **59**: 108-116.

Billings, R.F. 1985. Southern pine beetles and associated insects: effects of rapidly-released host volatiles on response to aggregation pheromones. *Zeitschrift für Angewandte Entomologie* **99**: 483-491.

Billings, R.F., and R.S. Cameron. 1984. Kairomonal responses of Coleoptera, *Monochamus titillator* (Cerambycidae), *Thanasimus dubius* (Cleridae), and *Temnochila virescens* (Trogositidae), to behavioral chemicals of southern pine bark beetles (Coleoptera: Scolytidae). *Environmental Entomology* **13**: 1542-1548.

Billings, R.F., R.I. Gara, and B.F. Hrutfiord. 1976. Influence of ponderosa pine resin volatiles on the response of *Dendroctonus ponderosae* to synthetic trans-verbenol. *Environmental Entomology* **5**: 171-179.

Borden, J.H. 1974. Aggregation pheromones in the Scolytidae. Pp. 135-169 *in* Pheromones, M.C. Birch (ed.). North-Holland Publ., Amsterdam. xxi + 495 pp.

Borden, J.H. 1977. Behavioral responses of Coleoptera to pheromones, allomones and kairomones. Pp. 169-198 *in* Chemical Control of Insect Behavior, H.H. Shorey and J.J. McKelvey, Jr. (eds.). John Wiley and Sons, New York. viii + 414 pp.

Borden, J.H. 1982. Aggregation pheromones. Pp. 74-139 *in* Bark Beetles in North American Conifers, J.B. Mitton and K.B. Sturgeon (eds.). University of Texas Press, Austin, Texas. xi + 527 pp.

Borden, J.H., B.S. Lindgren, and L. Chong. 1980. Ethanol and α-pinene as synergists for the aggregation pheromones of two *Gnathotrichus* species. *Canadian Journal of Forest Research* **10**: 290-292.

Borden, J.H., C.J. King, B.S. Lindgren, L. Chong, D.R. Gray, A.C. Oehlschlager, K.N. Slessor, and H.D. Pierce, Jr. 1982. Variations in response of *Trypodendron lineatum* from two continents to semiochemicals and trap form. *Environmental Entomology* **11**: 403-408.

Bordeh, J.H., J.E. Conn, L.M. Friskie, B.E. Scott, L.J. Chong, H.D. Pierce, Jr., and A.C. Oehlschlager. 1983. Semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in British Columbia: baited-tree studies. *Canadian Journal of Forest Research* **13**: 325-333.

Borden, J.H., D.W.A. Hunt, D.R. Miller, and K.N. Slessor. 1986. Orientation in forest Coleoptera: an uncertain outcome of responses by individual beetles to variable stimuli. Pp. 97-109 *in* Mechanisms in Insect Olfaction, T.L. Payne, M.C. Birch, and C.E.J. Kennedy (eds.). Oxford University Press, Oxford.

Borden, J.H., A.M. Pierce, H.D. Pierce, Jr., L.J. Chong, A.J. Stock, and A.C. Oehlschlager. 1987a. Semiochemicals produced by western balsam bark beetle, *Dryocetes confusus* Swaine (Coleoptera: Scolytidae). *Journal of Chemical Ecology* **13**: 823-836.

Borden, J.H., L.C. Ryker, L.J. Chong, H.D. Pierce, Jr., B.D. Johnston, and A.C. Oehlschlager. 1987b. Response of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests. *Canadian Journal of Forest Research* **17**: 118-128.

Boutz, G.E., J.W Brewer, and J.N. Bishop. 1985. Capture patterns of *Scolytus multistriatus* (Marsh.) (Col., Scolytidae) attracted to a pheromone-baited trap. *Zeitschrift für Angewandte Entomologie* **99**: 366-370.

Browne, L.E. 1978. A trapping system for the western pine beetle using attractive pheromones. *Journal of Chemical Ecology* **4**: 261-275.

Butovitsch, V. 1939. Zur Kenntnis der Paarung, Eiablage und Ernährung der Cerambyciden. *Entomologisk Tidskrift* 60: 206-258.

Byers, J.A., B.S. Lanne, J. Löfqvist, F. Schlyter, and G. Bergström. 1985. Olfactory recognition of host-tree susceptibility by pine shoot beetles. *Naturwissenschaften* **6**: 324-326.

Byrne, K.J., A.A. Swigar, R.M. Silverstein, J.H. Borden, and E. Stokkink. 1974. Sulcatol: Population aggregation pheromone in the scolytid beetle, *Gnathotrichus sulcatus*. *Journal of Insect Physiology* **20**: 1895-1900.

Cade, S.C., B.F. Hrutfiord, and R.I. Gara. 1970. Identification of a primary attractant for *Gnathotrichus sulcatus* isolated from western hemlock logs. *Journal of Economic Entomology* **63**: 1014-1015.

Campbell, J.M., and contributors. 1979. Coleoptera. Pp. 357-387 *in* Canada and its Insect Fauna, H.V. Danks (ed.). *Memoirs of the Entomological Society of Canada* Number 108. 573 pp.

Canadian Standards Association. 1982. Wood utility poles and reinforcing stubs. Canadian Standards Association Standard CAN3-015-M.

Cates, R.G., and H. Alexander. 1982. Host resistance and susceptibility. Pp. 212-263 *in* Bark Beetles in North American Conifers, J.B. Mitton and K.B. Sturgeon (eds.). University of Texas Press, Austin, Texas. xi + 527 pp.

Cerezke, H.F. 1975. White-spotted sawyer beetle in logs. *Canadian Forestry Service Information Report* NOR-X-129. 6 pp.

Champlain, A.B., and J.N. Knull. 1932. Fermenting baits for trapping Elateridae and Cerambycidae (Coleop.). *Entomological News* 43: 253-257.

Chapman, J.A. 1966. The effect of attack by the ambrosia beetle *Trypodendron lineatum* (Oliv.) on log attractiveness. *Canadian Entomologist* 98: 50-59.

Chapman, J.A., and J.M. Kinghorn. 1955. Window flight traps for insects. *Canadian Entomologist* 87: 46-47.

Chapman, J.A., and J.M. Kinghorn. 1958. Studies of flight and attack activity of the ambrosia beetle, *Trypodendron lineatum* (Oliv.), and other scolytids. *Canadian Entomologist* 90: 362-372.

Chararas, C. 1979. Écophysiologie des Insectes Parasites des Forêts. Édition C. Chararas, Paris. ii + 297 pp.

Clements, R.W., and H.G. Williams. 1981. Attractants, techniques, and devices for trapping bark beetles. *U.S.D.A. Forest Service Research Note* SE-309. 3 pp.

Coulson, R.N., D.N. Pope, J.A. Gagne, W.S. Fargo, P.E. Pulley, L.J. Edson, and T.L. Wagner. 1980. Impact of foraging by *Monochamus titillator* (Col.: Cerambycidae) on within-tree populations of *Dendroctonus frontalis* (Col.: Scolytidae). *Entomophaga* 25: 155-170.

Craighead, F.C. 1921. Hopkins host-selection principle as related to certain cerambycid beetles. *Journal of Agricultural Research (U.S.D.A.)* 22: 189-220.

Derfer, J.M., and M.M. Derfer. 1983. Terpenoids. Pp. 709-762 *in* Kirk-Othmer Encyclopedia of Chemical Technology (3rd ed.), Volume 22. John Wiley and Sons, New York. xxvi + 1002 pp.

Dillon, L.S., and E.S. Dillon. 1941. The tribe Monochamini in the western hemisphere (Coleoptera: Cerambycidae). Reading Public Museum and Art Gallery, Scientific Publication Number 1. 135 pp. + 5 plates.

Doppelreiter, H. 1979. Nachweis eines weiblichen Sexualpheromons beim Hausbockkäfer (*Hylotrupes bajulus* (L.)). *Zeitschrift für Angewandte Entomologie* 88: 56-59.

Drew, J., and G.D. Pylant, Jr. 1966. Turpentine from the pulpwoods of the United States and Canada. *Tappi* 49: 430-438.

Dropkin, V.H., A. Foudin, E. Kondo, M. Linit, M. Smith, and K. Robbins. 1981. Pinewood nematode: a threat to U.S. forests? *Plant Disease* 65: 1022-1027.

Dubbel, V., K. Kerck, M. Sohrt, and S. Mangold. 1985. Influence of trap color on the efficiency of bark beetle pheromone traps. *Zeitschrift für Angewandte Entomologie* **99**: 59-64.

Duffy, E.A.J. 1953. A Monograph of the Immature Stages of British and Imported Timber Beetles (Cerambycidae). British Museum of Natural History, London. viii + 349 pp.

Dyer, E.D.A. 1962. The effect of exposure of hibernation sites on the time of *Trypodendron* spring flight. *Canadian Entomologist* **94**: 910-915.

Dyer, E.D.A., and J.A. Chapman. 1965. Flight and attack of the ambrosia beetle, *Trypodendron lineatum* (Oliv.) in relation to felling date of logs. *Canadian Entomologist* **97**: 42-57.

Dyer, L.J., and W.D. Seabrook. 1975. Sensilla on the antennal flagellum of the sawyer beetles *Monochamus notatus* (Drury) and *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae). *Journal of Morphology* **146**: 513-532.

Dyer, L.J., and W.D. Seabrook. 1978a. Some aspects of oviposition site selection in *Monochamus notatus* and *M. scutellatus* (Coleoptera: Cerambycidae). *Journal of Chemical Ecology* **4**: 199-210.

Dyer, L.J., and W.D. Seabrook. 1978b. Evidence for the presence of acceptor sites for different terpenes on one receptor cell in male *Monochamus notatus* (Drury) (Coleoptera: Cerambycidae). *Journal of Chemical Ecology* **4**: 523-529.

Eidmann, H.H., P. Baeckström, S. Harding, T. Norin, J. Vrkoc, and J. Weslien. 1987. Methylbutynol effectively replaces methylbutenol, a pheromone component of *Ips typographus* (L.) (Coleoptera: Scolytidae). *Journal of Chemical Ecology* **13**: 1555-1560.

Evans, D.A., and M.D. Higgs. 1975. Mono-oxygenated monoterpenes from the frass of the wood-boring beetle *Hylotrupes bajulus* (L.). *Tetrahedron Letters* **41**: 3585-3586.

Evans, W.G. 1966. Morphology of the infra-red sense organ of *Melanophila acuminata*. *Annals of the Entomological Society of America* **59**: 873-877.

Fatzinger, C.W. 1985. Attraction of the black turpentine beetle (Coleoptera: Scolytidae) and other forest Coleoptera to turpentine-baited traps. *Environmental Entomology* **14**: 768-775.

Francke, W., and J.P. Vité. 1983. Oxygenated terpenes in pheromone systems of bark beetles. *Zeitschrift für Angewandte Entomologie* **96**: 146-156.

Furniss, R.L., and V.M. Carolin. 1977. Western forest insects. *U.S.D.A. Forest Service Miscellaneous Publication* Number 1339. vii + 654 pp.

Galford, J.R. 1977. Evidence for a pheromone in the locust borer. *U.S.D.A. Forest Service Research Note* NE-240. 3 pp.

Galford, J.R. 1980. Bait bucket trapping for red oak borers (Coleoptera: Cerambycidae). *U.S.D.A. Forest Service Research Note* NE-293. 2pp.

Gardiner, L.M. 1957. Collecting wood-boring beetle adults by turpentine and smoke. *Canadian Forestry Service Bi-monthly Research Notes* **13**: 2.

Gardiner, L.M. 1969. Immature stages and biology of eastern Canadian Cerambycidae (Coleoptera) in the Sault Ste. Marie collection. *Canadian Forestry Service Internal Report* O-14. ii + 109 pp.

Gardiner, L.M. 1975. Insect attack and value loss in wind-damaged spruce and jack pine stands in northern Ontario. *Canadian Journal of Forest Research* **5**: 387-398.

Garth, G.S., and C.H. Shanks, Jr. 1978. Some factors affecting infestations of strawberry fields by the black vine weevil in western Washington. *Journal of Economic Entomology* **71**: 443-448.

Graham, K. 1968. Anaerobic induction of primary chemical attractancy for ambrosia beetles. *Canadian Journal of Zoology* **46**: 905-908.

Groberman, L.J., and J.H. Borden. 1981. Behavioral response of *Dendroctonus pseudotsugae* and *Trypodendron lineatum* (Coleoptera: Scolytidae) to selected wavelength regions of the visible spectrum. *Canadian Journal of Zoology* **59**: 2159-2165.

Groberman, L.J., and J.H. Borden. 1982. Electrophysiological response of *Dendroctonus pseudotsugae* and *Trypodendron lineatum* (Coleoptera: Scolytidae) to selected wavelength regions of the visible spectrum. *Canadian Journal of Zoology* **60**: 2180-2189.

Guenther, E. 1949. The Essential Oils. Volume Two. The Constituents of Essential Oils. D. Van Nostrand Co., Princeton. xiii + 852 pp.

Hanover, J.W. 1975. Physiology of tree resistance to insects. *Annual Review of Entomology* **20**: 75-95.

Hellrigl, K.G. 1971. Die Bionomie der europäischen *Monochamus* Arten (Coleopt., Cerambycid.) und ihre Bedeutung für die Forst- und Holzwirtschaft. *Redia* **52**: 367-509.

Hertel, G.D. 1970. Response of the pales weevil to loblolly pine seedlings and cut stems. *Journal of Economic Entomology* **63**: 995-997.

Higgs, M.D., and D.A. Evans. 1978. Chemical mediators in the oviposition behaviour of the house longhorn beetle, *Hylotrupes bajulus*. *Experientia* **34**: 46-47.

Hilker, M. 1984. Untersuchungen über die Attraktivität von Weißfarben unterschiedlicher (UV)-Lichtremission für *Pityogenes chalcographus* L. und *Ips typographus* L. (Coleoptera, Scolytidae). *Zeitschrift für Angewandte Entomologie* **98**: 463-473.

Hines, J.W., and H.J. Heikkenen. 1977. Beetles attracted to severed Virginia pine (*Pinus virginiana* Mill.). *Environmental Entomology* **6**: 123-127.

Holdeman, Q.L. 1980. The pinewood nematode (*Bursaphelenchus lignicolus* Mamyia & Kiyohara 1972) and the associated pine wilt disease of Japan. California Department of Food and Agriculture, and Agricultural Commission of California, Sacramento. 45 pp.

Hughes, A.L. 1979. Reproductive behavior and sexual dimorphism in the white-spotted sawyer *Monachamus scutellatus*. *Coleopterists' Bulletin* **33**: 45-47.

Hughes, A.L. 1981. Differential male mating success in the white spotted sawyer *Monochamus scutellatus* (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* **74**: 180-184.

Hunt, R.S., and E. von Rudloff. 1974. Chemosystematic studies in the genus *Abies*. I. Leaf and twig oil analysis of alpine and balsam firs. *Canadian Journal of Botany* **52**: 477-487.

Ikeda, T., and K. Oda. 1980. The occurrence of attractiveness for Monochamus alternatus Hope (Coleoptera: Cerambycidae) in nematode-infected pine trees. *Journal of the Japanese Forestry Society* **62**: 432-434.

Ikeda, T., N. Enda, A. Yamane, K. Oda, and T. Toyoda. 1980. Attractants for the Japanese pine sawyer, *Monochamus alternatus* Hope (Coleoptera: Cerambycidae). *Applied Entomology and Zoology* **15**: 358-361.

Ikeda, T., M. Miyazaki, K. Oda, A. Yamane, and N. Enda. 1981. The chemical ecology of *Monochamus alternatus* Hope on the relationship with pine wood nematodes and host tree. Proceedings of the XVII IUFRO World Congress, Division II, pp. 297-303.

Iwabuchi, K. 1982. Mating behavior of *Xylotrechus pyrrhoderus* Bates (Coleoptera: Cerambycidae). I. Behavioral sequences and existence of the male sex pheromone. *Applied Entomology and Zoology* **17**: 494-500.

Iwabuchi, K., J. Takahashi, Y. Nakagawa, and T. Sakai. 1985. Electroantennogram response of grape borer *Xylotrechus pyrrhoderus* Bates (Coleoptera: Cerambycidae) to its male sex pheromone components. *Journal of Chemical Ecology* **11**: 819-828.

Iwabuchi, K., J. Takahashi, Y. Nakagawa, and T. Sakai. 1986. Behavioral responses of female grape borer *Xylotrechus pyrrhoderus* Bates (Coleoptera: Cerambycidae) to synthetic male sex pheromone components. *Applied Entomology and Zoology* **21**: 21-27.

Iwabuchi, K., J. Takahashi, and T. Sakai. 1987. Occurrence of 2,3–octanediol and 2–hydroxy–3–octanone, possible male sex pheromone in *Xylotrechus chinensis* Chevrolat (Coleoptera: Cerambycidae). *Applied Entomology and Zoology* **22**: 110-111.

Johann, M. 1986. Zur Anlockung des Buchdruckers (*Ips typographus* L.). I. Die Lockwirkung natürlichen Brutmaterials. *Journal of Applied Entomology* **101**: 332-342.

Juillet, J.A. 1963. A comparison of four types of traps used for capturing flying insects. *Canadian Journal of Zoology* **41**: 219-223.

Kangas, E., V. Perttunen, and H. Oksanen. 1970. Responses of *Blastophagus minor* Hart. (Col., Scol.) to the pine phloem fraction known to be attractant to *Blastophagus piniperda* L. *Annales Entomologici Fennici* **36**: 120-122.

Kennedy, J.S. 1965. Mechanisms of host plant selection. *Annals of Applied Biology* **56**: 317-322.

Kerck, K. 1972. Äthylalkohol und Stammkontur als Komponenten der Primäranlockung bei *Xyloterus domesticus* L. (Col.: Scolytidae). *Naturwissenschaften* **59**: 423.

Klimetzek, D., and J.P. Vité. 1978. Einfluss des saisonbedingten Verhaltens beim Buchdrücker auf die Wirksamkeit von Flug- und Landefallen. *Allgemeine Forstzeitschrift* **33**: 1446-1447.

Knull, J.N. 1951. The checkered beetles of Ohio (Coleoptera: Cleridae). *Ohio Biological Survey Bulletin* Number 42 (volume 8[2]: 269-350).

Kobayashi, F. 1978. Pine bark beetle problem in Japan, referring to the discovery of the pine wood nematode, *Bursaphelenchus lignicolus* (Mamyia & Kiyohara). *Anzeiger für Schädlingskunde, Pflanzen- und Umweltschutz* **51**: 76-79.

Kohnle, U., and J.P. Vité. 1984. Bark beetle predators: strategies in the olfactory perception of prey species by clerid and trogositid beetles. *Zeitschrift für Angewandte Entomologie* **98**: 504-508.

Kuboki, M., K. Akutsu, A. Sakai, and T. Chuman. 1985. Bioassay of the sex pheromone of the udo longicorn beetle, *Acalolepta luxuriosa* Bates (Coleoptera: Cerambycidae). *Applied Entomology and Zoology* **20**: 88-89.

Kuwahara, Y., S. Matsuyama, and T. Suzuki. 1987. Identification of 2,3–octanediol, 2–hydroxy–3–octanone and 3–hydroxy–2–octanone from male *Xylotrechus chinensis* Chevrolat as possible sex pheromones (Coleoptera: Cerambycidae). *Applied Entomology and Zoology* **22**: 25-28.

Lanne, B.S., F. Schlyter, J.A. Byers, J. Löfqvist, A. Leufvén, G. Bergström, J.N.C. van der Pers, R. Unelius, P. Baeckström, and T. Norin. 1987. Differences in attraction to semiochemicals present in sympatric pine shoot beetles, *Tomicus minor* and *T. piniperda*. *Journal of Chemical Ecology* **13**: 1045-1067.

Lie, R., and A. Bakke. 1981. Practical results from the mass-trapping of *Ips typographus* in Scandinavia. Pp. 175-181 *in* Management of Insect Pests with Semiochemicals: Concepts and Practice, E.R. Mitchell (ed.). Plenum Press, New York. 514 pp.

Lindgren, B.S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). *Canadian Entomologist* **115**: 299-302.

Lindgren, B.S., and J.H. Borden. 1983. Survey and mass trapping of ambrosia beetles (Coleoptera: Scolytidae) in timber processing areas on Vancouver Island. *Canadian Journal of Forest Research* **13**: 481-493.

Lindgren, B.S., J.H. Borden, L. Chong, L.M. Friskie, and D.B. Orr. 1983. Factors influencing the efficiency of pheromone-baited traps for three species of ambrosia beetles (Coleoptera: Scolytidae). *Canadian Entomologist* **115**: 303-313.

Linsley, E.G. 1959. Ecology of Cerambycidae. *Annual Review of Entomology* **4**: 99-138.

Linsley, E.G. 1961. The Cerambycidae of North America. Part I. Introduction. *University of California Publications in Entomology* **18**: 1-97, + 35 plates.

Linsley, E.G., and J.A Chemsak. 1984. The Cerambycidae of North America, Part VII, No. 1: Taxonomy and classification of the subfamily Lamiinae, tribes Parmenini through Acanthoderini. *University of California Publications in Entomology* **102**: 1-258.

Mamiya, Y., and N. Enda. 1972. Transmission of *Bursaphelenchus lignicolus* (Nematoda: Aphelenchoididae) by *Monochamus alternatus* (Coleoptera: Cerambycidae). *Nematologica* **18**: 159-162.

Mares, J.T., and W.H. Robinson. 1986. Structure of the ovipositor of *Hylotrupes bajulus* (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* **79**: 344-349.

McLean, J.A., and J.H. Borden. 1975. Survey for *Gnathotrichus sulcatus* (Coleoptera: Scolytidae) in a commercial sawmill with the pheromone, sulcatol. *Canadian Journal of Forest Research* **5**: 586-591.

McLean, J.A., and J.H. Borden. 1977. Suppression of *Gnathotrichus sulcatus* with sulcatol-baited traps in a commercial sawmill and notes on the occurrence of *G. retusus* and *Trypodendron lineatum*. *Canadian Journal of Forest Research* **7**: 348-356.

McLean, J.A., and J.H. Borden. 1979. An operational pheromone-based suppression program for an ambrosia beetle, *Gnathotrichus sulcatus*, in a commercial sawmill. *Journal of Economic Entomology* **72**: 165-172.

McLean, J.A., A. Bakke, and H. Niemeyer. 1987. An evaluation of three traps and two lures for the ambrosia beetle *Trypodendron lineatum* (Oliv.) (Coleoptera: Scolytidae) in Canada, Norway, and West Germany. *Canadian Entomologist* **119**: 273-280.

Miller, J.R., and K.L. Strickler. 1984. Finding and accepting host plants. Pp. 127-157 *in* Chemical Ecology of Insects, W.J. Bell and R.T. Cardé (eds.). Chapman and Hall Ltd., London. xvi + 524 pp.

Mizell, R.F., J.L. Frazier, and T.E. Nebeker. 1984. Response of the clerid predator *Thanasimus dubius* (F.) to bark beetle pheromones and tree volatiles in a wind tunnel. *Journal of Chemical Ecology* **10**: 177-187.

Moeck, H.A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). *Canadian Entomologist* **102**: 985-995.

Moeck, H.A. 1971. Field test of ethanol as a scolytid attractant. *Canadian Forestry Service Bi-monthly Research Notes* **27**: 11-12.

Moeck, H.A. 1980. Field test of Swedish "drainpipe" pheromone trap with mountain pine beetle. *Canadian Forestry Service Bi-monthly Research Notes* **36**: 2-3.

Moeck, H.A., D.L. Wood, and K.Q. Lindahl, Jr. 1981. Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. *Journal of Chemical Ecology* **7**: 49-83.

Montgomery, M.E., and P.M. Wargo. 1983. Ethanol and other host-derived volatiles as attractants to beetles that bore into hardwoods. *Journal of Chemical Ecology* **9**: 181-190.

Moser, J.C., and L.E. Browne. 1978. A nondestructive trap for *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae). *Journal of Chemical Ecology* **4**: 1-7.

Niemeyer, H. 1985. Field response of *Ips typographus* L. (Col., Scolytidae) to different trap structures and white versus black flight barriers. *Zeitschrift für Angewandte Entomologie* **99**: 44-51.

Niemeyer, H., and G. Watzek. 1977. Lockstoff-Fallen: Versuche zur Bekämpfung des Buchdruckers (*Ips typographus*) ohne Fangbäume und Insektizide. *Allgemeine Forstzeitschrift* **32**: 1009-1010.

Niemeyer, H., T. Schröder, and G. Watzek. 1983. Eine neue Lockstoff-Falle zur Bekämpfung von rinden- und holzbrütenden Borkenkäfern. *Forst und Holzwirt* **38**: 105-112.

Nijholt, W.W., and J.A. Chapman. 1968. A flight trap for collecting living insects. *Canadian Entomologist* **100**: 1151-1153.

Nijholt, W.W.; and J. Schönherr. 1976. Chemical response behavior of scolytids in West Germany and western Canada. *Canadian Forestry Service Bi-monthly Research Notes* **32**: 31-32.

Oda, K. 1974. Volatile compounds from felled logs of *Pinus densiflora*. *Bulletin of the Government Foret Experiment Station* Number 266, 1-11.

Parmalee, F.T. 1941. Longhorned and flat headed borers attacking fire-killed coniferous timber in Michigan. *Journal of Economic Entomology* **34**: 377-380.

Payne, T.L., J.E. Coster, J.V. Richerson, L.J. Edson, and E.R. Hart. 1978a. Field response of the southern pine beetle to behavioral chemicals. *Environmental Entomology* **7**: 578-582.

Payne, T.L., J.E. Coster, J.V. Richerson, E.R. Hart, R.L. Heden, and L.J. Edson. 1978b. Reducing variation in field tests of behavioral chemicals for the southern pine beetle. *Journal of the Georgia Entomological Society* **13**: 85-90.

Payne, T.L., J.C. Dickens, and J.V. Richerson. 1984. Insect predator-prey coevolution via enantiomeric specificity in a kairomone-pheromone system. *Journal of Chemical Ecology* **10**: 487-492.

Perttunen, V. 1957. Reactions of two bark beetle species, *Hylurgops palliatus* Gyll. and *Hylastes ater* Payk. (Col., Scolytidae) to the terpene α-pinene. *Annales Entomologici Fennici* **23**: 101-110.

Perttunen, V., H. Oksanen, and E. Kangas. 1970. Aspects of the external and internal factors affecting the olfactory orientation of *Blastophagus piniperda* (Coleoptera: Scolytidae). *Contributions from Boyce Thompson Institute* **24**: 293-297.

Prebble, M.L., and L.M. Gardiner. 1958. Degrade and value loss in fire-killed pine in Mississagi area of Ontario. *Forestry Chronicle* **34**: 142-145.

Prentice, R.M., and A.E. Campbell. 1959. Volume loss of pulpwood in Manitoba caused by wood borers. *Forestry Chronicle* **35**: 142-145.

Raffa, K.F., and A.A. Berryman. 1982. Accumulation of monoterpenes and associated volatiles following inoculation of grand fir with a fungus transmitted by the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). *Canadian Entomologist* **114**: 797-810.

Raske, A.G. 1972. Biology and control of *Monochamus* and *Tetropium*, the economic wood borers of Alberta. *Canadian Forestry Service Internal Report* NOR-9. 48 pp.

Raske, A.G. 1973a. Taxonomic relationship between *Monochamus scutellatus* and *Monochamus oregonensis* (Coleoptera: Cerambycidae). *Canadian Entomologist* **105**: 795-806.

Raske, A.G. 1973b. Relationship between felling date and larval density of *Monochamus scutellatus*. *Canadian Forestry Service Bi-monthly Research Notes* **29**: 23-24.

Raske, A.G. 1975. Distribution of *Monochamus* larval entrance holes on lodgepole pine logs. *Canadian Forestry Service Bi-monthly Research Notes* **31**: 33.

Regnander, J., and C. Solbreck. 1981. Effectiveness of different types of pheromone traps used against *Ips typographus* (L.) (Col., Scolytidae) in Sweden. *Anzeiger für Schädlingskunde, Pflanzen- und Umweltschutz* **54**: 104-108.

Richmond, H.A., and R.R. Lejeune. 1945. The deterioration of fire-killed white spruce by wood-boring insects in northern Saskatchewan. *Forestry Chronicle* **21**: 168-192.

Rose, A.H. 1957. Some notes on the biology of *Monochamus scutellatus* (Coleoptera: Cerambycidae). *Canadian Entomologist* **89**: 547-553.

Rose, W.F., III, R.F. Billings, and J.P. Vité. 1981. Southern pine bark beetles: evaluation of non-sticky pheromone trap designs for survey and research. *Southwestern Entomologist* **6**: 1-9.

Rowe, J.S. 1972. Forest Regions of Canada. Canadian Forestry Service Publication Number 1300. x + 172 pp.

Rudinsky, J.A. 1966. Scolytid beetles associated with Douglas fir: response to terpenes. *Science* **152**: 218-219.

Safranyik, L., and A.G. Raske. 1970. Sequential sampling plan for larvae of *Monochamus* in lodgepole pine logs. *Journal of Economic Entomology* **63**: 1903-1906.

Sakai, T., Y. Nakagawa, J. Takahashi, K. Iwabuchi, and K. Ishii. 1984. Isolation and identification of the female sex pheromone of the grape borer *Xylotrechus pyrrhoderus* Bates (Coleoptera: Cerambycidae). *Chemistry Letters*, pp. 263-264.

Schlyter, F., G. Birgersson, J.A. Byers, J. Löfqvist, and G. Bergström. 1987a. Field response of spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates. *Journal of Chemical Ecology* **13**: 701-716.

Schlyter, F., J.A. Byers, and J. Löfqvist. 1987b. Attraction to pheromone sources of different quantity, quality, and spacing: density-regulation mechanisms in bark beetle *Ips typographus*. *Journal of Chemical Ecology* **13**: 1503-1523.

Schönherr, J. 1971. Beobachtungen über die Empfindlichkeit von Borkenkäfern gegenüber kurzwelligem Licht. *Zeitschrift für Angewandte Entomologie* **68**: 244-250.

Schönherr, J. 1976. Importance of visual stimuli in the host selection behavior of bark beetles (*Dendroctonus ponderosae* and *Ips montanus*). *Colloques Internationaux du Centre National de la Recherche Scientifique* **265**: 187-193.

Schroeder, L.M., and H.H. Eidmann. 1987. Gallery initiation by *Tomicus piniperda* (Coleoptera: Scolytidae) on Scots pine trees baited with host volatiles. *Journal of Chemical Ecology* **13**: 1591-1599.

Siegfried, B.D. 1987. In-flight responses of the pales weevil, *Hylobius pales* (Coleoptera: Curculionidae) to monoterpene constituents of southern pine gum turpentine. *Florida Entomologist* **70**: 97-102.

Solomon, J.D., L. Newsome, and W.N. Darwin. 1972. Carpenterworm moths and cerambycid hardwood borers caught in light traps. *Journal of the Georgia Entomological Society* **7**: 76-79.

Solomon, J.D., R.E. Doolittle, and T.J. Spilman. 1976. Cerambycid beetles captured in sticky-traps in Mississippi. *Coleopterists' Bulletin* **30**: 289-290.

Soper, R.S., Jr., and R.E. Olson. 1963. Survey of biota associated with *Monochamus* in Maine. *Canadian Entomologist* 95: 83-95.

Southwood, T.R.E. 1978. Ecological Methods. Chapman and Hall, London. xxiv+524 pp.

Stewart, P.A., and J.J. Lam, Jr. 1970. Capture of forest insects in traps equipped with blacklight lamps. *Journal of Economic Entomology* **63**: 871-873.

Svihra, P. 1972. Survey of the seasonal flight pattern of *Ips typographus* L. with an attractant trap in Slovakia. *Zeitschrift für Angewandte Entomologie* **72**: 80-92.

Thomas, H.A., and G.D. Hertel. 1969. Responses of the pales weevil to natural and synthetic host attractants. *Journal of Economic Entomology* **62**: 383-386.

Thomas, H.A., and G.D. Hertel. 1979. Responses of pales weevils to natural and synthetic traps under field conditions. *Journal of Economic Entomology* **72**: 342-345.

Thorsteinson, A.J. 1960. Host selection in phytophagous insects. *Annual Review of Entomology* **5**: 193-218.

Tilles, D.A., K. Sjödin, G. Nordlander, and H.H. Eidmann. 1986. Synergism between ethanol and conifer host volatiles as attractants for the pine weevil, *Hylobius abietis* (L.) (Coleoptera: Curculionidae). *Journal of Economic Entomology* **79**: 970-973.

Trägårdh, I. 1930. Some aspects in the biology of longicorn beetles. *Bulletin of Entomological Research* **21**: 1-8.

van Huizen, T.H.P. 1977. The significance of flight activity in the life cycle of *Amara plebeja* Gyll. (Coleoptera, Carabidae). *Oecologia* **29**: 27-41.

Vité, J.P. 1984. Erfahrungen und Erkenntnisse zur akuten Gefährdung des mitteleuropäischen Fichtenwaldes durch Käferbefall. *Allgemeine Forstzeitschrift* **39**: 249-254.

Vité, J.P., and A. Bakke. 1979. Synergism between chemical and physical stimuli in host colonization by an ambrosia beetle. *Naturwissenschaften* **66**: 528-529.

von Rudloff, E. 1969. Scope and limitations of gas chromatography of terpenes in chemosystematic studies. Pp. 127-162 *in* Recent Advances in Phytochemistry, Volume 2, M.K. Seikel and V.C. Runeckles (eds.). Appleton-Century-Crofts, New York. ix + 175 pp.

von Rudloff, E. 1975. Volatile leaf oil analysis in chemosystematic studies of North American conifers. *Biochemical Systematics and Ecology* **2**: 131-167.

Walsh, K.D., and M.J. Linit. 1985. Oviposition biology of the pine sawyer, *Monochamus carolinensis* (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* **78**: 81-85.

Wellso, S.G., G.V. Manley, and J.A. Jackman. 1976. Keys and notes on the Buprestidae (Coleoptera) of Michigan. *Great Lakes Entomologist* **9**: 1-22.

Werner, R.A. 1972a. Aggregation behaviour of the beetle *Ips grandicollis* in response to host-produced attractants. *Journal of Insect Physiology* **18**: 423-437.

Werner, R.A. 1972b. Response of the beetle, *Ips grandicollis*, to combinations of host and insect produced attractants. *Journal of Insect Physiology* **18**: 1403-1412.

Wickman, B.E. 1965. Insect-caused deterioration of windthrown timber in northern California, 1963-1964. *U.S.D.A. Forest Service Research Paper* PSW-20. 14 pp.

Wickman, B.E. 1968. The biology of the fir tree borer, *Semanotus litigiosus* (Coleoptera: Cerambycidae), in California. *Canadian Entomologist* **100**: 208-220.

Wickman, B.E. 1969. Wood borers attracted to turpentine in windthrown timber in northern California. *U.S.D.A. Forest Service Research Note* PSW-195. 4 pp.

Wilkening, A.J., J.L. Foltz, T.H. Atkinson, and M.D. Connor. 1981. An omnidirectional flight trap for ascending and descending insects. *Canadian Entomologist* **113**: 453-455.

Wilkinson, R.C. 1972. Monoterpenes as possible attractants to the white-pine weevil, *Pissodes strobi*. Abstract, 2nd North American Forest Biology Workshop, Oregon State University, Corvallis, Oregon. (cited in Wilkinson 1980)

Wilkinson, R.C. 1980. Relationship between cortical monoterpenes and susceptibility of eastern white pine to white-pine weevil attack. *Forest Science* **26**: 581-589.

Wilson, L.F. 1961a. Calculating volume loss in balsam fir pulpwood from wood-boring insects. *U.S.D.A. Forest Service Technical Note* LS-599. 2 pp.

Wilson, L.F. 1961b. Attraction of wood-boring insects to freshly cut pulpsticks. *U.S.D.A. Forest Service Technical Note* LS-610. 2 pp.

Wilson, L.F. 1962. White-spotted sawyer. *U.S.D.A. Forest Service Forest Pest Leaflet* Number 74. 7 pp.

Wingfield, M.J., and R.A. Blanchette. 1983. Transmission of the pine wood nematode, *Bursaphelenchus xylophilus* during oviposition of *Monochamus carolinensis*, *M. scutellatus* and *M. mutator*. *Phytopathology* **73**: 839 (Abstract A578).

Wood, D.L. 1972. Selection and colonization of ponderosa pine by bark beetles. Pp. 101-117 *in* Insect/Plant Relationships, H.F. van Emden (ed.). Symposium of the Royal Entomological Society of London Number 6. Blackwell, Oxford. viii + 215 pp.

Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Review of Entomology* **27**: 411-446.

Wroblewska, H., A.H. Conner, and J.W. Rowe. 1977. Lightwood formation in red pine treated with paraquat. *Wood Science* **10**: 1-4.

Younan, E.G., and F.P. Hain. 1982. Evaluation of five trap designs for sampling insects associated with severed pines. *Canadian Entomologist* **114**: 789-796.

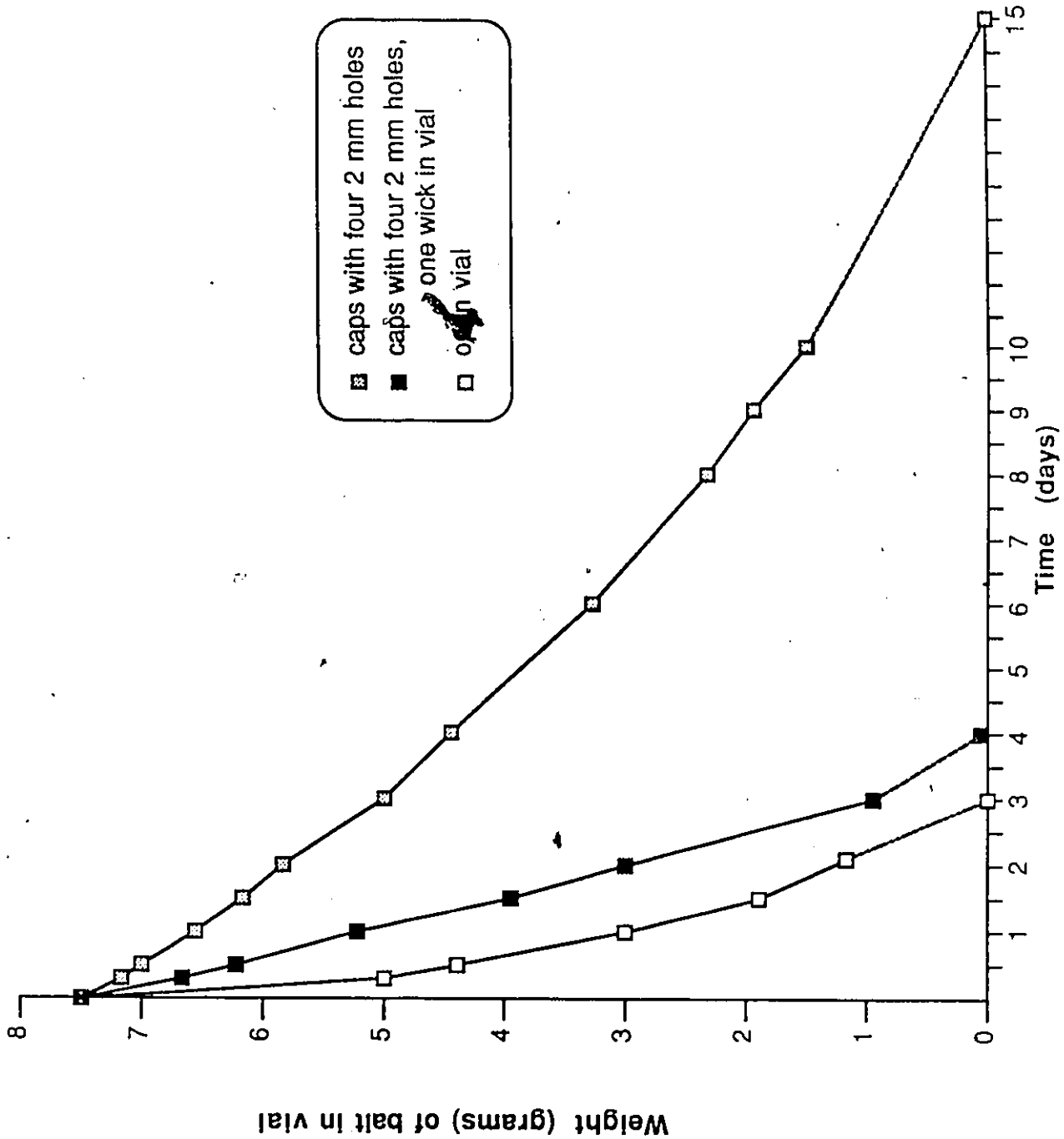
Zar, J.H. 1984. Biostatistical Analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J. xiv + 718 pp.

Zavarin, E. 1968. Chemotaxonomy of the genus *Abies*—II. Within tree variation of the terpenes in cortical oleoresin. *Phytochemistry* **7**: 92-107.

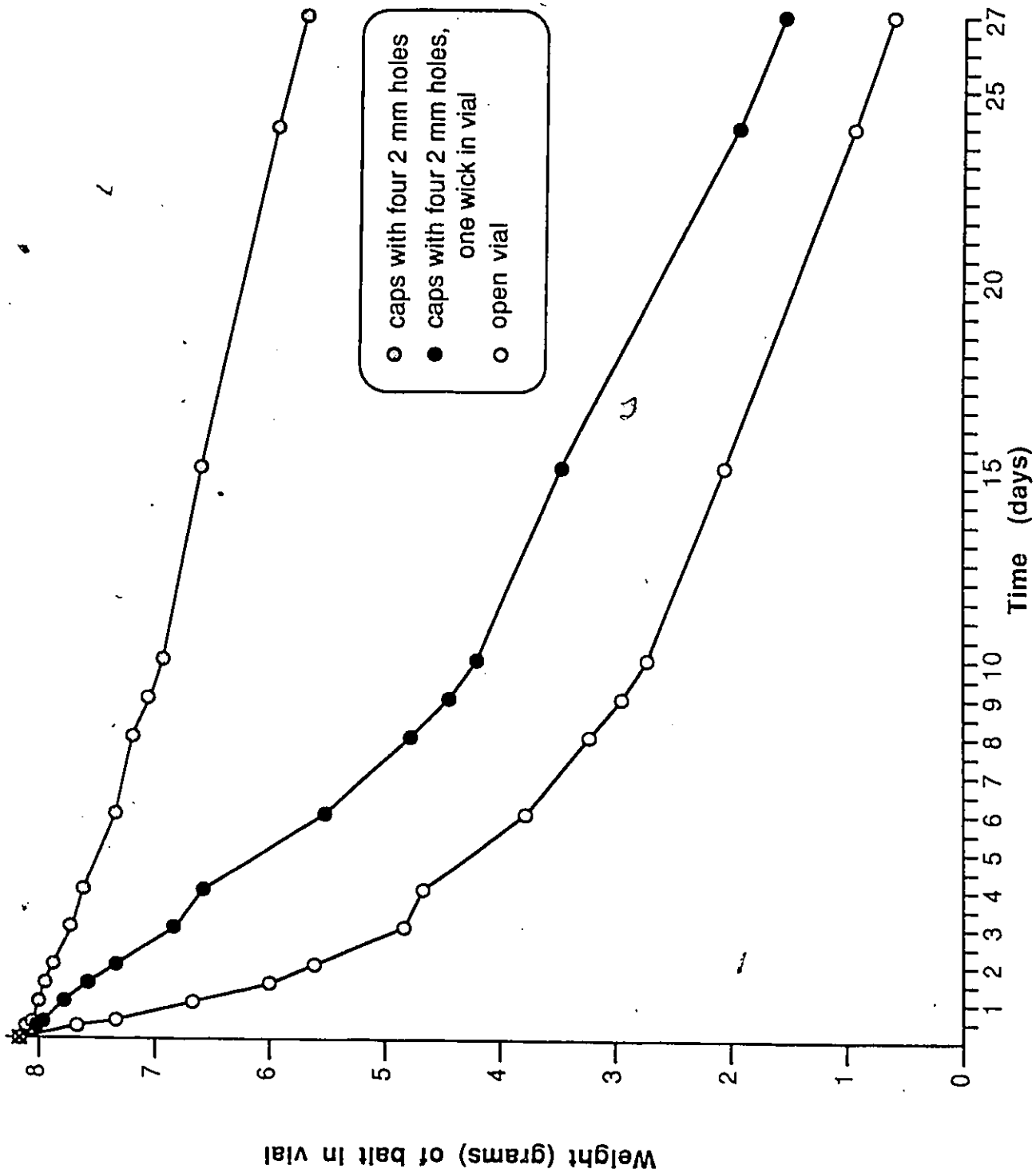
Zavarin, E., and K. Snajberk. 1965. Chemotaxonomy of the genus *Abies*—I. Survey of the terpenes present in the *Abies* balsams. *Phytochemistry* **4**: 141-148.

APPENDICES

Appendix 1. Rates of ethanol vaporisation in the laboratory.



Appendix 1. Rates of monoterpene vaporisation in the laboratory.



Appendix 2. Equations used for non-parametric analyses of data.

Abbreviations:

a = number of treatments
b = number of replicates
c = Scheffé contrast coefficient
N = count of all samples ($N = a \cdot b$)
q = Studentised range critical value
R = rank sum for treatment
t_i = number of ties in the ith group of ties
ΣT = correction for ties
U = Mann-Whitney statistic
Z = normal deviate
μ_U = mean of U distribution
σ_U = standard error of U distribution
χ^2_r = Friedman χ^2 (based on ranks)

Friedman test (Zar 1984, eq.13.37):

$$\text{Friedman } \chi^2_r = \frac{12}{ba(a+1)} \Sigma R^2 - 3b(a+1)$$

Friedman test corrected for ties (Zar 1984, modified from eq.13.38 and eq.13.39):

$$\text{Friedman } \chi^2_r = \frac{\Sigma R^2 - (\Sigma R)^2 / a}{\frac{ba(a+1)}{12} - \frac{\Sigma T}{12(a-1)}}$$

where $\Sigma T = \Sigma (t_i^3 - t_i)$, such that $\Sigma T = \Sigma T$ of eq. 11.33.

Standard error (S.E.) for Tukey and Newman-Keuls comparisons (Zar 1984, eq.13.42):

$$\text{S.E.} = \left[\frac{ba\,(a+1)}{12} \right]^{1/2}$$

and then using critical values of $q_{\alpha,\infty,k}$ for comparisons of rank sums.

Standard error (S.E.) for Tukey and Newman-Keuls comparisons, corrected for ties (Zar 1984, modified from eq.13.42 and eq.13.48, referring to sections 12.6, 12.7, 13.9):

$$\text{S.E.} = \left[\left(\frac{ba(a+1)}{12} - \frac{\Sigma T}{12(a-1)} \right)\right]^{1/2}$$

where $\Sigma T = \Sigma\,(t_i^3 - t_i)$,
and then using critical values of $q_{\alpha,\infty,k}$ for comparisons of rank sums.

Standard error (S.E.) for Scheffé-type multiple contrasts, corrected for ties (Zar 1984, modified from eq.13.48):

$$\text{S.E.} = \left[\left(\frac{ba(a+1)}{12} - \frac{\Sigma T}{12(a-1)} \right) \cdot \Sigma c^2 \right]^{1/2}$$

where $\Sigma T = \Sigma\,(t_i^3 - t_i)$,
and then using critical values of $([\chi^2_r]_{\alpha,a,b})^{1/2}$ or of $(\chi^2_{\alpha,a-1})^{1/2}$ for contrasts of rank sums.

Mann-Whitney test corrected for ties using normal approximation (Zar 1984, section 9.9):

$$U = b^2 + (\,b\,[b+1] + 2\,) - R_1$$

$$\sigma_U = \left(\frac{b^2}{N^2 - N} \cdot \frac{N^3 - N - \Sigma T}{12} \right)^{1/2}, \text{ where } \Sigma T = \Sigma\,(t_i^3 - t_i).$$

$$\mu_U = b^2 + 2$$

$$Z = \frac{|\,U - \mu_U\,| - 0.05}{\sigma_U}$$

and then using critical values of $t_{\alpha,\infty}$

APPENDIX 3. MAJOR BEETLE SPECIES CAPTURED IN STICKY STOVEPIPE TRAPS, MULTIPLE FUNNEL TRAPS, AND FLIGHT INTERCEPTION TRAPS (BAITED AND UNBAITED) AT CHALK RIVER, ONTARIO, CANADA. *

CARABIDAE
Notobia terminata (Say)

LEIODIDAE
Anisotoma sp.

SILPHIDAE
Oiceoptoma noveboracense (Forster)
Nicrophorus defodiens Mannerheim
Nicrophorus orbicollis Say
Nicrophorus sayi Laporte
Nicrophorus tomentosus Weber

SCARABAEIDAE
Serica atracapilla Kirby
Phyllophaga anxia LeConte

BUPRESTIDAE
Chalcophora virginiensis (Drury)
Chalcophora liberta (Germar)
Dicerca tenebrosa (Kirby)
Dicerca dumolini (Gory & Laporte)
Dicerca callosa callosa Casey
Dicerca tenebrica (Kirby)
Dicerca divaricata (Say)
Poecilonota cyanipes (Say)
Buprestis salisburyensis (Herbst)
Buprestis sulcicollis (LeConte)
Buprestis maculipennis Gory
Buprestis maculativentris Say
Buprestis nuttalli (Kirby)
Melanophila fulvoguttata (Harris)
Melanophila aeneola Melsheimer
Chrysobothris floricola Gory
Chrysobothris rugosiceps Melsheimer
Chrysobothris femorata (Olivier)
Chrysobothris verdigripennis Frost
Chrysobothris dentipes (Germar)
Chrysobothris scabripennis Castelnau & Gory
Chrysobothris trinervia (Kirby)
Chrysobothris sexsignata (Say)
Agrilus vittaticollis (Randall)
Agrilus anxius Gory
Agrilus liragus Barter & Brown

ELATERIDAE
Lacon brevicornis (LeConte)
Lacon obtecus (Say)
Limonius aurifer LeConte
Limonius aeger LeConte
Athous brightwelli (Kirby)
Athous rufifrons (Randall)
Denticollis denticornis (Kirby)
Ctenicera spinosa (LeConte)
Ctenicera hamata (Say)
Ctenicera propola propola (LeConte)
Ctenicera triundulata (Randall)
Ctenicera mediana (Germar)
Ctenicera inflata (Say)
Ctenicera hieroglypha (Say)
Ctenicera pulchra (LeConte)
Hemicrepidius memnonius (Herbst)
Hemicrepidius brevicollis (Candeze)
Dalopius cognatus Brown
Sericus brunneus (Linnaeus)
Agriotes stabilis (LeConte)
Agriotes collaris (LeConte)
Agriotes limosus (LeConte)
Ampedus pullus Germar
Ampedus sanguinipennis (Say)
Ampedus apicatus (Say)
Ampedus evansi Brown
Ampedus mixtus (Herbst)
Ampedus luctuosus (LeConte)
Ampedus melsheimeri (Leng)
Ampedus rubricollis (Herbst)
Melanotus castanipes (Paykull)
Melanotus similis (Kirby)
Cardiophorus convexulus LeConte

LAMPYRIDAE
Lucidoda atra (Fabricius)
Ellychnia corrusca (Linnaeus)
Pyractonema angulata (Say)
Photuris pennsylvanica (DeGeer)

CANTHARIDAE
Cantharis rotundicollis Say

CLERIDAE
Phyllobaenus humeralis difficilis (LeConte)
Thanasimus dubius (Fabricius)
Thanasimus undulatus (Say)
Thanasimus undulatus nubilus Klug
Enoclerus nigripes rufiventris (Spinola)
Enoclerus nigrifrons gerhardi Wolcott
Enoclerus muttkowskii (Wolcott)
Trichodes nutalli (Kirby)
Phlogistosternus dislocatus (Say)

CEPHALOIDAE
Cephaloon lepturides Newman

ALLECULIDAE
Isomira quadristriata Couper
Hymenorus niger Melsheimer
Hymenorus molestus Fall

MELANDRYIDAE
Penthe pimelia (Fabricius)
Eustrophinus bicolor (Fabricius)
Orchesia castanea Melsheimer
Dircaea quadrimaculata (Say)
Serropalpus sp.
Phleootrya sp.

MORDELLIDAE
Tomoxia inclusa LeConte

CERAMBYCIDAE
Prioninae
Orthosoma brunneum (Forster)
Tragosoma depsarius (Linnaeus)
Aseminae
Asemum striatum (Linnaeus)
Tetropium cinnamopterum cinnamopterum Kirby
Atimia confusa confusa (Say)
Lepturinae
Evodinus monticola monticola (Randall)
Anthophylax attenuatus (Haldeman)
Rhagium inquisitor (Linnaeus)
Acmaeops proteus proteus (Kirby)
Pseudogaurotina abdominalis (Bland)
Gnathacmaeops pratensis (Laicherting)
Bellamira scalaris (Say)
Analeptura lineola (Say)
Judolia montivagans montivagans (Couper)
Pygoleptura nigrella nigrella (Say)
Typocerus velutinus velutinus (Olivier)
Typocerus sparsus LeConte
Leptura subhamata Randall
Trachysida aspera brevifrons (Howden)
Stictoleptura canadensis canadensis (Olivier)
Trigonarthris proxima (Say)
Cosmosalia chrysocoma (Kirby)
Cerambycinae
Purpuricenus humeralis (Fabricius)
Elaphidionoides villosus (Fabricius)
Pronocera collaris collaris (Kirby)
Phymatodes dimidiatus (Kirby)
Calloides nobilis nobilis (Harris)
Xylotrechus sagittatus sagittatus (Germar)
Xylotrechus colonus (Fabricius)
Xylotrechus annosus annosus (Say)
Xylotrechus undulatus (Say)
Neoclytus muricatulus muricatulus (Kirby)
Clytus ruricola (Olivier)
Cyrtophorus verrucosus (Olivier)
Lamiinae
Monochamus scutellatus scutellatus (Say)
Monochamus carolinensis (Olivier)
Monochamus notatus (Drury)
Microgoes oculatus (LeConte)
Pogonocherus penicillatus LeConte
Aegomorphus morrisi (Uhler)
Amniscus sexguttata (Say)
Hyperplatys aspersa (Say)
Neacanthocinus pusillus (Kirby)
Saperda obliqua Say
Saperda candida Fabricius
Saperda calcarata Say
Saperda tridentata Olivier
Saperda lateralis Fabricius
Oberea tripunctata (Swederus)

CURCULIONIDAE
Pissodes strobi (Peck)
Hylobius pales (Herbst)

SCOLYTIDAE
Scolytus piceae (Swaine)
Hylurgops pinifex (Fitch)
Hylastes porculus Erichson
Dendroctonus valens LeConte
Polygraphus rufipennis (Kirby)
Trypodendron lineatum (Olivier)
Dryocetes autographus (Ratzeburg)
Dryocetes affaber (Mannerheim)
Xyleborus dispar (Fabricius)
Pityogenes hopkinsi Swaine
Orthotomicus caelatus (Eichhoff)
Ips pini (Say)
Ips calligraphus (Germar)
Ips grandicollis (Eichhoff)

---

* Voucher specimens for all species retained in the author's collection; voucher specimens for most species also deposited in the collection of the National Museum of Natural Sciences, Ottawa, Canada.