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ASPECTS OF HOST SELECTION BEHAVIOUR IN *PISSODES STROBI* PECK

(COLEOPTERA: CURCULIONIDAE)

by

Teunis Jacob Dirk VanderSar

B.Sc., University of Toronto, 1967

M.Sc., University of Toronto, 1969

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE OF

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ABSTRACT

In laboratory feeding bioassays, *Pissodes strobi* adults discriminated between preferred and non-host conifer species on the basis of close-range or contact chemoreception. In two-way choice bioassays both sexes preferred to feed on Sitka spruce rather than western red cedar. Females preferred Sitka spruce to Douglas-fir, whereas males did not discriminate between these two species. When presented either Sitka spruce or one of the three non-host species alone, however, starved weevils of both sexes fed equally on Sitka spruce, Douglas-fir, and western hemlock. Neither sex fed on cedar, and weevils were seldom observed in contact with this species. Both sexes preferred to feed on water-soaked Sitka spruce sections rather than on those soaked in cedar exudate, suggesting that cedar contains chemical repellents and/or feeding deterrents. Sustained feeding by both sexes on elderberry pith discs containing a 50 per cent ethanol extract of Sitka spruce leader bark suggested that host bark contains feeding stimulants. As only female *P. strobi* exhibited a concentration dependent feeding response, females may be more sensitive to chemostimulants than are males.

Additional feeding bioassays were conducted to examine the host preference of three distinct *P. strobi* populations reared from naturally-infested leaders of three allopatric conifer species; eastern white pine, Engelmann spruce, and Sitka spruce. Whereas each *P. strobi* population failed to discriminate between these three native hosts in forced feeding

experiments, the results of three-way choice bioassays suggested that eastern white pine is the ancestral host of both western *P. strobi* populations. Whereas *P. strobi* reared from eastern white pine preferred to feed on its natural host rather than on either of the western spruces, *P. strobi* reared from Engelmann spruce did not discriminate between eastern white pine and its natural host, Engelmann spruce, but fed significantly less on Sitka spruce. *P. strobi* reared from Sitka spruce, however, fed equally on all three host species. These results suggested that *P. strobi* has dispersed west across North America, adapting its host selection behaviour in turn to Engelmann spruce and then Sitka spruce. The data support the contention of Smith and Sugden (1969) that the two western weevil populations are ecotypes of *P. strobi* Peck rather than distinct species.

Vision plays an important role in initial orientation of overwintered *P. strobi* adults to potential host conifers. Results of laboratory orientation experiments using black cardboard silhouettes suggested that both sexes are predisposed to attack vertical or near-vertical Sitka spruce leaders that are approximately 3 cm in silhouette width and above average in length. Field data confirmed that both sexes selected only the longer, larger-diameter host leaders from among the available leader population. For brood hosts re-attacked the second year, stepwise discriminant analysis was performed on several host characteristics to distinguish weevilled and unattacked lateral branches in host crowns. The single most efficient lateral branch property to achieve this classification was lateral branch length. In conjunction with angular deviation from vertical, and midpoint diameter, 68.2 per cent of lateral branches were correctly classified.

The selection of oviposition sites by gravid female *P. strobi* on excised host leaders in the laboratory is governed by positive phototaxis and negative geotaxis. These mechanisms, however, exert relatively little influence on the selection of feeding sites, the position of which may be largely determined by chemoreception. During the spring oviposition period, positive phototaxis appears to be the more predominant orientation response. Either mechanism alone or both acting in concert, can account for the oviposition pattern produced by *P. strobi* each spring in the apical region of erect Sitka spruce leaders.

To Cornelis Van Der Sar and Aartje Andeweg

who encouraged their children to learn,

and gave to them as best they could

There be four things which are little
upon the earth, but they are exceeding wise:
The ants are a people not strong, yet they
prepare their meat in the summer;
The conies are but a feeble folk, yet make
they their houses in the rocks;
The locusts have no king, yet go they
forth all of them by bands;
The spider taketh hold with her hands,
and is in kings' palaces.

Proverbs of Solomon 30:24-28

Frontispiece. *Pissodes strobi* initiating flight from the terminal bud of a Sitka spruce lateral branch

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ASPECTS OF HOST SELECTION BEHAVIOUR IN *PISSODES STROBI* PECK

(COLEOPTERA: CURCULIONIDAE)

INTRODUCTION

Pissodes strobi Peck is a nearctic weevil species damaging to the terminal shoot of young conifer regeneration, particularly eastern white pine, *Pinus strobus* L., Engelmann spruce, *Picea engelmannii* Parry, and Sitka spruce, *P. sitchensis* (Bong.) Carr. Following flight dispersal from previously attacked brood hosts (Overhulser 1973), females oviposit in May and early June in feeding cavities excavated in the bark of vigorous, one-year-old host leaders. The eggs hatch after about two weeks, and the legless larvae feed downwards within the cambial zone consuming phloem and cortical tissues (Belyea and Sullivan 1956; Stevenson 1967; Silver 1968). Concealed beneath the intact periderm, older larvae eventually congregate to form a united feeding front or ring, which results in the girdling and death of at least two years' leader growth. Leader etiolation and red needle discolouration are both indicative of successful *P. strobi* attack on hosts in the field by late July. Fourth-instar larvae may pupate within the pith of larger-diameter leaders, or construct chip cocoons of shredded wood fibres on the pitted surface of the xylem. New generation adults of *P. strobi*, which is univoltine, emerge from desiccated, dead host leaders in late August and early September, chewing exit holes through the thin periderm. Pre-wintering weevils feed in the living bark of the lower stem and lateral branches of brood hosts until unfavourable weather forces the weevils to seek shelter within the forest floor litter (Belyea and Sullivan 1956). In the milder winter climate of the Pacific Northwest, *P. strobi* may overwinter on brood host lateral branches, feeding intermittently when temperatures permit (Gara et al. 1971; McMullen and Condrashoff 1973).

Considerable resources in both time and research effort have been allocated to the selection of host conifers resistant to weevilling by *P. strobi* (Wright and Gabriel 1959; Gerhold 1966; Connola 1966; Fowler and Heimburger 1969; Garrett 1973; Mitchell et al. 1974). These studies, however, lacked a fundamental appreciation of the weevil-host interaction in terms of the factors that govern host susceptibility. As a consequence, decisions pertaining to reforestation programs of susceptible species cannot be rooted in reliable experimental evidence.

The present study was designed to investigate several discrete steps in the host selection behaviour of *P. strobi*. My broad objectives were to investigate: the role of chemoreception in host species discrimination; the role of vision in *P. strobi* orientation to potential hosts following flight dispersal; and the role of geotaxis and phototaxis in the selection by female *P. strobi* of feeding and oviposition sites within the microhabitat of single host leaders.

ROLE OF CHEMORECEPTION IN THE HOST SELECTION BEHAVIOUR OF *PISSODES STROBI*

In the process of host selection in its Pacific Coast habitat, *P. strobi* must discriminate between its natural host, Sitka spruce and a number of coincident conifer species that include Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, western hemlock, *Tsuga heterophylla* (Raf.) Sarg., and western red cedar, *Thuja plicata* Donn. Although factors such as vision and olfaction are implicated in the selection by *P. strobi* of larger-diameter leaders of vigorous hosts in even-aged stands (Kriebel 1954; Silver 1968), ultimate selection between potential host species is likely made on the basis of chemical stimuli perceived at close range (Dethier 1954). This close-range perception would fall in the second, third, or possibly fourth categories of Beck's (1965) four-phase phytophagous insect feeding behaviour sequence: (1) host plant recognition and orientation, (2) biting response, (3) maintenance of feeding, and (4) cessation of feeding followed by dispersal. That such discrimination exists in the white pine weevil is indicated by findings that more bark feeding cavities were produced on its preferred host *P. strobus* L., than on either of two alternate hosts, *P. banksiana* Lambert, and *P. resinosa* Ait. (Plank and Gerhold 1965).

My objectives were: (1) to develop a simple laboratory feeding preference bioassay for *P. strobi*, (2) to determine the effect of host diameter on feeding preference, and (3) to determine the chemical basis of host selection by *P. strobi* through choice and forced feeding experiments utilizing natural and extracted host material.

Methods and Materials

Pre-wintering weevils were collected in the laboratory in late summer 1974 and 1975 following emergence from successfully attacked Sitka spruce leaders. These terminals had been field-collected in late July and mid-August from three localities; the Kelsey Bay region of Vancouver Island, the University of British Columbia Research Forest, Maple Ridge, B.C., and the District of Mission Municipal Forest, Mission, B.C. Following collection, the leaders were stored at 0 to 2°C and moved to room temperature as new adult weevils were required.

After emergence, each weevil was isolated and sexed, and groups of weevils were held in jars at 0 to 2°C on Sitka spruce lateral branch sections. Prior to each experiment, weevils were conditioned for 24 hours at 20 to 21°C with access to water (moist cotton) but not food.

In both forced and choice feeding experiments, lateral branch sections were used. With one exception, all branch sections within an experiment were of approximately equal cross-sectional diameter. Fresh 3 or 4 cm sections of current or one-year-old lateral branches were used in each feeding bioassay. All cut surfaces were sealed with paraffin wax to preclude excessive release of host volatiles and weevil feeding on exposed tissues.

In all experiments, single weevils of either sex were exposed to various test materials or stimuli. In contrast to other experiments on *P. strobi* (Plank and Gerhold 1965), or other insects such as *Scolytus multistriatus* Marsham (Loschiavo et al. 1963) in which groups of insects were tested, use of a single insect per replicate precludes interaction among beetles, and allows an assessment of individual capability and variation in host discrimination within a population.

The experimental bioassay apparatus consisted of a 448 ml glass jar inverted over a filter paper floor on which rested the horizontal test materials. As many as 80 individual assays in some experiments were run simultaneously on a countertop in a laboratory maintained at approximately 20 to 21°C. Within any bioassay series (e.g., 10 replicates of individual females on Douglas-fir), the host material in each apparatus was clipped from different trees. Therefore, each feeding experiment incorporated maximum variability of both insect and host components. During an experiment, the position of each weevil in the apparatus was recorded periodically. These observations provided an indication of the speed and accuracy of host plant recognition and orientation. Feeding on each test material in the case of forced feeding bioassays was assessed by counting feeding punctures in the bark and by weighing the fecal material produced over the 24-hour test interval. The total number of feeding cavities produced on a lateral branch is a measure of the biting response that initiates feeding on a potential host. Maintenance of feeding activity involves actual food intake and was hypothesized to be correlated more closely with the weight of feces produced. In most choice feeding bioassays, only the number of punctures produced on each lateral section was counted.

Preference of *P. strobi* for larger- or smaller-diameter lateral branches was assessed in a choice experiment. In each of 10 replicates for each sex, the larger-diameter branch section was cut from the base of a Sitka spruce lateral of the current year, whereas the smaller-diameter section was cut from the tip of the same lateral. In this manner, differences in chemical composition and physical parameters such as bark texture and needle distribution within a replicate were minimized.

Feeding behaviour by pre-wintering *P. strobi* on Sitka spruce and other Pacific Coast conifers, Douglas-fir, western hemlock, and western red cedar was determined by exposing a weevil to a single host or non-host lateral section for 24 hours. Two experiments were conducted, the first replicated five times and the second 10 times for each sex and conifer species. Visual observation of weevil position and determination of feces weight were carried out only in the second 10 replicate experiment. Analysis of variance (ANOVA) was performed on the feeding puncture data of the combined 15 replicates and also on the feces weight data obtained in the 10 replicate experiment.

The ability of pre-wintering *P. strobi* adults to discriminate between host and non-host conifer species was assessed by exposing single weevils to a two-way choice of host laterals, one of which was always Sitka spruce, and the other either Douglas-fir, western hemlock, or western red cedar. The choice of lateral sections was usually between material of the same age, i.e., both were current-year or one-year-old laterals. However, to satisfy equal cross-sectional diameter requirements, it was sometimes necessary to pair one-year-old Douglas-fir or western hemlock laterals with current-year Sitka spruce materials. The choice experiment involved 10 replicates for each sex and host choice combination.

The hypothesis that western red cedar contains a repellent and/or a feeding deterrent for *P. strobi* was investigated by utilizing a cedar exudate. This exudate was obtained by pressing lateral branches (stripped of scale-like leaves) in a 15-ton hydraulic press. A clear amber liquid was obtained following filtration to remove particulate matter from the exudate. Control branch sections were soaked in tap water for four days, and the experimental sections in the filtered exudate for an equal duration. Adjacent 3 cm sections from current-year Sitka spruce branches were used as the control and experimental host material in each replicate. This procedure minimized possible differences in chemical composition and physical parameters (e.g., branch diameter) between experimental and control sections. Following immersion, the paired sections were air-dried on cheesecloth prior to use in the bioassay. The two-way choice experiment comprised 11 replicates for each sex.

The nature of chemical host selection factors in Sitka spruce was further determined through extraction and bioassay procedures. In early spring 1975, unattacked Sitka spruce leaders were collected from the District of Mission Municipal Forest, and stripped of all needles and the terminal bud. The bark tissue was peeled from the xylem and immediately extracted with 50 per cent ethanol in a blender for 15 minutes. Following vacuum filtration, the reddish solution was tested* for feeding stimulant activity at three concentrations: 0.185, 0.093, and 0.046 gram equivalents of fresh bark tissue.

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*In this bioassay only, overwintered *P. strobi* adults collected from Sitka spruce leaders in early spring 1975, were used rather than pre-wintering weevils.

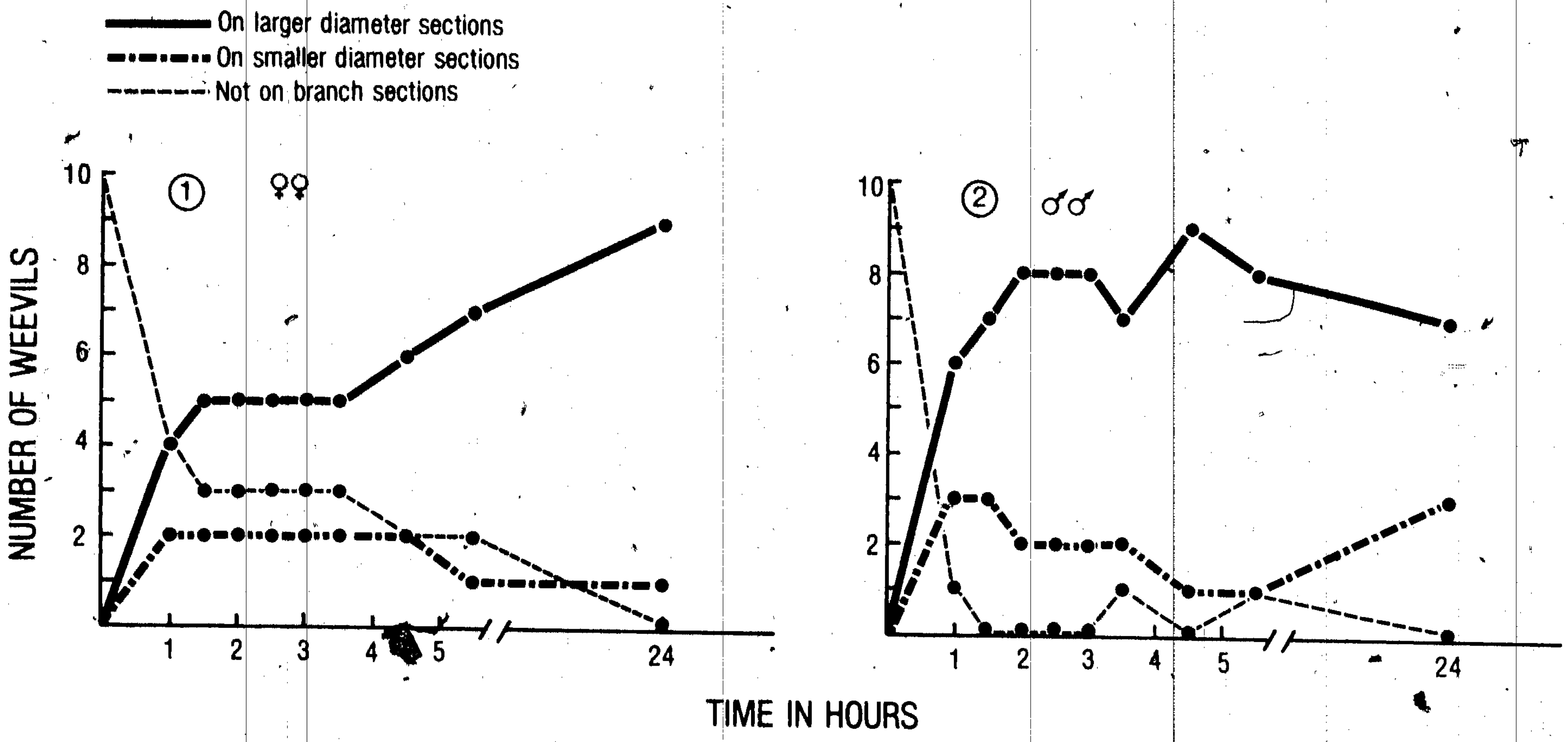
As in similar experiments with other insects (Loschiavo 1965; Norris and Baker 1967), elderberry pith discs were used as the inert substrate in which the extracts were tested. Pith discs (approximately 3 mm thick and 12 mm in diameter) were placed inside and flush with the rim of small, plastic vial caps. Approximately 0.075 ml of the 50 per cent ethanolic extract were added to the experimental discs and an equivalent amount of 50 per cent ethanol to the control discs. Each experimental apparatus consisted of a plastic petri dish inverted over a filter paper floor on which rested the experimental and control plastic caps. A single weevil of either sex was used per replicate, and its position in the apparatus recorded at five or 10 minute intervals until feeding activity subsided. Ten replicates were used for each sex and for each stimulus concentration.

Results

Effect of Host Diameter on Feeding Rate

Both sexes of *P. strobi* preferred to feed on larger-diameter Sitka spruce lateral branch sections (t-test, $P<0.05$). Following their release on the filter paper floor of the apparatus, the majority of weevils oriented to the larger-diameter spruce sections early in the experiment (Figs. 1, 2). Females produced a mean of 4.3 feeding punctures on host sections 5.2±0.9 mm in diameter, whereas a mean of 0.5 feeding cavities were initiated on smaller-diameter host sections 3.9±0.9 mm in cross-section. Male weevils produced a mean of 4.7 feeding punctures on Sitka spruce sections 5.3±1.0 mm in diameter, whereas a mean of 1.6 feeding punctures were produced on smaller-diameter spruce sections 3.9±0.8 mm

Figs. 1, 2. Position of pre-wintering *Pissodes strobi* adults over 24-hour period when presented a choice of different diameter, 3 cm sections from the same, current-year lateral branch of Sitka spruce. One weevil per replicate; 10 replicates for each sex and choice combination


On larger diameter sections
On smaller diameter sections
Not on branch sections
NUMBER OF WEEVILS
①
♀♀
②
♂♂
10
8
6
4
2
1
2
3
4
5
24
TIME IN HOURS

in cross-section. Ninety per cent of both male and female *P. strobi* fed on larger-diameter host sections at some time during the 24-hour test.

Feeding on Host and Non-host Species

ANOVA of the forced feeding results indicated a significant host effect. *P. strobi* produced significantly more feeding punctures on both Sitka spruce and Douglas-fir than on western hemlock, and significantly more feeding cavities on the latter species than on western red cedar (Table I).

The ANOVA based on feces weights indicated that *P. strobi* fed equally on Sitka spruce, Douglas-fir, and western hemlock, but fed significantly less on western red cedar (Table I).

Although the weevils oriented fairly rapidly to Sitka spruce, Douglas-fir, and western hemlock (Figs. 3-8), neither sex exhibited marked orientation to western red cedar (Figs. 9, 10).

Feeding Preference between Host and Non-host Species

Females preferred to feed on Sitka spruce in all species comparisons, whereas male *P. strobi* failed to distinguish between Sitka spruce and Douglas-fir (Table II). The weevils made an early and distinct choice in favour of Sitka spruce rather than western red cedar (Figs. 11, 12), but were slightly more often found in contact with western hemlock (Figs. 13, 14) and Douglas-fir (Figs. 15, 16) than western red cedar.

Bioassay of Western Red Cedar for Repellents and/or Feeding Deterrents

Both sexes of *P. strobi* preferred to feed on the water-soaked

Table I. Feeding activity of pre-wintering *Pissodes strobi* adults when presented with 4 cm sections of host or non-host lateral branches for 24 hours. One weevil per replicate. Feeding puncture data and feces weight data based on 15 and 10 replicates for each sex and conifer species respectively

Conifer Species	Mean number of feeding punctures produced per weevil			Mean weight of feces produced per weevil (mg)		
	Males	Females	Total[1]	Males	Females	Total[1]
Sitka spruce	3.5	4.3	3.9a	0.166	0.204	0.185a
Douglas-fir	2.9	4.3	3.6a	0.080	0.226	0.153a
Western hemlock	2.0	2.3	2.2b	0.175	0.219	0.197a
Western red cedar	0.1	0.3	0.2c	0	0	0b

[1] Means in a column followed by the same letter not significantly different (Newman-Keuls, $P<0.05$).

Figs. 3-10. Number of pre-wintering *Pissodes strobi* adults on 4 cm lateral branch sections of four conifer species presented singly over a 24-hour period. One weevil per replicate; 10 replicates for each sex and conifer species

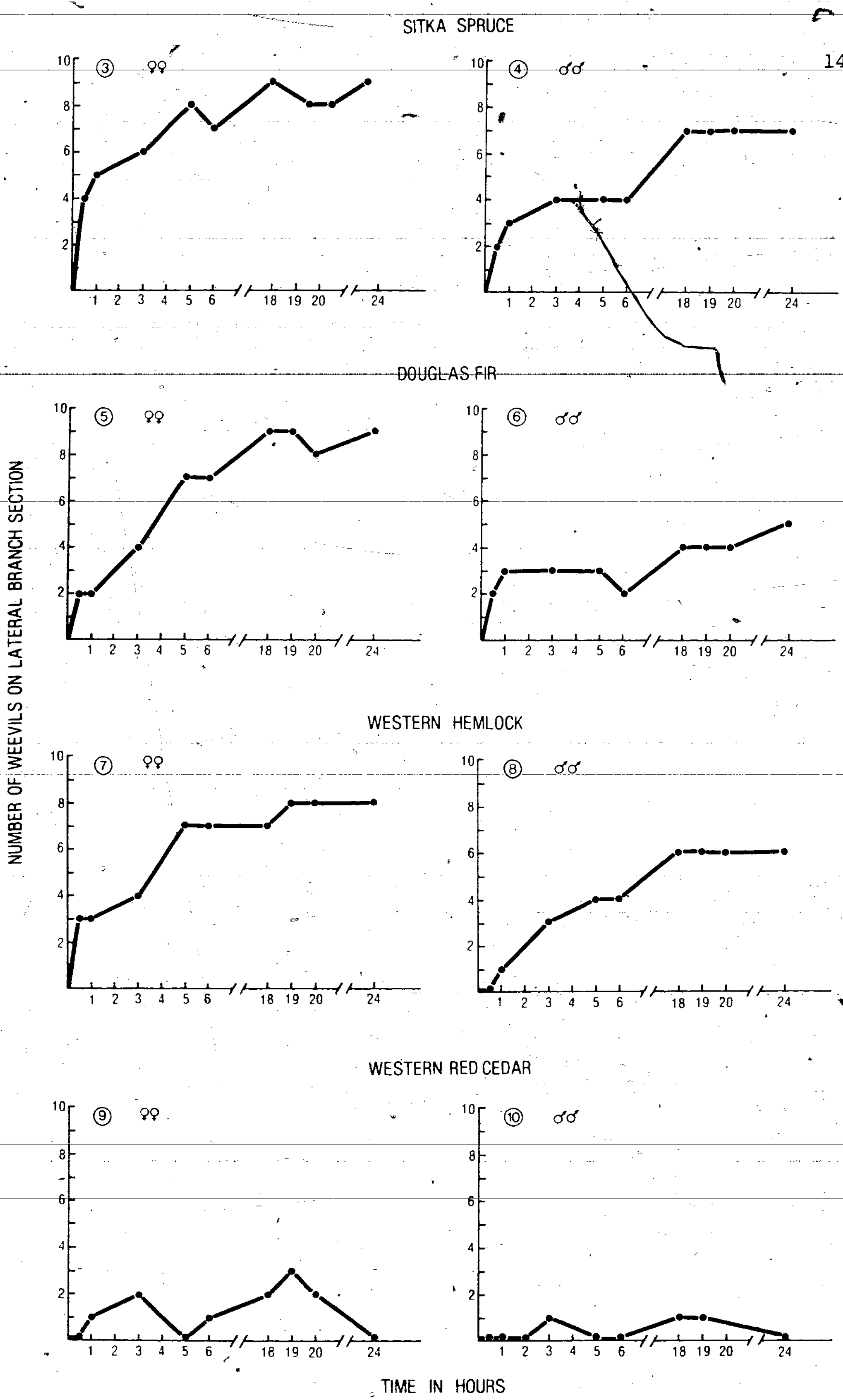

SITKA SPRUCE
③ ♀♀
④ ♂♂
DOUGLAS FIR
⑤ ♀♀
⑥ ♂♂
WESTERN HEMLOCK
⑦ ♀♀
⑧ ♂♂
WESTERN RED CEDAR
⑨ ♀♀
⑩ ♂♂
NUMBER OF WEEVILS ON LATERAL BRANCH SECTION
10
8
6
4
2
1 2 3 4 5 6 18 19 20 24
TIME IN HOURS

Table II. Feeding response of pre-wintering *Pissodes strobi* adults when presented a choice of 3 cm sections of host and non-host lateral branches for 24 hours. One weevil per replicate; 10 replicates for each sex and two-choice combination

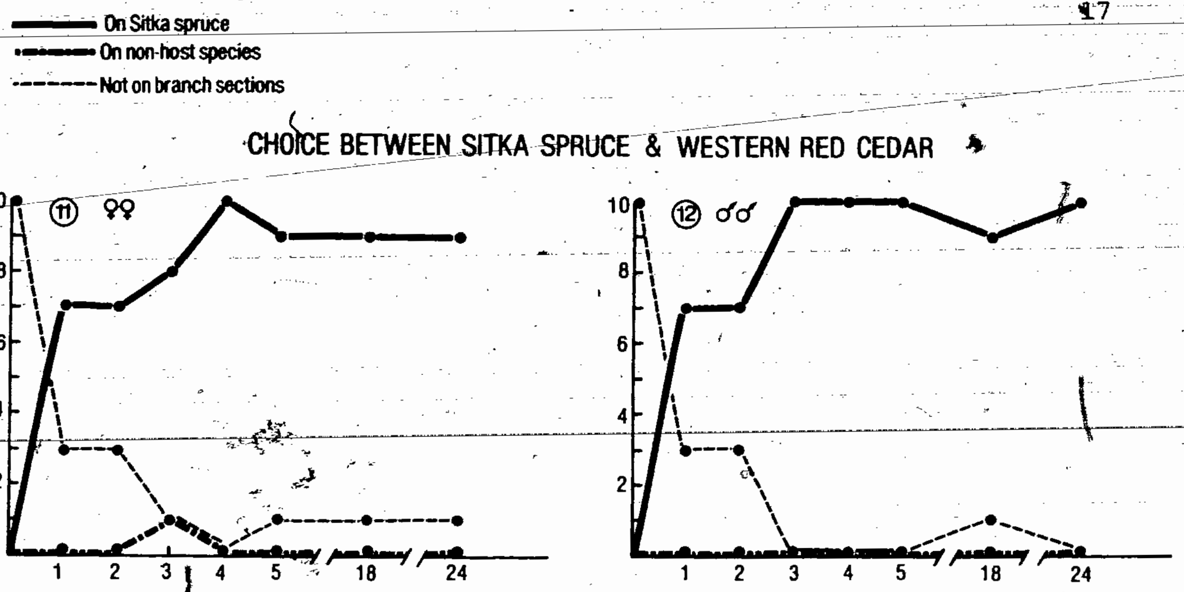
Choice of tree species	No. of weevils feeding at some time on either species	Mean no. feeding punctures/weevil[1,2]
Females		
Sitka spruce	8[3]	6.1
Douglas-fir	2	1.1*
Sitka spruce	7[3]	6.3
Western hemlock	1	0.7*
Sitka spruce	9[3]	7.0
Western red cedar	0	0*
Males		
Sitka spruce	8	4.6
Douglas-fir	5	2.6
Sitka spruce	9	6.4
Western hemlock	4	1.4*
Sitka spruce	10	6.0
Western red cedar	0	0*

[1] Each mean calculated by dividing value for each host choice by the total number of surviving weevils.

[2] t-test significance levels between paired means: *($P<0.01$).

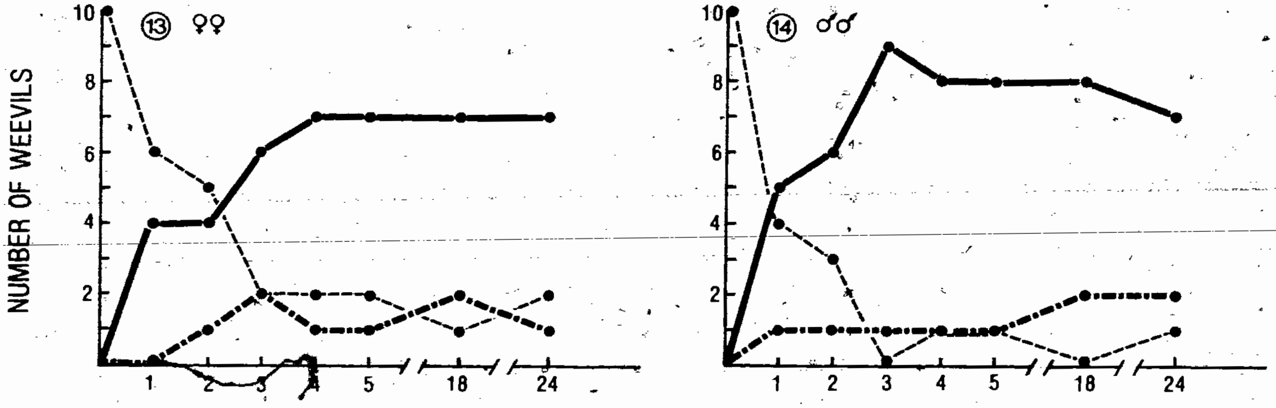
[3] Weevil died during 24-hour test. Replicate discounted.

Figs. 11-16. Position of pre-wintering *Pissodes strobi* adults over 24-hour period when presented a choice of 3 cm lateral branch sections of Sitka spruce and one of three non-host species. One weevil per replicate; 10 replicates for each sex and choice combination

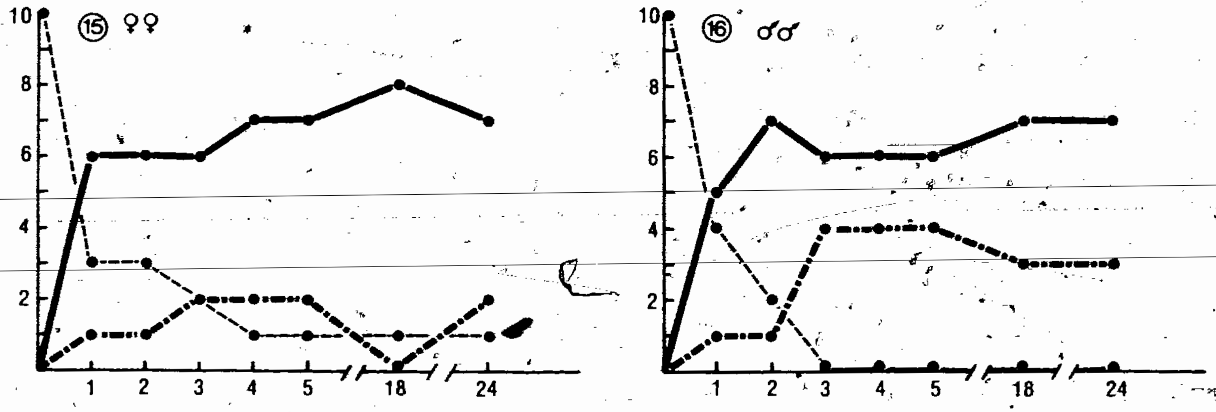


CHOICE BETWEEN SITKA SPRUCE & WESTERN RED CEDAR

CHOICE BETWEEN SITKA SPRUCE & WESTERN HEMLOCK



CHOICE BETWEEN SITKA SPRUCE & DOUGLAS-FIR



TIME IN HOURS

Sitka spruce lateral sections rather than on host sections soaked in cedar exudate, although this difference in feeding rates was not significant for males (Table III). Up to four individuals of either sex were in contact with the exudate-treated sections at some time in the experiment, and a low contact rate persisted throughout the test (Figs. 17, 18). Moreover, although not all weevils in contact with exudate-treated sections initiated test punctures, the production of feces by males that did not feed on untreated sections (Table III) indicates that food ingestion did occur once a weevil had initiated a test puncture on an exudate-treated section.

Bioassay of Extracts Prepared from Sitka Spruce Bark

Although the feeding response was variable (Table IV), significantly more female *P. strobi* fed longer on pith discs containing the highest concentration of spruce bark extract than on the solvent-treated controls (χ^2, $P<0.025$). The number of females feeding on extracts of lower concentrations was not significantly different from the number of *P. strobi* feeding at some time on control discs. However, with decreasing concentration of the 50 per cent ethanol extract, the number of females feeding on extract-treated discs decreased, but remained consistently greater than the number feeding on the solvent controls (Table IV). In addition, feeding duration per female decreased with decreasing concentration of the Sitka spruce leader bark extract. The feeding duration of male *P. strobi* indicated a consistent low level feeding response to the Sitka spruce bark extract that did not appear to be concentration dependent (Table IV).

Table III. Feeding response of pre-wintering *Pissodes strobi* adults when presented a choice of 3 cm sections of current-year Sitka spruce lateral branches soaked for four days in western red cedar exudate or sections soaked for an equal duration in tap water. One weevil per replicate; 11 replicates for each sex and choice combination

Treatment of host laterals	Weevils feeding at some time on either section	Mean no. feeding punctures/weevil[1,2]	Mean wt. feces/weevil (mg)[1,2]
Females			
Water-soaked	9	4.6	0.296
Cedar exudate-soaked	1[3]	0.4*	0.016*
Males			
Water-soaked	8	4.5	0.220
Cedar exudate-soaked	2[3]	1.5	0.060

[1] Each mean calculated by dividing value for each host choice by the total number of weevils.

[2] t-test significance levels between paired means: *(P<0.01).

[3] The single female produced punctures on both lateral sections. Total feces weight in this replicate was divided in the proportion that punctures were produced on each host lateral section. The two males each fed on only one section.

Figs. 17, 18. Position of pre-wintering *Pissodes strobi* adults over 24-hour period when presented a choice of 3 cm sections of current-year Sitka spruce lateral branches soaked for four days in western red cedar exudate, or sections soaked for an equal duration in water. One weevil per replicate; 11 replicates for each sex and choice combination

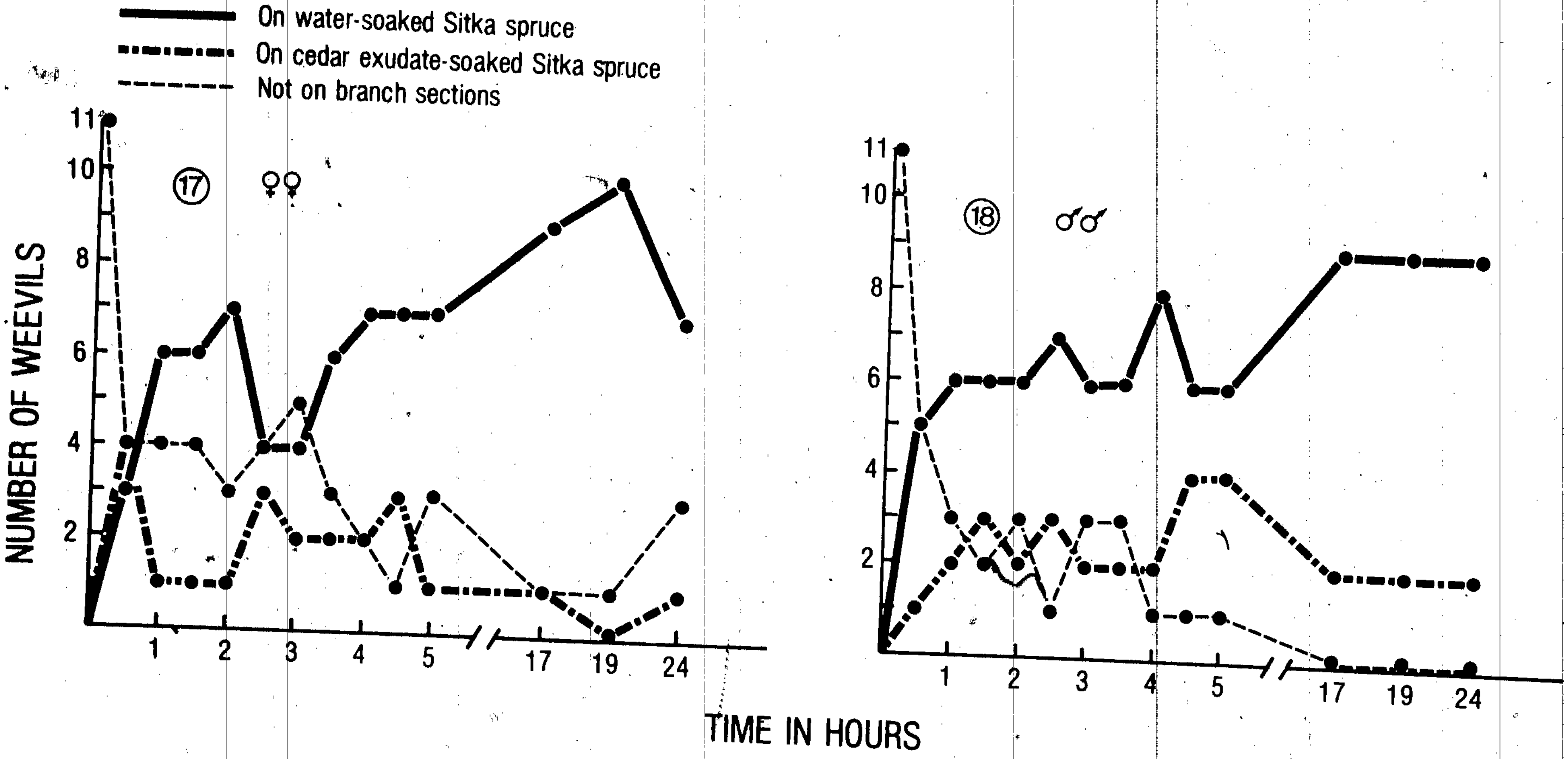

On water-soaked Sitka spruce
On cedar exudate-soaked Sitka spruce
Not on branch sections
⑰ ♀♀
⑱ ♂♂
NUMBER OF WEEVILS
11
10
8
6
4
2
1
2
3
4
5
17
19
24
TIME IN HOURS

Table IV. Feeding response of overwintered *Pissodes strobi* when presented a choice of 50 per cent ethanol extract of Sitka spruce leader bark or a solvent control, both solutions applied to elderberry pith discs. One weevil per replicate; 10 replicates for each sex and stimulus concentration

Stimulus	Concentration	No. weevils feeding at some time on either stimulus	Mean feeding duration/feeding weevil (min.)
		Females	
SS[1] bark extract	0.185 g.equiv.	10	53.5
50% ethanol	0.075 ml	1	10.0
SS bark extract	0.093 g.equiv.	7	27.1
50% ethanol	0.075 ml	2	20.0
SS bark extract	0.046 g.equiv.	6	6.7
50% ethanol	0.075 ml	3	16.7
		Males	
SS bark extract	0.185 g.equiv.	5	25.0
50% ethanol	0.075 ml	3	23.3
SS bark extract	0.093 g.equiv.	5	34.0
50% ethanol	0.075 ml	1	15.0
SS bark extract	0.046 g.equiv.	5	23.0
50% ethanol	0.075 ml	0	0

[1] SS = Sitka spruce.

Discussion

Effect of Host Diameter on Feeding Behaviour

Since chemical differences between paired Sitka spruce lateral sections of different diameter were minimal, *P. strobi* likely expressed a true visual response that determines initial orientation to the larger-diameter host. This hypothesis is supported by the observation that the majority of weevils orient to the larger-diameter host sections early in the experiment (Figs. 1, 2). After the initial choice had been made, 10 transfers to the alternate host section were observed (five in each direction) involving 35 per cent of the adults.

The orientation to and subsequent feeding preference for larger-diameter host material is of adaptive significance to *P. strobi* in host selection. The volume of the feeding cavities excavated by *P. strobi* on Sitka spruce is related to both the bark thickness and the distribution of cortical resin ducts, as the weevils will avoid rupturing the epithelial cells surrounding the resin canals (Overhulser 1973). Should it be impossible for the weevil to feed around a resin duct, the feeding cavity is abandoned. It is known that thinner bark (Kriebel 1954) and shallow resin ducts (Stroh and Gerhold 1965) are resistance factors in white pine weevil attack on *P. strobus*. Both factors result in fewer feeding punctures. In smaller-diameter, thin-barked host material, the likelihood of a feeding weevil contacting an outside or inside resin duct is greater, due simply to reduced radial distance between canals. In addition, oviposition behaviour is also adversely affected on thin-barked host material. Oviposition in spring follows the excavation of suitable feeding cavities that must be of sufficient depth to accommodate the ovoid eggs. Sullivan (1961) indicated that host bark thinner than about 0.8 mm is likely unsuitable for the deposition of eggs which average 0.8 by 0.5 mm. Both feeding and oviposition behaviour, therefore, are favoured on larger-diameter host material likely to have thicker bark.

These results also indicate that in any choice bioassays, lateral branch sections of equal diameter should be employed to eliminate bias on the basis of diameter.

Feeding on Host and Non-host Species

The sustained feeding by *P. strobi* on two non-host species, Douglas-fir and western hemlock (Table I), was somewhat unexpected. However, the wide host range of *P. strobi* suggests that several non-host species have some of the requisite host characteristics to induce host-positive feeding behaviour in the absence of an established host. This hypothesis is supported by the readiness of the white pine weevil to feed on western white pine, *Pinus monticola* Dougl. (Soles et al. 1970) in the laboratory although the species is not an acceptable host under more natural field conditions.

Whereas *P. strobi* oriented fairly rapidly to Sitka spruce, Douglas-fir, and western hemlock (Figs. 3-8), neither sex exhibited marked orientation to (Figs. 9, 10) or sustained feeding on western red cedar (Table I). In some instances, hunger apparently induced the weevils to attempt test punctures, but lack of feces production indicated lack of food intake (Table I). More test punctures were observed on the filter paper floor of the apparatus containing western red cedar than other conifer species, suggesting that this species is repellent even to starved weevils deprived of food for 24 hours.

Feeding Preference Between Host and Non-host Species

When given a choice, female *P. strobi* can discriminate among four common conifer species in its Pacific coast habitat, whereas males do not distinguish between Sitka spruce and Douglas-fir (Table II). Choice feeding bioassays suggest that western red cedar emits volatile repellents that block host recognition and prevent initial orientation to this species. Olfactory and gustatory chemoreception are implicated in the rejection of western red cedar. Weevils are rarely found in contact with it (Figs. 11, 12), and do not attempt test feeding punctures (Table II), suggesting repellency. However, in forced feeding bioassays, the lack of sustained feeding after test punctures have been made (Table I) indicates gustatory chemoreception followed by rejection of western red cedar as a host.

Sitka spruce, on the other hand, is attractive to *P. strobi* such that the full complement of feeding behaviour is repeated cyclically. Chemical stimulants present in the bark apparently promote sustained feeding on this species. It can be inferred from the data that both Douglas-fir and western hemlock contain feeding stimulants in less than optimal concentrations. In the absence of more suitable host material (i.e., Sitka spruce), hunger likely promotes continued feeding of starved weevils. It is not known, however, whether Douglas-fir and western hemlock contain the nutritive factors required for long-term weevil maintenance and reproduction.

Bioassay of Western Red Cedar for Repellents and/or Feeding Deterrents

The bioassay results clearly indicate that the largely aqueous western red cedar exudate contains compounds that convert an acceptable host to one that is unacceptable (Table III). Reduced feeding by the single female that fed on the exudate-treated section suggests that feeding deterrents are present. The two males that fed on exudate-treated sections showed intermediate feeding rates relative to controls. In addition, constituents from cedar apparently stimulated increased locomotor activity. Eighty per cent of the females and 30 per cent of the males moved at least once from the host lateral section initially chosen, the highest transfer rate recorded in any experiment.

The nature of the active components in western red cedar is not known. However, the species contains water-soluble organic tropolones and phenolics of known antibiotic activity (Barton and MacDonald 1971). The possibility of naturally occurring quinones such as juglone, a feeding deterrent for *S. multistriatus* in the bark of *Carya ovata* (Mill.) K. Koch (Gilbert et al. 1967) should also be considered. Such compounds are considered to act by blocking sulfhydryl groups on receptor neuron membrane proteins (Norris et al. 1970). The isolation and identification of feeding repellents and deterrents for *P. strobi* from western red cedar could lead to their use in pest management, by preventing feeding and oviposition on susceptible hosts until critical seasonal and phenological periods had passed.

Bioassay of Extracts Prepared from Sitka Spruce Bark

Weevil feeding response to the 50 per cent ethanol extracts of Sitka spruce leader bark (Table IV) suggests that host compounds which are soluble in a polar solvent act as feeding stimulants for *P. strobi*. Female feeding response appears to be concentration dependent, whereas males do not demonstrate an increase in feeding duration with increasing concentration of the spruce bark extract.

Refinement of both extraction methods and bioassay techniques may allow the isolation and subsequent identification of feeding stimulants for *P. strobi*. Knowledge of the key compounds could be applied to such pursuits as the selection of resistant provenances which produce them in suboptimal concentrations.

In summary, host selection in *P. strobi* is a complex process in which chemoreception plays a pivotal role. Although the mechanisms that mediate long-range orientation of *P. strobi* to potential host trees remain undefined, results of the host diameter experiments suggest vision as a potentially fertile area of further research. Close-range discrimination between tree species involves olfaction and contact chemoreception. Repellent compounds and/or feeding deterrents render western red cedar an unacceptable host, whereas Sitka spruce bark contains optimal concentrations of compounds that promote sustained feeding activity. Under appropriate physical conditions, these same compounds may also release oviposition behaviour in *P. strobi*. Feeding and oviposition may therefore constitute a behavioural continuum that is subject to physical, chemical, and environmental input at various stages of the host selection sequence.

The results suggest that female *P. strobi* respond more sensitively than males to active compounds present in both western red cedar and Sitka spruce. In addition, only female *P. strobi* discriminate between the preferred host, Sitka spruce, and Douglas-fir in choice experiments. Female weevils may therefore be more instrumental in host selection following dispersal, than male *P. strobi*.

HOST PREFERENCE OF *PISSODES STROBI* REARED FROM THREE NATIVE HOSTS*

The white pine weevil, *P. strobi*, is a species first described from the leading shoot of "Weymouth pine," *Pinus strobus* (Peck 1817). Currently recognized as a major pest throughout the range of eastern white pine (Fig. 19) from the Atlantic Coast to south-eastern Manitoba, the weevil has been instrumental in the curtailment of reforestation programs (Belyea and Sullivan 1956). Two western weevil populations that are damaging to Engelmann spruce, *P. engelmannii* regeneration (Fig. 19) in the interior mountains (Stevenson 1967), and to Sitka spruce, *P. sitchensis* plantations (Fig. 19) on the Pacific Coast (Silver 1968), were both accorded species status by Hopkins (1911) on the basis of his host selection principle.

The behavioural ecology of the three weevil populations on their respective hosts is essentially identical (Belyea and Sullivan 1956; Stevenson 1967; Silver 1968).

In studies on the taxonomic status of the genus *Pissodes* Germar, Manna and Smith (1959) and Smith (1962) were unable to distinguish Hopkins' (1911) species *engelmanni* and *sitchensis* from *P. strobi* on basis of morphological or cytogenetic evidence. Accordingly, Smith and Sugden (1969) concluded that the two western weevil populations were in fact geographic races or ecotypes of *P. strobi*.

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*In this section, the three weevil populations are identified by the host from which they emerged as follows: from eastern white pine (ex EWP), from Engelmann spruce (ex ES), from Sitka spruce (ex SS).

Fig. 19. Geographical distribution (from Fowells 1965) of three preferred host conifers of three *Pissodes strobi* populations. Collection sites of weevilled leaders of each of the three host species are indicated

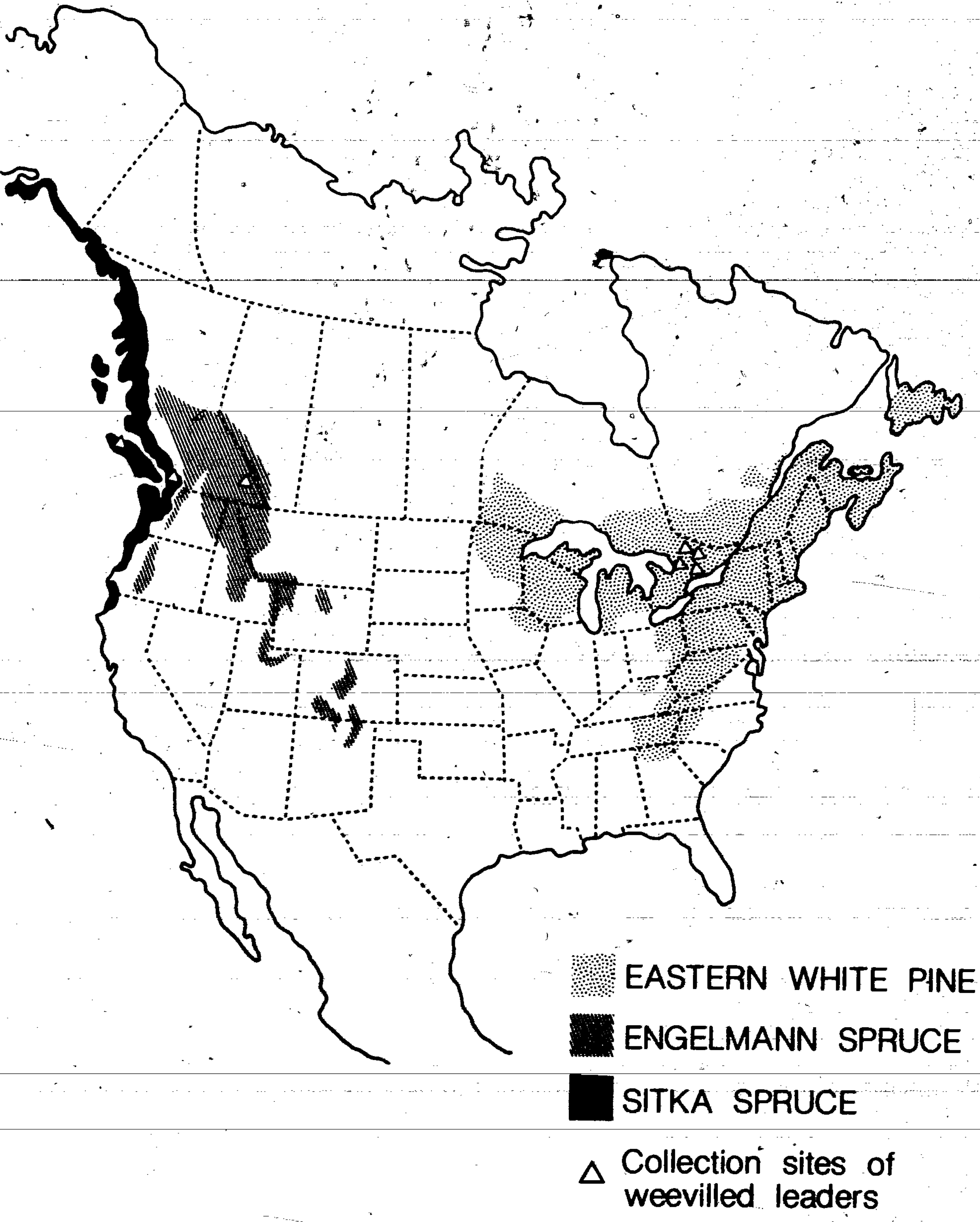

EASTERN WHITE PINE
ENGELMANN SPRUCE
SITKA SPRUCE
△ Collection sites of weevilled leaders

Table V lists the host trees that are commonly reported for the three *P. strobi* populations (Belyea and Sullivan 1956; Stevenson 1967; Smith and Sugden 1969; Mitchell et al. 1974). All reported host species possess vigorous erect terminals.

My objectives were: (1) to test the host specificity of the three weevil populations on each of the three preferred natural hosts using forced and choice feeding bioassays, and (2) to assess the revised taxonomic status of the former *P. engelmanni* and *P. sitchensis* on the basis of their feeding preferences relative to *P. strobi*.

Methods and Materials

New generation adult weevils were reared from naturally-infested host material as described in Methods and Materials on page 4. Infested Sitka spruce leaders were collected in mid-July 1975, from three localities; the Kelsey Bay region of northern Vancouver Island, the University of British Columbia Research Forest, Maple Ridge, B.C., and the District of Mission Municipal Forest, Mission, B.C. Weevilled Engelmann spruce leaders were collected in late August from natural regeneration in Kootenay National Park, B.C. Infested eastern white pine terminals were collected from plantations and natural regeneration in several south-eastern Ontario localities. Collection sites are indicated in Fig. 19. Owing to the proximity of the Maple Ridge and Mission, B.C. sites, however, a single triangle denotes these two collection areas of weevilled Sitka spruce leaders.

For both the forced and choice feeding experiments, the methods and evaluation procedures described in Methods and Materials on pages

Table V. Native and exotic host species commonly reported for the three populations of *Pissodes strobi*

Host species	*P. strobi* (ex EWP)	*P. strobi* (ex ES)	*P. strobi* (ex SS)
Pinus strobus L.	x[1]		
P. sylvestris L.[2]	x		
P. banksiana Lamb.	x		
P. resinosa Ait.	x		
P. rigida Mill.	x		
P. pungens Lamb.	x		
P. contorta Dougl.		x	
Picea abies (L.) Karst.[2]	x	x	x
P. glauca (Moench) Voss	x	x	x
P. mariana (Mill.) BSP	x	x	x
P. pungens Engelm.	x	x	x
P. rubens Sarg.	x		
P. sitchensis (Bong.) Carr			x[1]
P. engelmannii Parry		x[1]	
P. glauca (Moench) Voss *albertiana* (S. Brown) Sarg.[3]		x	
Picea x *lutzii* Little[4]			x

[1] Preferred natural host species.

[2] Exotic species.

[3] Natural hybrid between *P. engelmannii* and *P. glauca*.

[4] Natural hybrid between *P. sitchensis* and *P. glauca*.

4 to 6 were utilized, except for modifications as noted. Current-year Sitka spruce and eastern white pine lateral branches were obtained from plantations in the University of British Columbia Research Forest, Maple Ridge, B.C. Engelmann spruce lateral branches were clipped from natural regeneration in Manning Provincial Park, B.C. and the Merritt region of interior British Columbia. The branches were brought to the laboratory the day of collection, and stored at 0 to 4°C. All bioassays were conducted within one to two days of field collection of the lateral branches.

In the forced feeding bioassays, individual weevils were presented a single lateral branch section of one of the three preferred natural hosts. These experiments were conducted on three different days over a three-week period in September to October 1975. On each day, four replicates for each sex of each weevil population on each of the three host species, *Pinus strobus, Picea engelmannii,* and *P. sitchensis,* were completed. Each replicate tested a lateral branch section from a different tree, such that variability in the host-insect interaction was maximized. After 24 hours, the feeding punctures initiated on each host lateral branch section were counted, and the weight of feces determined for each replicate.

In the choice feeding bioassays, each weevil was presented a choice of three, 4 cm lateral branch sections, one each of eastern white pine, Engelmann spruce and Sitka spruce. Each replicate consisted of a 448 ml glass jar inverted over a filter paper floor on which rested the three branch sections. Thirty replicates were used for each sex of each weevil population. The choice bioassay was conducted in two parts;

18 replicates were completed on 16 October, and an additional 12 replicates on 8 December 1975. At intervals during the choice bioassays, the position of each weevil in the apparatus was recorded. After 24 hours, the number of feeding punctures on each host lateral branch section was counted.

In the forced feeding bioassays, analysis of variance (ANOVA) was performed on both the feeding puncture and feces weight data. Separate ANOVA on the number of feeding punctures initiated on each host species in the 16 October and 8 December choice bioassays indicated that differences between groups were not significant. Therefore, the feeding puncture data for all 30 replicates were combined in a single multivariate analysis of variance (MANOVA) using the numbers of feeding punctures produced on each of the three host species as variables. Hypothesis (H) and error (E) cross-product matrices were calculated using computer program BMD12V. Greatest characteristic roots of each HE^{-1} matrix were determined using computer program SFU-EIGENP. Critical values were subsequently calculated and compared to Heck Charts. After carrying out a Profile Analysis, multiple comparisons were made to determine significant differences between numbers of feeding punctures produced by each weevil population on each of the three host conifer species (Harris 1975, Morrison 1976).

To assess one population variable which may have influenced observed differences in feeding rates, 25 weevils of each sex of each weevil population were weighed on 2 February 1976. Prior to weighing, all weevils had been maintained at 2°C on lateral branch sections of their respective natural hosts. An analysis of variance was performed on the body weight data.

Results

All three *P. strobi* populations initiated shallow and deep bark punctures on eastern white pine, in addition to feeding cavities in the needles, needle fascicles and needle traces of this host. On both spruce species, however, nearly all feeding punctures were deeper bark cavities initiated on the sterigmatal ridges, and needle punctures were rarely observed. This between-host variability in the location and depth of feeding punctures may be related to the depth of inside and outside cortical resin canals (Stroh and Gerhold 1965). Since eastern white pine resin is repellent to *P. strobi* (Anderson and Fisher 1956), shallow punctures contacting the resin ducts may be abandoned. Such behaviour has also been observed in *P. strobi* feeding on Sitka spruce (Overhulser 1973).

Each feeding puncture is considered to represent the biting response that initiates feeding on a given host species. For this reason, an analysis of variance was performed on the total number of feeding punctures. However, the disparity in location and relative depth of feeding punctures both within and between host species precludes a simple correlation of numbers of punctures with the amount of food ingested. For this reason, it is hypothesized that fecal weight is a more accurate and reliable measure of actual food intake. It was not feasible to measure this additional variable in the choice bioassays, however, as 19.4 per cent of the weevils produced punctures on more than one host lateral branch section.

Forced Feeding Bioassay

In the forced feeding bioassay, analysis of variance indicated there were no significant differences in the number of feeding cavities initiated on each of the three host species by all three *P. strobi* populations combined, nor a significant effect due to weevil sex. However, *P. strobi* (ex EWP) initiated significantly more feeding cavities on the three host species combined than did either *P. strobi* (ex ES) or *P. strobi* (ex SS) (Table VI).

The feces weight ANOVA indicated that there were no significant differences in the weight of feces produced on each of the three host species by all three weevil populations combined, nor a significant effect due to beetle population. Female weevils, however, produced significantly more feces feeding on the three hosts combined than did the males (Table VII).

Choice Feeding Bioassays

The results of the MANOVA indicated a significant weevil population effect ($P<0.01$), but no significant sex effect or beetle by sex interaction. In addition, the parallelism, flatness, and levels hypotheses were rejected ($P<0.01$) indicating significantly different feeding rates on the three host species by each beetle population, differential feeding on each of the three host species, and differential feeding by each beetle population, respectively. Multiple comparisons between the means of each weevil population feeding on the three host species showed that *P. strobi* (ex EWP) produced significantly more feeding punctures on eastern white pine than on Engelmann spruce and significantly more

Table VI. Feeding punctures produced by pre-wintering weevils of three *Pissodes strobi* populations on current-year, 4 cm lateral branch sections of three preferred hosts presented singly during 24-hour period. One weevil per replicate; 12 replicates for each sex of each *Pissodes* population on each host species

Weevil Population	# feeding punctures initiated by males			# feeding punctures initiated by females			Total[1]
	Eastern white pine	Engelmann spruce	Sitka spruce	Eastern white pine	Engelmann spruce	Sitka spruce	
P. strobi (ex EWP)	106	80	64	119	105	121	595a
P. strobi (ex ES)	93	51	57	72	56	83	412b
P. strobi (ex SS)	68	46	83	75	63	78	413b

[1] Totals followed by the same letter not significantly different (Newman-Keuls test, $P<0.05$).

Table VII. Weight of feces produced by pre-wintering weevils of three *Pissodes strobi* populations feeding on current-year, 4 cm lateral branch sections of three preferred hosts presented singly for 24 hours. One weevil per replicate; 12 replicates for each sex of each *Pissodes* population on each host species

Wt. of feces produced on eastern white pine (mg)			Wt. of feces produced on Engelmann spruce (mg)			Wt. of feces produced on Sitka spruce (mg)			Total[1]
P. strobi (ex EWP)	*P. strobi* (ex ES)	*P. strobi* (ex SS)	*P. strobi* (ex EWP)	*P. strobi* (ex ES)	*P. strobi* (ex SS)	*P. strobi* (ex EWP)	*P. strobi* (ex ES)	*P. strobi* (ex SS)	
Females									
3.484	2.113	3.422	3.735	4.362	4.695	3.868	3.829	4.324	33.832
Males									
2.520	3.303	2.834	2.956	3.254	3.114	2.082	2.106	3.505	25.674

[1] Totals significantly different, ANOVA; $P<0.01$.

punctures on the latter host than on Sitka spruce (Table VIII). While the difference between mean number of feeding punctures produced on eastern white pine and Engelmann spruce by *P. strobi* (ex ES) was not significant (Table VIII), significantly fewer feeding cavities were produced on Sitka spruce than on either of the other two hosts. *P. strobi* (ex SS) did not show any preference for any of the three host species (Table VIII).

When the mean number of feeding punctures produced on each host species were compared, *P. strobi* (ex EWP) produced significantly more punctures on its natural host, eastern white pine, than did the two western weevil populations combined ($P<0.05$). Although the differences between mean numbers of feeding punctures produced on Sitka spruce were not significant, *P. strobi* (ex SS) tended to produce more feeding cavities on its natural host, Sitka spruce, than did either *P. strobi* (ex EWP) or *P. strobi* (ex ES). In addition, the mean number of feeding punctures produced on Engelmann spruce by *P. strobi* (ex ES) was not significantly different from the mean number of feeding punctures produced on this host by either *P. strobi* (ex EWP) or *P. strobi* (ex SS). The mean number of feeding cavities produced on Engelmann spruce by *P. strobi* (ex EWP) was, however, significantly greater than the number of feeding punctures initiated on this host by *P. strobi* (ex SS).

Weevil positions during the 24-hour test (Figs. 20-25) reflect the results shown in Table VIII. All three host species were contacted by weevils of both sexes soon after the start of each bioassay. However, after 24 hours, the majority of weevils of all three populations were found in contact with either eastern white pine or Engelmann spruce,

Table VIII. Mean number of feeding punctures produced on each host by pre-wintering weevils of three *Pissodes strobi* populations when presented a choice of three, 4 cm host lateral branch sections, one each of eastern white pine, Engelmann spruce, and Sitka spruce for 24 hours. One weevil per replicate; 30 replicates for each sex of each population on the three-host combination

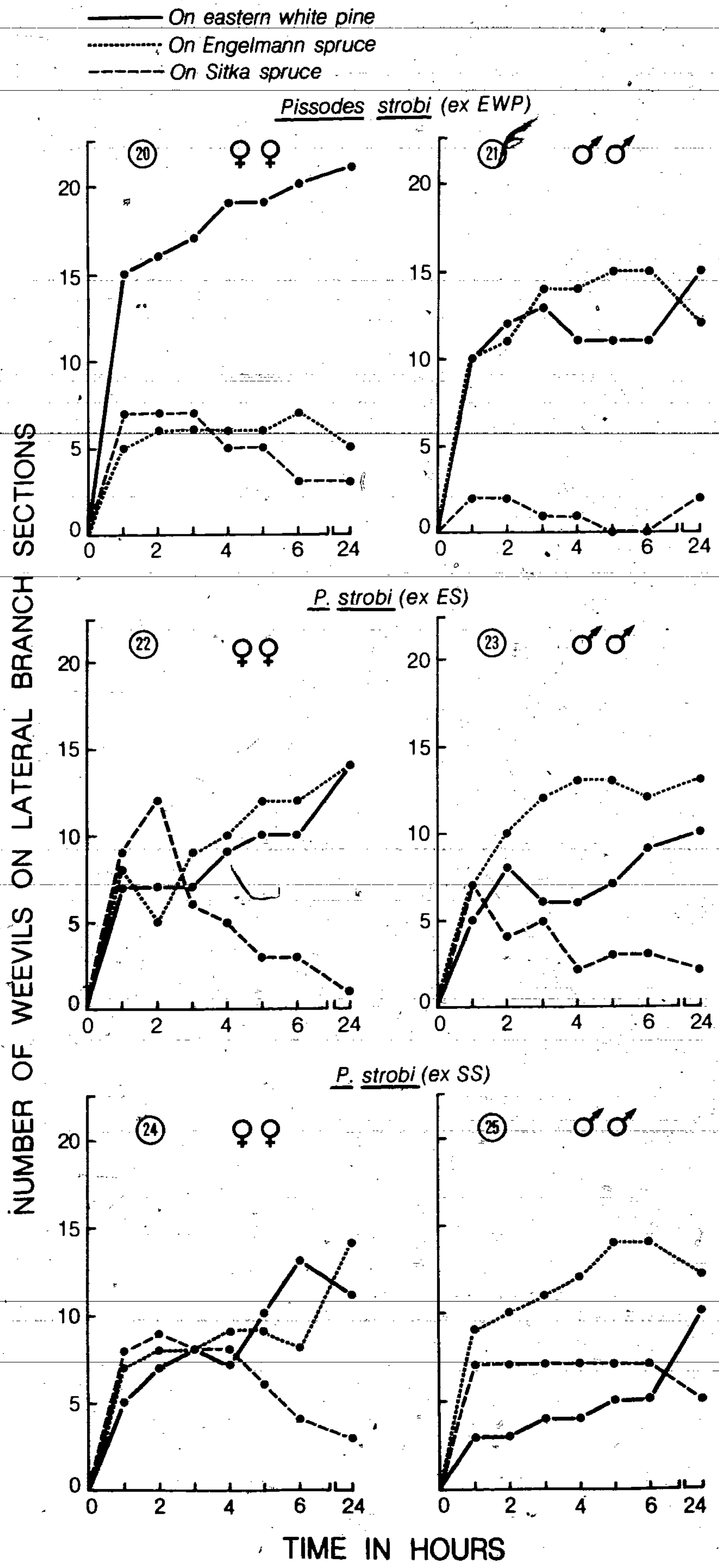
Host species	Weevil population[1]			Mean # feeding punctures produced on each host species[2]
	P. strobi (ex EWP)	*P. strobi* (ex ES)	*P. strobi* (ex SS)	
Eastern white pine	8.45a	4.10a	2.60a	5.05
Engelmann spruce	3.60b	2.43a	1.88a	2.64
Sitka spruce	0.43c	0.42b	1.13a	0.66
Mean # feeding punctures produced/weevil in each population[3]	4.16	2.32	1.87	

[1] Differences between means in the same column followed by same letter not significant (MANOVA, $P<0.05$).

[2] Flatness hypothesis rejected (MANOVA, Profile Analysis, $P<0.01$).

[3] Levels hypothesis rejected (MANOVA, Profile Analysis, $P<0.01$).

Figs. 20-25. Position of pre-wintering adults of three *Pissodes strobi* populations when presented a choice of three, 4 cm host lateral branch sections, one each of eastern white pine, Engelmann spruce, and Sitka spruce for 24 hours. One weevil per replicate; 30 replicates for each sex of each weevil population on the three-host combination


On eastern white pine
On Engelmann spruce
On Sitka spruce
Pissodes strobi (ex EWP)
⑳ ♀♀
㉑ ♂♂
P. strobi (ex ES)
㉒ ♀♀
㉓ ♂♂
P. strobi (ex SS)
㉔ ♀♀
㉕ ♂♂
NUMBER OF WEEVILS ON LATERAL BRANCH SECTIONS
0
5
10
15
20
0
2
4
6
24
TIME IN HOURS

rather than Sitka spruce. The greatest incidence of weevils in contact with Sitka spruce after 24 hours was 14.5 per cent of *P. strobi* (ex SS).

The body weight of female weevils was significantly greater than that of males (Table IX). In addition, the weight of the *P. strobi* (ex SS) population was significantly greater than the body weight of either the *P. strobi* (ex EWP) or the *P. strobi* (ex ES) populations (Table IX).

Discussion

Significantly more feeding by female weevils in the forced feeding bioassay (Table VII), is partially attributed to their significantly greater body weight (Table IX). It may also be related to the physiological requirements of ovary maturation prior to spring dispersal. The significantly greater number of feeding punctures initiated by *P. strobi* (ex EWP) on all three host species combined in the forced feeding bioassays may reflect the observation that this population did not feed extensively on its native host in holding jars, and therefore, were more strongly stimulated to feed. However, all weevils were conditioned equally by deprivation of food for 24 hours prior to each experiment. Moreover, food ingestion (as measured by feces weight) by *P. strobi* (ex EWP) was approximately equal to that of the remaining two populations (Table VII), suggesting similar satiation levels.

The lack of discrimination between hosts in the forced feeding bioassay indicates that all three host species are acceptable to all three *P. strobi* populations. In choice feeding bioassays, however, the failure of the two western *P. strobi* populations to discriminate between their respective natural hosts (i.e., the conifer species from which they

Table IX. Mean body weight for weevils of three *Pissodes strobi* populations. N=25 in each category

Weevil population	Mean body weight ±S.D. (mg)		
	Females	Males	Both sexes combined[1]
P. strobi (ex EWP)	9.266±1.483	8.938±1.745	9.102±1.611a
P. strobi (ex ES)	9.311±1.707	7.852±1.598	8.581±1.795a
P. strobi (ex SS)	10.087±1.857	9.136±1.916	9.611±1.928b
Three populations combined[2]	9.554±1.709	8.642±1.825	

[1] Means followed by same letter not significantly different (Newman-Keuls, P<0.01).

[2] Females significantly heavier than males (ANOVA, P<0.01).

emerged) and eastern white pine (Table VIII) suggests that the latter conifer is their ancestral host. Since *P. strobi* (ex EWP) prefers to feed on eastern white pine, *P. strobi* (ex ES) prefers to feed on both eastern white pine and Engelmann spruce, and *P. strobi* (ex SS) feeds on all three host species equally, these results suggest that *P. strobi* has dispersed west across the North American continent probably utilizing an alternate host species such as *P. glauca*. White spruce is sympatric with both Engelmann spruce and Sitka spruce in central and north-western British Columbia, and hybridizes readily with both species (Roche 1969). Engelmann and Sitka spruces, however, are allopatric species.

In retrospect, Hopkins (1911) was premature in according species status to the two western weevil populations on the basis of his host selection principle. The experimental results support Smith and Sugden's (1969) contention that the three *P. strobi* populations are ecotypes or geographic races.

VISUAL ORIENTATION OF *PISSODES STROBI* IN RELATION TO HOST SELECTION BEHAVIOUR

Host selection in phytophagous insect species is essentially a two-stage process in which initial orientation to a potential host plant is followed by acceptance or rejection of same as a host suitable for feeding and/or oviposition activity (Dethier 1954). *P. strobi* is capable of discriminating among at least six native conifer species by close-range or contact chemoreception as indicated in choice feeding bioassays. Little is known, however, of the sensory modalities that govern initial orientation to, and subsequent arrival at potential host trees. Since Anderson and Fisher (1960) showed that essential oils, steam-distilled from eastern white pine bark, are repellent to *P. strobi*, olfactory attraction to this preferred host appears unlikely.

In nature, *P. strobi* selects the more vigorous, larger-diameter, upright leaders of dominant and co-dominant trees in even-aged stands for spring feeding and subsequent oviposition (Kriebel 1954; Sullivan 1961; Stroh and Gerhold 1965; Connola 1966; Harman and Kulman 1969). One hypothesis which could account for this host preference in the field is that *P. strobi* adults discriminate visually between some physical characteristics of available leaders.

My objectives were: (1) to ascertain the physical characteristics or properties that are important in the visual attraction and subsequent orientation of *P. strobi* to simple geometric shapes, (2) to determine the capability of *P. strobi* to discriminate deviation of simple geometric shapes from the vertical plane, and (3) to relate these findings to the observed host preferences of *P. strobi* in the field.

Methods and Materials

Laboratory Orientation Experiments

Preliminary flight experiments conducted in spring 1975 with *P. strobi* that had overwintered naturally, indicated both sexes were attracted to land on vertical black cardboard strips mounted around the 196 cm circumference of a white cardboard cylinder (χ^2, $P<0.005$). Owing to the reluctance of *P. strobi* to fly under a variety of experimental conditions, however, subsequent orientation experiments were conducted with walking weevils.

Overwintered *P. strobi* adults were collected during April to June 1976, from the leaders of Sitka spruce planted in four localities; the University of British Columbia Research Forest, Maple Ridge, B.C., the District of Mission Municipal Forest, Mission, B.C., and two plantations in the vicinity of Port Renfrew, Vancouver Island, B.C.

The orientation of overwintered *P. strobi* adults to black cardboard shapes was tested at 20 to 23°C inside an upright cylinder (61 cm diameter x 61.5 cm height) of white cardboard (Fig. 26) resting on a Kraft paper floor that was replaced after each experiment. Uniform illumination of the arena was provided by fluorescent lights mounted 10 cm above the cylinder.

Descriptions of the various black cardboard patterns used to test the orientation response of walking *P. strobi* are summarized in Table X. Experiments 1 and 6 were designed to test the null hypothesis that *P. strobi* orient randomly to the cylinder periphery, whereas experiments 2

Fig. 26. Diagram of apparatus used to test the visual orientation of walking *Pissodes strobi* adults. Dotted silhouettes depict experiment 5 on the inside circumference of the white cardboard cylinder

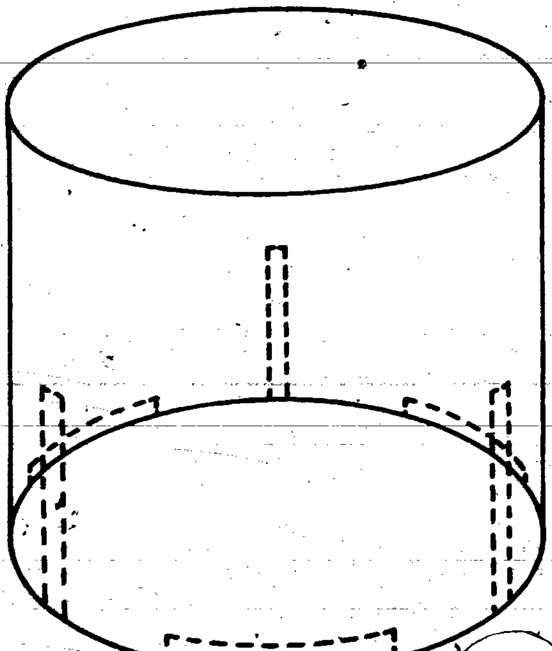


Table X. Description of black cardboard patterns presented to walking *Pissodes strobi* adults around the base of a white cardboard cylinder 192 cm in circumference. Experiments conducted during July and August 1976, with spring adults that had overwintered naturally in the field

Exp. no.[1]	Description of black cardboard silhouette pattern
1	Six vertical rectangles, 3x15 cm, spaced 29 cm apart
2	Three vertical rectangles, 2x15 cm, alternated with three vertical rectangles, 6x15 cm, each spaced 28 cm apart
3	Three vertical rectangles, 3x15 cm, alternated with three vertical rectangles, 3x30 cm, each spaced 29 cm apart
4	Three vertical rectangles, 2x18 cm, alternated with three squares, 6x6 cm, each spaced 28 cm apart
5	Three vertical rectangles, 3x15 cm, alternated with three horizontal rectangles, 3x15 cm, each spaced 23 cm apart
6	Experiment 4 raised 4 cm above the Kraft paper floor of the cylinder above a 4x192 cm strip of black cardboard mounted around the base of the cylinder circumference
7	Six, 30 cm^2 rectangles presented around the circumference at the base of the white cardboard cylinder in the random order: 1x30 cm, 7x4.3 cm, 3x10 cm, 5x6 cm, 11x2.7 cm, 9x3.3 cm, each spaced 26 cm apart
8	Experiment 7 randomly reordered as follows: 1x30 cm, 3x10 cm, 11x2.7 cm, 7x4.3 cm, 9x3.3 cm, 5x6 cm, each spaced 26 cm apart
9	Six, 45 cm^2 parallelograms each with a 3 cm wide base, that deviated 0°, 15°, 30°, 45°, 60° and 90°, respectively, from the vertical, presented around the circumference at the base of the white cardboard cylinder in the random order: vertical rectangle, 60°, 30°, 15° off-vertical parallelograms, horizontal rectangle and 45° off-vertical parallelogram, each spaced 21.2 cm apart
10	Experiment 9 randomly reordered as follows: vertical rectangle, 45°, 60°, 15°, 30° off-vertical parallelograms and horizontal rectangle, each spaced 21.2 cm apart

[1] In experiments 1-8 distances between adjacent black silhouettes were measured edge-to-edge; whereas in experiments 9 and 10 distances between adjacent black silhouettes were measured edge-to-edge following projection of each off-vertical parallelogram along the cylinder base.

and 3 tested weevil orientation to silhouette width and height, respectively. *P. strobi* orientation to silhouette area was tested in experiments 4, 7, and 8, whereas the effect of silhouette position was examined in experiments 5, 9, and 10.

Weevils of either sex were released--facing in random directions --in small groups of six to 10 individuals in the centre of the arena floor and allowed to walk to the cylinder wall. Weevils inadvertently released on their back were not assisted in righting themselves, as this action prompted escape behaviour rather than orientation to the cylinder periphery. Each insect was scored at the point it first contacted the wall of the white cardboard cylinder with either its proboscis or prothoracic legs. No time limit was imposed on the response of each beetle.

Null hypotheses regarding weevil orientation to silhouette patterns in experiments 1 to 6 were tested using Chi-square at one degree of freedom. Yates' correction for continuity was applied when sample size was less than 40 individuals. *P. strobi* orientation responses to the multiple patterns presented in experiments 7 and 8, and 9 and 10, were examined using analysis of variance (ANOVA). Six replicates of approximately 22 weevils each were completed in both experiments 7 and 8, whereas four replicates of about 25 weevils each were completed in each of experiments 9 and 10. The proportional responses obtained in each replicate were transformed to the arcsin of the square root prior to each analysis of variance.

The same group (or proportion thereof) of *P. strobi* of either sex was tested to each silhouette pattern described in Table X. When not being tested in the walking arena (Fig. 26), all weevils were held at 20 to 23°C on Sitka spruce lateral branch sections in glass jars. During long between-test intervals, however, the glass jars were transferred to 2 to 4°C to minimize weevil mortality.

Field Data

During the spring 1976 field collections of overwintered *P. strobi* adults, the length and width at midpoint (measured both with and without the needles) were obtained for each one-year-old Sitka spruce leader on which a single weevil of either sex was found feeding or resting. To assess whether the means of these host leader characteristics differed significantly from the population means, identical data were obtained in autumn 1976, for a random sample of current-year host leaders at each of the three Sitka spruce plantations used to collect the overwintered *P. strobi* the previous spring. In addition, the host leader population data were used to assess the biological significance of *P. strobi* orientation in experiments 7 and 8 (Table X).

To determine the relationship of weevil orientation in experiments 9 and 10 (Table X) to actual field conditions, the length, diameter at midpoint (excluding needles), and angular deviation from vertical; were measured for each first-whorl lateral branch in the crown of 44 multiple-top Sitka spruce that had been weevilled in both 1975 and 1976. As many as five lateral branches of the first whorl below the dead 1975 leader, may compete for apical dominance in 1976 to create a multiple-top host. Ten such hosts were located in the District of Mission Municipal Forest, Mission, B.C., 20 trees were located in the University of British Columbia

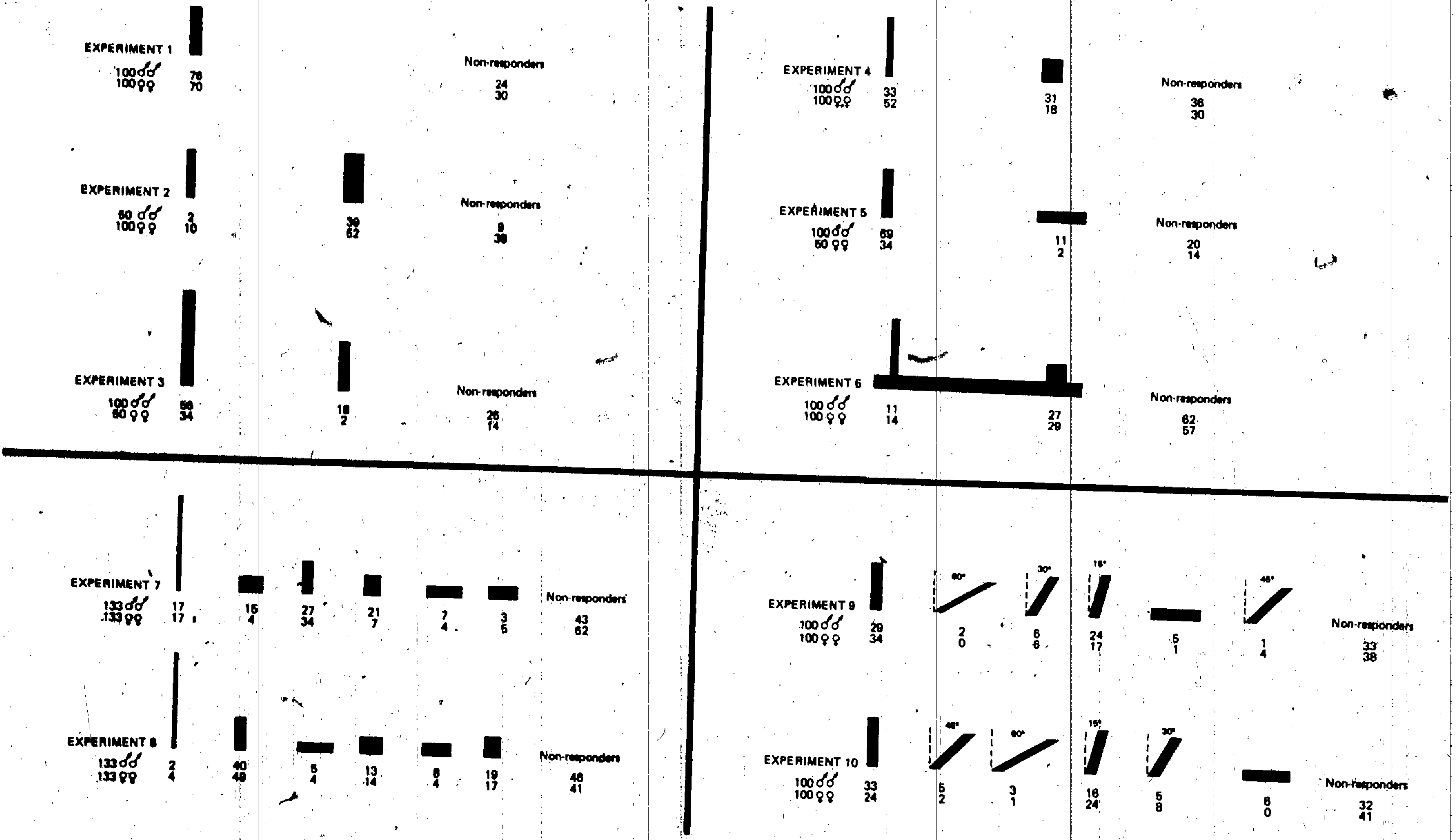
Research Forest, Maple Ridge, B.C., and the remainder in natural Sitka spruce regeneration located south of Kelsey Bay, Vancouver Island, B.C. In addition, stepwise discriminant analysis, program BMD07M (Sampson 1976) was applied to these host lateral branch characteristics in order to ascertain their contribution to the classification of weevilled and unattacked lateral branches.

Results

Laboratory Orientation Experiments

The orientation response of *P. strobi* in each experiment is given in Fig. 27. Non-responders refer to those weevils in experiments 1 to 5 and 7 to 10 that contacted the cylinder periphery at white, or, in experiment 6, those weevils that contacted black at points other than directly below the black silhouettes. In experiment 1, the null hypothesis states that weevils randomly contact the cylinder periphery in the ratio that black and white are presented around the basal circumference of the cardboard cylinder, and was rejected for both sexes (χ^2, $P<0.005$). Both sexes of *P. strobi* were attracted to and climbed the black silhouettes presented. Similarly, neither sex contacted the 4x192 cm black cardboard strip randomly in experiment 6 (χ^2, $P<0.005$), but oriented to points directly below the black silhouettes presented. These results discount the hypothesis that *P. strobi* is attracted to black silhouettes as a result of their somewhat higher temperature in relation to white cardboard that is equidistant from the experimental light source. As a result of ~~the~~ significant visual orientation response to black silhouettes in experiments 1 and 6, those weevils contacting the 192 cm cylinder

Fig. 27. Number of overwintered *Pissodes strobi* adults of each sex that oriented to black cardboard silhouettes in 10 experiments. Numbers of beetles used and the total response to each silhouette pattern are given below each diagram. Non-responders represent those beetles that contacted the white cylinder wall, or in experiment 6, the black 4 cm strip at points other than directly below the silhouettes presented. Descriptions of silhouette patterns and randomized placement are given in Table X


EXPERIMENT 1
100 ♂♂
100 ♀♀
76
70
Non-responders
24
30
EXPERIMENT 2
50 ♂♂
100 ♀♀
2
10
39
52
Non-responders
9
38
EXPERIMENT 3
100 ♂♂
60 ♀♀
56
34
18
2
Non-responders
26
14
EXPERIMENT 4
100 ♂♂
100 ♀♀
33
52
31
18
Non-responders
36
30
EXPERIMENT 5
100 ♂♂
50 ♀♀
69
34
11
2
Non-responders
20
14
EXPERIMENT 6
100 ♂♂
100 ♀♀
11
14
27
29
Non-responders
62
57
EXPERIMENT 7
133 ♂♂
133 ♀♀
17
17
15
4
27
34
21
7
7
4
3
5
Non-responders
43
62
EXPERIMENT 8
133 ♂♂
133 ♀♀
2
4
40
49
5
4
13
14
8
4
19
17
Non-responders
46
41
EXPERIMENT 9
100 ♂♂
100 ♀♀
29
34
60°
2
0
30°
6
6
15°
24
17
5
1
45°
1
4
Non-responders
33
38
EXPERIMENT 10
100 ♂♂
100 ♀♀
33
24
45°
5
2
60°
3
1
15°
16
24
30°
5
8
6
0
Non-responders
32
41

circumference at white were excluded from further statistical consideration in the analysis of results of experiments 2 to 5 and 7 to 10.

In experiment 2, the null hypothesis stating that *P. strobi* orient to black silhouettes randomly, and consequently in the 3:1 ratio of their widths, was rejected for males (χ^2, $P<0.005$), but accepted for females (χ^2, $P<0.50$). Only male *P. strobi* oriented preferentially to the wider of the two black silhouettes. In experiment 3, both sexes preferred to contact the taller of the two silhouettes (Fig. 27). In this instance, the null hypothesis states random orientation to the silhouettes in the 1:1 ratio of their widths and was rejected for both sexes (χ^2, $P<0.005$). Experiment 4 was designed to assess the relative importance of silhouette height and width in the visual orientation of *P. strobi* to silhouettes of equal area. Since male *P. strobi* oriented to the black silhouettes in the 1:1 ratio of their areas (χ^2, $P<0.70$), the result suggests silhouette height and width are equally significant in the response. Female *P. strobi* preferred to orient to the taller silhouette (χ^2, $P<0.005$), and therefore, apparently respond more to silhouette height than width. Both male and female *P. strobi* preferred to orient to the vertical silhouette (χ^2, $P<0.005$) in experiment 5. Evidently, a preferred silhouette is no longer acceptable when rotated through 90° to the horizontal position. Both sexes of *P. strobi* oriented randomly to the silhouettes in experiment 6 in the 3:1 ratio of their widths (χ^2, $P<0.90$). This result is different from the *P. strobi* orientation response in experiment 4 (Table X, Fig. 27), and suggests that both sexes were not choosing between the silhouettes mounted above the 4 cm black strip, but rather between those silhouettes which included the 4 cm height increment.

Extending the results of experiments 4 and 5, ANOVA applied to the orientation response of male *P. strobi* in experiments 7 and 8 (Fig. 27) indicated that significantly more males were attracted to the 3x10 cm vertical rectangle than to any of the five remaining black silhouettes of equal area (Newman-Keuls test, $P<0.05$). In addition, more males were attracted to both the 5x6 cm and the 7x4.3 cm silhouettes than to either the 9x3.3 cm or the 11x2.7 cm horizontal rectangles (Newman-Keuls test, $P<0.05$). The experiment by silhouette interaction was significant, but involved only the least preferred horizontal silhouettes. The parallel ANOVA for female *P. strobi* orientation in experiments 7 and 8 indicated that more females were attracted to the 3x10 cm vertical rectangle than to any of the five remaining black silhouettes (Newman-Keuls text, $P<0.05$). As was the case for male orientation, the experiment by silhouette interaction was significant, but again involved the least preferred horizontal silhouettes.

ANOVA applied to the orientation of male *P. strobi* in experiments 9 and 10 (Fig. 27) indicated that significantly more males were attracted to both the vertical rectangle and the 15° off-vertical parallelogram, than to the remaining four silhouettes (Newman-Keuls text, $P<0.05$). Silhouette dimensions and orientation, therefore, are important parameters that govern visual discrimination in males, although in experiments 9 and 10, silhouette orientation is unavoidably confounded by the varying cross-sectional diameter and length of parallelograms of equal area, all on a 3 cm base (Fig. 27). The parallel ANOVA for female *P. strobi* orientation tested in experiments 9 and 10 (Fig. 27) yielded the identical result obtained for males (Newman-Keuls test, $P<0.05$). In addition, however, significantly more females oriented to the 30° off-vertical parallelogram than to either the 60° off-vertical parallelogram or the horizontal rectangle (Newman-Keuls test, $P<0.05$).

Field Data

Both sexes of *P. strobi* in spring 1976, were found on one-year-old host leaders that are significantly longer and of greater midpoint diameter than current-year host leaders measured at the same Sitka spruce plantations in autumn 1976 (Table XI). In addition, female *P. strobi* were present on Sitka spruce leaders that possessed a significantly greater silhouette width than the population mean (Table XI). Barring major climatological perturbation, there is unlikely to be a significant change in host leader properties at the same plantation site in successive growing seasons.

Table XII summarizes the physical properties of weevilled and unattacked lateral branches competing for dominance in multiple-top Sitka spruce hosts. Weevilled branches were significantly longer and deviated less from the vertical than those not attacked in spring 1976.

Table XIII summarizes the stepwise discriminant analysis applied to three properties of Sitka spruce lateral branches measured in autumn 1976, to select the character that best separated weevilled from unattacked lateral branches. In this stepwise procedure, additional host properties were selected only if these contributed significantly to group separation when combined in a linear function with the property

Table XI. Characteristics of Sitka spruce leaders measured in three plantations from which overwintered *Pissodes strobi* were collected in April-June 1976

Description of Sitka spruce leaders	Number of leaders	Mean leader length±S.D.[1] (cm)	Mean leader width at midpoint (including needles) ±S.D.[1] (cm)	Mean leader width at midpoint (excluding needles) ±S.D.[1] (cm)
Autumn 1976 leaders	494	45.2±16.1a	3.07±0.73a	0.80±0.22a
Spring 1976 leaders from which single male *P. strobi* were collected	36	55.4±16.0b	3.16±0.65a	1.12±0.28b
Spring 1976 leaders from which single female *P. strobi* were collected	119	50.4±14.8b	3.23±0.67b	1.10±0.28b

[1] Means in each column followed by different letter are significantly different (t-test, $P<0.05$).

Table XII. Physical characteristics of weevilled and unattacked first-whorl lateral branches competing for apical dominance in the crowns of Sitka spruce trees

Lateral branch class	Number examined	Mean length ±S.D.[1] (cm)	Mean width at midpoint (excluding needles) ±S.D. (cm)	Mean angular deviation from vertical ±S.D.[1] (degrees)
weevilled	51	38.9±11.4	1.1±0.3	2.0±3.9
not attacked	56	30.8±6.5	1.0±0.3	12.7±16.4

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[1] Difference between means in column is significant (t-test, P<0.01).

Table XIII. Properties of Sitka spruce lateral branches ranked in order of selection by stepwise discriminant analysis

Host property	F value to enter stepwise discriminant analysis	Probability level	Per cent of host lateral branches correctly classified		
			Weevilled	Unattacked	Total
Length	20.7	<0.001	54.9	87.5	72.0
Angular deviation from vertical	10.4	<0.001	68.6	60.7	64.5
Diameter at midpoint	3.7	<0.05	66.7	69.6	68.2

first selected. The most efficient host character was lateral branch length. Of decreasing importance were angular deviation of the lateral branch from vertical, and lateral branch diameter measured at the mid-point (Table XIII). Of the 107 Sitka spruce lateral branches examined on 44 trees, 68.2 per cent of these were correctly classified as weevilled or unattacked on the basis of these three measured host characters.

Discussion

Vision is of significant importance in initial stages of host selection by *P. strobi*. Consistent orientation in the laboratory to vertical rather than horizontal silhouettes suggests that overwintered *P. strobi* are predisposed to respond to vertical Sitka spruce leaders rather than horizontal lateral branches in a field situation. The orientation preference expressed by both sexes for the vertical silhouette, 3 cm in width, in experiments 7 and 8, corresponds well with field data in which the mean silhouette width of Sitka spruce leaders measured in three weevil-infested plantations was 3.07 cm (Table XI). When presented two vertical silhouettes of the preferred 3 cm width in the laboratory, both sexes of *P. strobi* oriented preferentially to the taller of these. Similarly, under natural field conditions, both male and female *P. strobi* select those host leaders that are significantly longer than the mean length of the overall leader population (Table XI). Although female *P. strobi* were collected in spring 1976, from host leaders that possess a significantly greater silhouette width than the host population mean (Table XI), one cannot infer from available data that females discriminate this 5.2 per cent difference visually following flight dispersal.

Predisposition of *P. strobi* to orient to Sitka spruce leaders rather than lateral branches, is an adaptive reproduction strategy for several reasons. Longer, more vigorous leaders can accommodate larger weevil broods to maturity--feeding in the cambial zone beneath the periderm--than is possible in either suppressed host leaders, or smaller-diameter lateral branches. Secondly, rapid weevil development to the adult stage must be completed prior to late autumn, as *P. strobi* can successfully overwinter as larvae only in milder maritime climates. Rapid brood development is favoured by the generally higher than ambient temperature regimes in host leaders exposed to direct solar insolation (Sullivan 1960). Lastly, successful weevilling of a vigorous host leader often results in a multiple-top crown due to first-whorl lateral branch competition for apical dominance. Increased availability of optimal oviposition sites in years following the initial host attack favours rapid population growth of *P. strobi* particularly on Sitka spruce. This host is geographically restricted to a mild winter climate such that lateral branch competition following successful leader attack is often resolved in a single growing season.

The selection by *P. strobi* of host leaders of significantly larger diameter than the leader population mean (Table XI), likely involves close-range assessment of the physical characteristics of potential hosts during test feeding. The lack of statistical correlation between leader silhouette width and true diameter (r=0.32), precludes the visual selection of larger-diameter leaders on the basis of their silhouette width alone. Thicker bark (Kriebel 1954) and wider separation of cortical resin canals (Stroh and Gerhold 1965), are two physical properties that are expected to favour the selection by *P. strobi* of only the larger-diameter host leaders available in the field.

On Sitka spruce hosts with multiple tops, female *P. strobi* are attracted to feed and oviposit on those lateral branches that most closely approximate leaders in physical characteristics. Weevilled lateral branches are longer, and deviate significantly less from the upright, vertical position than competing branches that were not attacked in 1976 (Table XII). These field data are in agreement with results of laboratory orientation of *P. strobi* in experiments 9 and 10, in which both sexes were most attracted to the vertical or near vertical silhouettes. Stepwise discriminant analysis confirmed that lateral branch length is the single most efficient property to achieve separation of weevilled from unattacked lateral branches in multiple-top hosts (Table XIII). In conjunction with two additional variables, angular deviation from vertical, and diameter measured at midpoint, the total percentage of lateral branches correctly classified decreased, but the percentage of host lateral branches correctly classified in both the weevilled and unattacked categories is more equitable (Table XIII). Host selection among competing lateral branches of spruce successfully attacked the previous year, may not involve the dispersing *P. strobi* population. Repeated attack on a brood host in the second year, may be accomplished by a resident *P. strobi* population that did not disperse following autumn emergence. Although this difference is not significant, 15.8 per cent of regeneration Sitka spruce successfully weevilled in 1975, were again weevilled in 1976, whereas only 9.9 per cent of the host population was weevilled for the first time in 1976. Silver (1968) reported that the percentage of Sitka spruce re-attacked in each of five successive years (1960-64) was, without exception, greater than the proportion of hosts attacked for the first time. These data suggest that Sitka spruce initially attacked by dispersing *P. strobi* are more susceptible to re-attack the following year due simply to the presence of progeny on the host that do not disperse, rather than intrinsic physical or chemical factors. It is hypothesized that resident *P. strobi* respond to gravitational stimuli in rejecting those host lateral branches that deviate considerably from the normal vertical orientation of host leaders. On the other hand, the mechanisms of negative geotaxis and positive phototaxis (Sullivan 1959) either alone or acting in concert, can account for the successful weevilling by resident *P. strobi* of the longer host lateral branches that deviate least from the vertical orientation.

Although the visual orientation response of *P. strobi* to black silhouettes was tested using walking weevils, there is no evidence to suggest the results do not apply equally well to flying weevils. Visual perception of form is expected to be independent of the method of locomotion employed by *P. strobi* during dispersal. In trapping studies conducted during the spring flight of *P. strobi* to new Sitka spruce hosts, Overhulser and Gara (1975) concluded that the majority of weevils fly at a height somewhat below the level of the host leaders. This finding suggests that flying *P. strobi* can evaluate host leader properties such as length, orientation, and silhouette width in order to discriminate visually between preferred and unsuitable leaders in initial stages of the host selection sequence.

ROLE OF GEOTAXIS AND PHOTOTAXIS IN THE FEEDING AND OVIPOSITION BEHAVIOUR OF OVERWINTERED *PISSODES STROBI*

Whereas both sexes of adult *P. strobi* feed on Sitka spruce lateral branches for most of the year (Gara et al. 1971; McMullen and Condrashoff 1973), feeding activity on Sitka spruce leaders is confined to the early growing season, and is largely restricted to the females as necessary physiological and physical prerequisites to oviposition (Overhulser and Gara 1975). Males are more mobile than females on Sitka spruce leaders following spring dispersal, and largely confine their activity to mating behaviour. Female weevils initiate oviposition each spring, just below the terminal bud cluster of Sitka spruce leaders, and continue lower down these leaders as spring advances to early summer.

Negative geotaxis and positive phototaxis are two orientation mechanisms that could account for this observed preference in the location of oviposition sites. Sullivan (1959) found that overwintered *P. strobi* adults are more strongly photopositive under a variety of conditioning regimes, and become more photonegative at higher temperatures than the same generation pre-wintering adults. He concluded that this behaviour of the overwintered adults served to maintain *P. strobi* on exposed host leaders for spring feeding and oviposition.

The role of negative geotaxis in the oviposition behaviour of *P. strobi* has not been extensively investigated. Gara et al. (1971) postulated that gravitational stimuli have little influence on the distribution of oviposition punctures and successful weevilling of Sitka spruce leaders. In field studies, caged weevils fed and oviposited on one-year-old Sitka spruce leaders bent into a horizontal position. In laboratory studies, however, *P. strobi* did oviposit in one-, two-, and three-year-old vertical lateral branches (Gara et al. 1971), suggesting that host orientation may be important in releasing oviposition behaviour.

My objectives were: (1) to determine the effect of host leader and lateral branch position on the distribution of feeding and oviposition punctures along their length under both forced and choice experimental conditions, and (2) to determine the relative influence of geotactic and phototactic mechanisms on the distribution of feeding and oviposition punctures along the length of excised Sitka spruce leaders.

Methods and Materials

Overwintered *P. strobi* adults were collected in spring 1975 and 1976, from the leaders of Sitka spruce planted in four different localities; the University of British Columbia Research Forest, Maple Ridge, B.C., the District of Mission Municipal Forest, Mission, B.C., and plantations established in the vicinity of Port Renfrew and Kelsey Bay, Vancouver Island, B.C. Only those *P. strobi* recovered from Sitka spruce leaders that bore oviposition punctures were used in laboratory oviposition experiments to ensure their physiological maturity.

The cut end of each unattacked one-year-old host leader or lateral branch used in oviposition experiments was immersed in water in a 4 or 8 oz Nalgene washbottle sealed at the neck with paraffin wax. Each trial in forced oviposition experiments consisted of a single host leader or lateral branch supported inside a screened, wooden cage by means of a clamp and support stand. In choice oviposition experiments, pairs of host leaders clamped in two different positions, or one host leader paired with one host lateral branch, each clamped in a different position, were used in each trial.

The overwintered weevils were allowed to feed and oviposit for varying periods, after which the number of both feeding and oviposition punctures produced per 1 cm segment along each host leader or lateral branch were counted. Chi-square tests were applied to the distributions of each type of weevil puncture along the length of each host leader or lateral branch. The null hypothesis stated that each type of puncture was produced in equal numbers in the apical and basal halves of host leaders or lateral branches.

Forced Oviposition Experiments

In experiments 11 to 15, two females and a single male *P. strobi* were released in the needles at the midpoint of Sitka spruce leaders of similar length clamped in one of the following positions, respectively: vertical and upright; 30° off-vertical; 60° off-vertical; horizontal; and vertical but inverted.* Three trials, each of three days' duration, were completed in each of experiments 11 to 15. Experiment 16 was identical to experiment 11, except that one-year-old Sitka spruce lateral branches (15 cm in length) cut from the topmost whorl directly below the host one-year-old leader were used. The light intensity measured at the level of host leaders or lateral branches in experiments 11 to 16, was

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*See Figs. 28 to 41 for diagrammatic representation of experimental design.

560 lux, provided by overhead fluorescent lights.

Choice Oviposition Experiments

Only female *P. strobi* were used in choice oviposition experiments in order to eliminate that proportion of feeding punctures produced by male weevils in experiments 11 to 16. In experiment 17, females were released in the needles at the point of contact of a horizontal host leader with a vertical, upright lateral branch clipped from the same host. Six trials were completed, two with two females for seven days, three with five females for six days, and one with six females for four days. Asymmetrical trials were often necessary depending on the field availability of gravid female weevils. In experiment 18, two females were released in the needles at the point of contact of a vertical, upright host leader with a horizontal lateral branch clipped from the same host. Two trials were completed, each of seven days' duration. In experiment 19, female weevils were released in the needles at the point of contact of a vertical, upright host leader with a 45° off-vertical leader, both clipped from a single multiple-top host to minimize chemical and physical differences between them. Six trials were completed, two with two females for seven days, and four with four females for four days. As in the forced oviposition experiments, the light intensity provided by overhead fluorescent tubes was 560 lux.

Influence of Geotactic and Phototactic Mechanisms on the Distribution of Feeding and Oviposition Punctures

In each of experiments 20 to 24, a single, unattacked host leader was supported inside a screened, wooden cage (46x31x31 cm) in the following positions, respectively: vertical and upright; vertical and inverted; vertical and inverted again; horizontal; and vertical but upright. In experiments 20 and 21, the cage was entirely covered in a double thickness of 4 mil black plastic to exclude light. In experiments 22, 23, and 24, all cage surfaces except the single surface perpendicular to the host leader and closest to the leader apex, were covered in 4 mil black plastic. A light source consisting of three parallel fluorescent tubes was placed 30 cm to one side of, below, and above, the uncovered cage surface in experiments 22 to 24, respectively, such that the leader apex was closest to the light source in each case. Light intensity measured at the leader apex was 3120 lux. Three female weevils in each of two trials in experiment 20, and five females in each of two, three, six, and three trials for experiments 21 to 24, respectively, were released in the needles at the midpoint of each host leader at the start of each test. The number of weevil-days per replicate in experiments 20 to 24 is approximately constant.

Results

Forced Oviposition Experiments

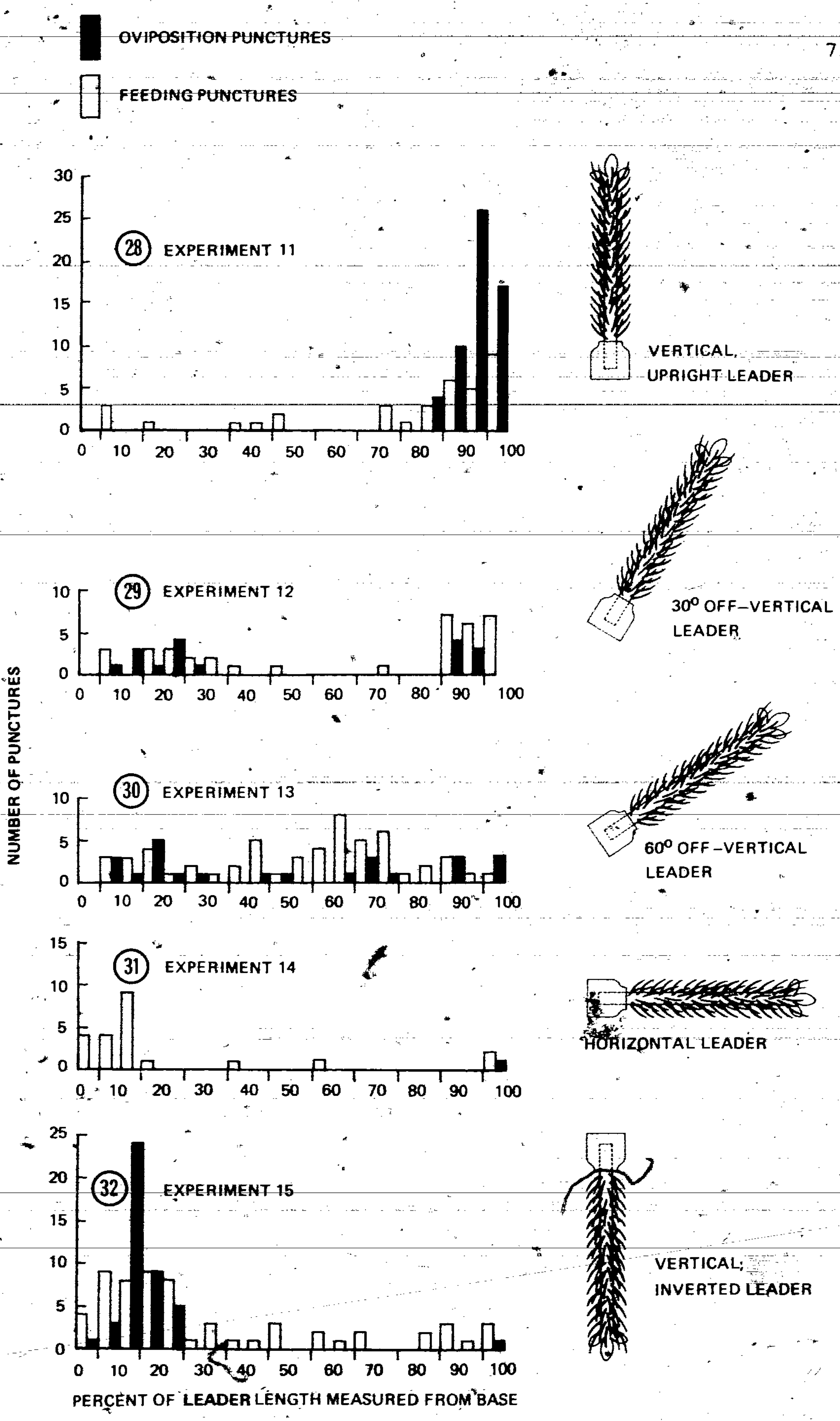
Table XIV indicates that overwintered *P. strobi* produced significantly more feeding punctures in the apical half of upright host leaders than in the basal half (Fig. 28). This result is reversed in the case of both horizontal leaders (Fig. 31), and vertical, inverted leaders (Fig. 32). Although weevils produced more feeding punctures in the apical half of 30° off-vertical leaders, 60° off-vertical leaders, and vertical, upright host lateral branches, than in the basal halves (Figs. 29, 30,

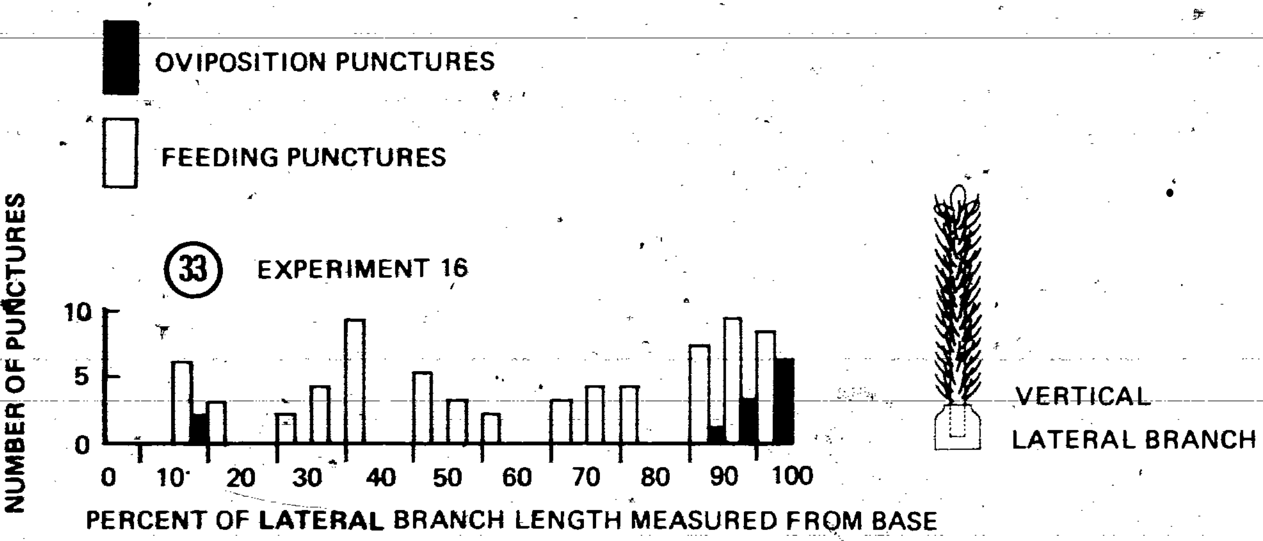
Table XLV. Distributions of feeding and oviposition punctures produced by overwintered *Pissodes strobi* in the apical and basal regions of Sitka spruce leaders and lateral branches

Experiment no.	Distribution of feeding punctures				Distribution of oviposition punctures			
	Basal half	Apical half	χ^2	Probability level[1]	Basal half	Apical half	χ^2	Probability level[1]
11	8	27	10.6	<0.005	0	57	57.0	<0.005
12	15	21	0.1	N.S.	10	7	0.1	N.S.
13	22	34	2.6	N.S.	13	11	0	N.S.
14	19	3	11.6	<0.005	0	1	--	--
15	46	14	17.1	<0.005	42	1	38.2	<0.005
16	29	40	1.1	N.S.	2	10	5.3	<0.025

[1] N.S. = not significant ($p<0.05$).

Figs. 28-33. Distributions of feeding and oviposition punctures produced by overwintered *Pissodes strobi* adults on Sitka spruce leaders or lateral branches oriented in the positions shown inside wooden, screened cages


OVIPOSITION PUNCTURES
FEEDING PUNCTURES
28
EXPERIMENT 11
VERTICAL, UPRIGHT LEADER
29
EXPERIMENT 12
30° OFF–VERTICAL LEADER
30
EXPERIMENT 13
60° OFF–VERTICAL LEADER
31
EXPERIMENT 14
HORIZONTAL LEADER
32
EXPERIMENT 15
VERTICAL; INVERTED LEADER
NUMBER OF PUNCTURES
0
5
10
15
20
25
30
0
10
20
30
40
50
60
70
80
90
100
PERCENT OF LEADER LENGTH MEASURED FROM BASE


■ OVIPOSITION PUNCTURES
□ FEEDING PUNCTURES
㉝ EXPERIMENT 16
NUMBER OF PUNCTURES
10
5
0
0
10
20
30
40
50
60
70
80
90
100
PERCENT OF LATERAL BRANCH LENGTH MEASURED FROM BASE
VERTICAL
LATERAL BRANCH

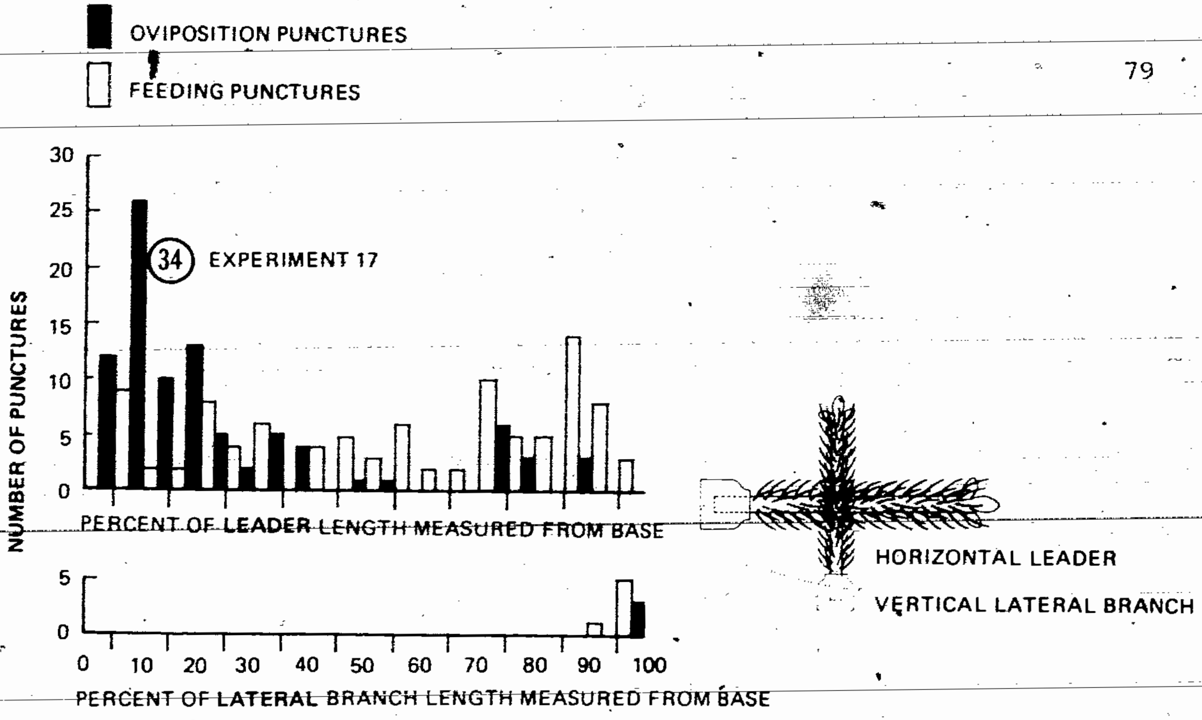
and 33), these differences in each case were not significant (Table XIV).

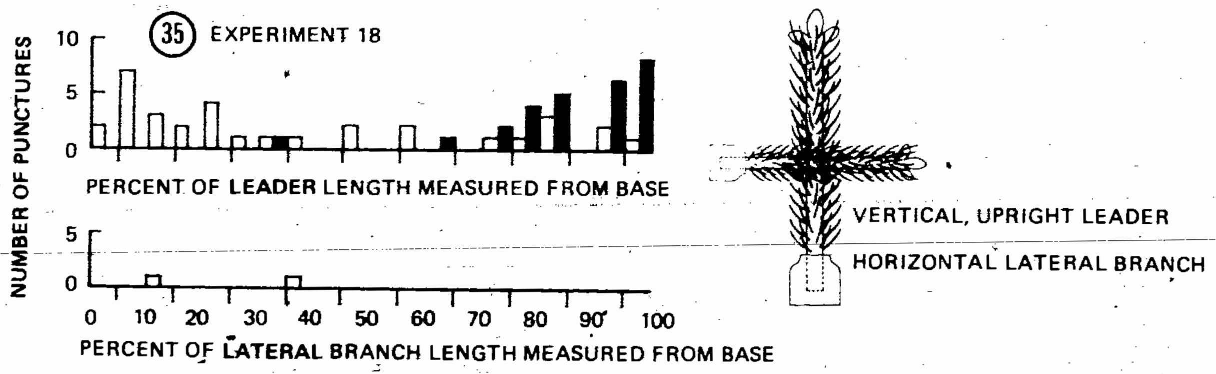
Female weevils produced significantly more oviposition punctures in the apical half of both vertical, upright host leaders and lateral branches than in the basal half (Figs. 28 and 33, Table XIV). Significantly more oviposition cavities were produced in the basal half of inverted host leaders than in the lower, apical half (Fig. 32, Table XIV). The numbers of oviposition punctures produced in each half of both the 30° and 60° off-vertical host leaders were not significantly different (Figs. 29 and 30, Table XIV), whereas only a single egg was deposited at the apex of a horizontal host leader (Fig. 31, Table XIV).

Choice Oviposition Experiments

In experiment 17, female weevils produced significantly more feeding and oviposition punctures in the bark of the horizontal host leader than in the vertical, upright lateral branch clipped from the same tree (Fig. 34, Table XV). Although more feeding punctures were produced in the apical half of horizontal host leaders than in the basal half, this difference was not significant (Fig. 34, Table XVI). In both experiments 18 and 19, female weevils produced significantly more feeding and oviposition punctures in the vertical, upright host leaders than in either the horizontal host lateral branch or the 45° off-vertical host leader (Figs. 35 and 36, Table XV). Significantly more feeding punctures were produced in the basal half of the vertical, upright host leaders than in the apical half in experiment 18, but the reverse was true in the case of vertical, upright host leaders in experiment 19 (Table XVI). In both experiments, significantly more oviposition punctures were

Figs. 34-36. Distributions of feeding and oviposition punctures produced by overwintered *Pissodes strobi* females on Sitka spruce leaders and lateral branches when presented a two-way choice of host materials oriented in the positions shown inside wooden, screened cages


OVIPOSITION PUNCTURES
FEEDING PUNCTURES
34
EXPERIMENT 17
NUMBER OF PUNCTURES
30
25
20
15
10
5
0
PERCENT OF LEADER LENGTH MEASURED FROM BASE
5
0
0
10
20
30
40
50
60
70
80
90
100
PERCENT OF LATERAL BRANCH LENGTH MEASURED FROM BASE
HORIZONTAL LEADER
VERTICAL LATERAL BRANCH


35
EXPERIMENT 18
NUMBER OF PUNCTURES
10
5
0
PERCENT OF LEADER LENGTH MEASURED FROM BASE
5
0
0
10
20
30
40
50
60
70
80
90
100
PERCENT OF LATERAL BRANCH LENGTH MEASURED FROM BASE
VERTICAL, UPRIGHT LEADER
HORIZONTAL LATERAL BRANCH

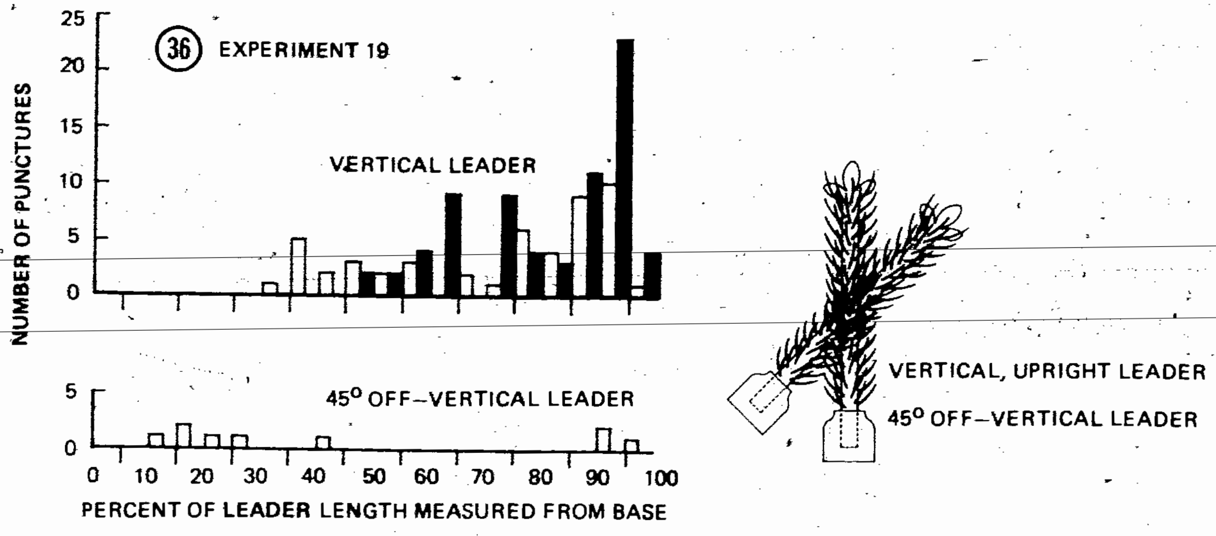

36
EXPERIMENT 19
NUMBER OF PUNCTURES
25
20
15
10
5
0
VERTICAL LEADER
5
0
45° OFF–VERTICAL LEADER
0
10
20
30
40
50
60
70
80
90
100
PERCENT OF LEADER LENGTH MEASURED FROM BASE
VERTICAL, UPRIGHT LEADER
45° OFF–VERTICAL LEADER

Table XV. Distributions of feeding and oviposition punctures produced by overwintered female *Pissodes strobi* when presented a choice of two host sections

Experiment no.	Distribution of feeding punctures				Distribution of oviposition punctures			
	Vertical host section	Off-vertical or horizontal host section	X^2	Probability level	Vertical host section	Off-vertical or horizontal host section	X^2	Probability level
17	6	102	85.4	<0.005	3	91	82.4	<0.005
18	33	2	28.3	<0.005	28	0	28.0	<0.005
19	52	9	30.8	<0.005	71	0	71.0	<0.005

Table XVI. Distributions of feeding and oviposition punctures produced by overwintered female *Pissodes strobi* along the length of preferred host leaders in choice experiments

Experiment no.	Distribution of feeding punctures				Distribution of oviposition punctures			
	Basal half	Apical half	X^2	Probability level[1]	Basal half	Apical half	X^2	Probability level[1]
17	44	58	0.2	N.S.	78	13	47.0	<0.005
18	23	10	5.3	<0.025	1	26	24.1	<0.005
19	11	41	17.3	<0.005	2	69	64.1	<0.005

[1] N.S. = not significant.

produced in the apical half of vertical, upright host leaders than in the basal half (Table XVI).

Influence of Geotactic and Phototactic Mechanisms on the Distribution of Feeding and Oviposition Punctures

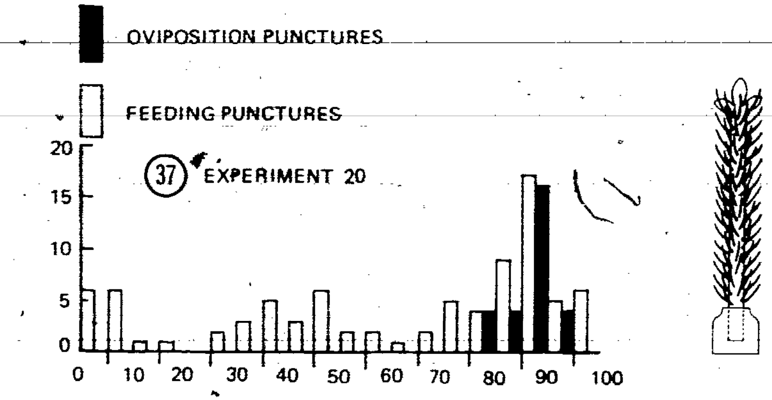
In the absence of light, overwintered *P. strobi* produced significantly more feeding and oviposition punctures in the apical half of vertical, upright host leaders (Fig. 37, Table XVII), but in the basal half of vertical, inverted host leaders (Fig. 38, Table XVII). With a light stimulus placed 30 cm below vertical, inverted host leaders, *P. strobi* produced significantly more feeding and oviposition punctures in the apical half, although considerable oviposition was observed in the upper, basal half of these inverted leaders (Fig. 39, Table XVII). Although female weevils produced more feeding punctures proximal to the light source in the apical half of both horizontal and vertical, upright leaders in experiments 23 and 24, respectively, this difference was not significant in either experiment (Figs. 40 and 41, Table XVII). Significantly more oviposition punctures, however, were produced by *P. strobi* proximal to the light source, in the apical half of both the horizontal and vertical, upright host leaders in experiments 23 and 24 (Table XVII).

Discussion

Forced and Choice Oviposition Experiments

Both feeding and oviposition behaviour of overwintered *P. strobi* adults are influenced by the orientation of excised Sitka spruce leaders and lateral branches on which the beetles are released. Weevils preferred to feed and oviposit in the apical half of vertical, upright host

Figs. 37-41. Distributions of feeding and oviposition punctures produced by overwintered *Pissodes strobi* females on Sitka spruce leaders oriented in the positions shown inside wooden, screened cages. Cages covered in black plastic except that single side closest to the light source in experiments 22 to 24

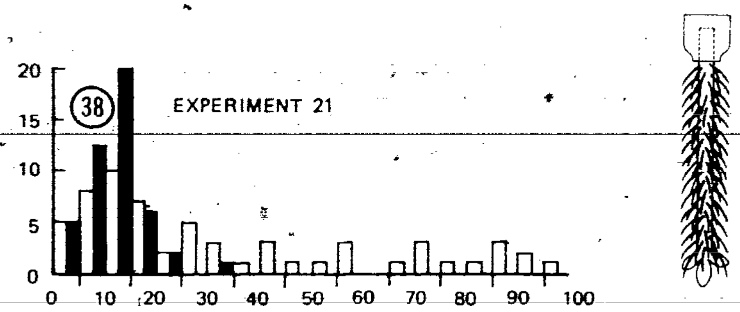


㊲ EXPERIMENT 20

VERTICAL, UPRIGHT LEADER

CAGE DARKENED

2 REPLICATES,
3 WEEVILS / REPLICATE
7 DAYS DURATION

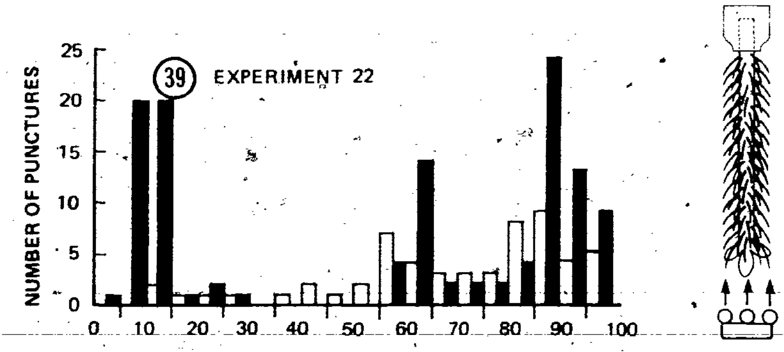


㊳ EXPERIMENT 21

VERTICAL, INVERTED LEADER

CAGE DARKENED

2 REPLICATES,
5 WEEVILS / REPLICATE
4 DAYS DURATION

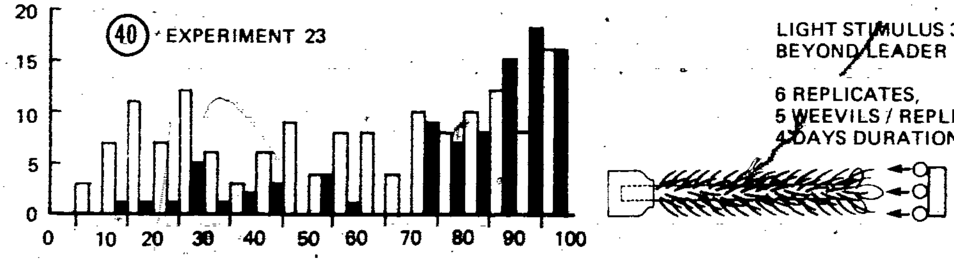


㊴ EXPERIMENT 22

VERTICAL, INVERTED LEADER

LIGHT STIMULUS 30 cm
BELOW CAGE

3 REPLICATES,
5 WEEVILS / REPLICATE
4 DAYS DURATION

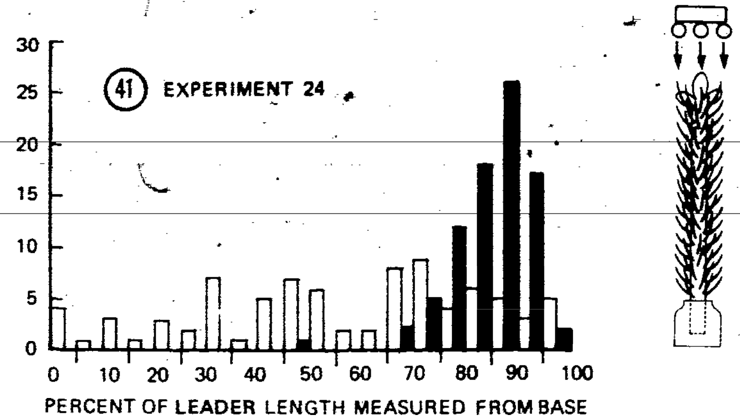


㊵ EXPERIMENT 23

HORIZONTAL LEADER

LIGHT STIMULUS 30 cm
BEYOND LEADER APEX

6 REPLICATES,
5 WEEVILS / REPLICATE
4 DAYS DURATION



㊶ EXPERIMENT 24

VERTICAL, UPRIGHT LEADER

LIGHT STIMULUS 30 cm
ABOVE CAGE

3 REPLICATES,
5 WEEVILS / REPLICATE
4 DAYS DURATION

Table XVII. Distributions of feeding and oviposition punctures produced by overwintered female *Pissodes strobi* in the apical and basal regions of Sitka spruce leaders

Experiment no.	Distribution of feeding punctures				Distribution of oviposition punctures			
	Basal half	Apical half	χ^2	Probability level[1]	Basal half	Apical half	χ^2	Probability level[1]
20	33	53	4.7	<0.05	0	28	28.0	<0.005
21	45	16	13.8	<0.005	47	0	47.0	<0.005
22	9	48	26.7	<0.005	45	74	7.1	<0.01
23	64	88	3.8	N.S.	14	78	44.5	<0.005
24	34	50	3.1	N.S.	1	82	81.0	<0.005

[1] N.S. = not significant.

leaders in experiment 11, and in the upper, basal half of vertical, inverted host leaders in experiment 15. In addition, *P. strobi* preferred to oviposit in the apical half of vertical, upright host lateral branches in experiment 16. This result is in agreement with the work of Gara et al. (1971). Deviation of Sitka spruce leaders from the natural, vertical orientation resulted in reduced oviposition activity by females in experiments 12, 13, and 14. In experiments 12 and 13, the distributions of both feeding and oviposition punctures were random along the length of both 30° and 60° off-vertical host leaders, suggesting a lack of preference.

In choice experiments 18 and 19, female weevils selected the vertical, upright host leaders, and preferred to oviposit in the apical half of each of these. No oviposition punctures were produced on either the horizontal host lateral branches in experiment 18, or on the 45° off-vertical host leaders in experiment 19.

Heavy oviposition by *P. strobi* along the length of horizontal host leaders in choice experiment 17 was rather unexpected. Although caged weevils will oviposit in the field on one-year-old Sitka spruce leaders bent into the horizontal plane (Gara et al. 1971), females apparently rejected the horizontal host leaders in experiment 14. Only a single egg puncture was counted in the bark at the leader apex, the lowest oviposition score recorded in any experiment. On the other hand, *P. strobi* did oviposit in the apical half of the vertical, upright host lateral branches in experiment 16. Oviposition in lateral branches may have been restricted by the relatively thin bark in both forced experiment 16 and choice experiment 17, whereas only in the latter experiment, did gravid females have the option to oviposit in the thicker bark of the horizontal host leaders. Alternatively, host leaders may contain optimal concentrations of chemicals that induce or promote feeding and subsequent oviposition behaviour. I have no explanation, however, for the concentration of oviposition punctures in the basal half of the horizontal leaders (Table XVI).

More difficult to interpret are the apparent preferences in feeding site location in experiments 14, 17, 18, and 19. Whereas weevils preferred to feed in the basal half of horizontal host leaders in experiment 14, the distribution of feeding punctures was random along the length of horizontal host leaders in choice experiment 17. Also, *P. strobi* preferred to feed in the basal half of vertical, upright host leaders in experiment 18, but in the apical half of vertical, upright host leaders in experiment 19. As these disparate results gave me reason to suspect that light conditions, in addition to host orientation, influenced weevil feeding and oviposition behaviour, light direction was manipulated in the design of experiments 20 to 24.

Influence of Geotactic and Phototactic Mechanisms on the Distributions of Feeding and Oviposition Punctures

The exclusion of light as an orientation cue in experiments 20 and 21, demonstrated that negative geotaxis alone was sufficient to induce female weevils to feed and oviposit in the apical half of vertical, upright host leaders. Chemicals acting as feeding and/or ovipositional stimulants which are present exclusively in the apical, meristematic region of Sitka spruce leaders can be discounted, as females oviposited at the base of vertical, inverted leaders in experiment 21. The bimodal distribution of oviposition punctures in experiment 22, is apparently the result of both negative geotaxis and positive phototaxis. Such a distribution could result from each female responding to both photic and gravitational stimuli but at different times, or individual females responding consistently in only one, or the other, direction of orientation. Since five females were used in each trial, competition for oviposition sites on a single host leader may have promoted the bimodal orientation response of *P. strobi* in experiment 22. In experiment 23, photic stimuli resulted in *P. strobi* orientation towards the illuminated, apical half of the horizontal host leaders such that significantly more oviposition punctures were excavated in this zone. In experiment 24, negative geotaxis and positive phototaxis may act in concert, such that females oriented to the apical half of the vertical, upright host leaders, and oviposited in this region. Although the differences were not significant (Table XVII) females produced more feeding cavities in the illuminated, apical half of both horizontal host leaders in experiment 23, and vertical, upright host leaders in experiment 24. This result, added to the fact that *P. strobi* will feed but not oviposit on the horizontal host lateral branches in experiment 18 and on the 45° off-vertical host leaders in experiment 19, suggest that the feeding behaviour of overwintered *P. strobi* is not as closely governed by photic and gravitational cues as is the more critical activity of oviposition.

I conclude that although choice between host lateral branches and leaders as sites for feeding and oviposition may in part by chemically mediated, there is no evidence that the choice of oviposition site within a leader is the result of chemical stimuli. Both negative geotaxis and positive phototaxis can act independently or in concert, to guide overwintered *P. strobi* to initiate oviposition at the apex of vigorous, erect Sitka spruce leaders.

Adaptive Significance of Negative Geotaxis and Positive Phototaxis in Host Selection Behaviour

The oviposition behaviour of *P. strobi* is an adaptive strategy as it reduces interference between siblings, yet allows maximum utilization of a limited food source. Younger larvae that hatch lower in the spruce leader, cannot immediately girdle the terminal, and consequently do not deprive their older siblings, higher in the leader, of food. In addition, Sitka spruce terminals possess a greater basal diameter than apical cross-section. Consequently, as the weevil brood increases in number lower down the attacked leader, a concomitant increase in food availability is encountered.

CONCLUDING DISCUSSION

Using the results of this study in conjunction with the published literature, it is feasible to reconstruct a host selection sequence for *P. strobi*. Weevils overwinter within the forest floor litter at the base of brood hosts from which these adults had emerged the previous autumn (Belyea and Sullivan 1956; Stevenson 1967). In the Pacific Northwest, adults may remain on the brood host lateral branches, feeding intermittently as mild winter temperatures permit (Gara et al. 1971; McMullen and Condrashoff 1973). In April, overwintered adults crawl from the duff, and orient visually to the prominent vertical trunks of nearby trees. Providing that conifer regeneration is closely-spaced, a proportion of *P. strobi* may disperse to new hosts by crawling during this period.

Responding with negative geotaxis and/or positive phototaxis, starved weevils climb to the upper trunk, and begin to feed in the bark which lacks a thick periderm. Mating activity also occurs on brood hosts during this feeding period in late April.

Overhulser (1973) reported that *P. strobi* initiate flight at a threshold temperature of 21°C, from the previous year's dead leader, the upper portion of the living bole, and the exposed tips of lateral branches. In trapping studies, daily weevil catches were greatest between 1000 and 1400 hours, on warm, sunny days, when relative humidity and wind velocity were low.

Anderson and Fisher (1956, 1960) examined the response of *P. strobi* to the odour of ground-up bark tissue and steam-distilled essential oils derived from the bark of a preferred host, eastern white pine.

They concluded that bark volatiles were repellent to the white pine weevil, and suggested that a factor(s) other than olfaction was involved in primary host attraction. The present study suggests that *P. strobi* relies on vision to discriminate between the physical characteristics of acceptable and unsuitable host leaders. Longer, erect leaders, approximately 3 cm in silhouette width are preferred by both sexes. The field trapping studies conducted by Overhulser (1973), confirmed that weevil flight is concentrated at a height somewhat below the level of susceptible host leaders. This fact would allow the flying beetles to assess visually the physical properties of new potential hosts. Weevil flight activity during spring dispersal is rather limited. Harman (1975) studied the movement of individually marked *P. strobi* within an eastern white pine plantation, and found that 64 per cent of weevil flights were terminated within 12.2 m of the starting point. In addition, 57 per cent of released weevils moved only once during the May and June flight period, and no adults moved more than four times. The longest flight recorded for males was 46.4 m, and for females, 53.0 m.

After arrival on new hosts, the physical and chemical properties of the leader bark likely determine ultimate host acceptance or rejection. Chemical compounds that promote weevil feeding behaviour characterize a preferred host, such as Sitka spruce, and encourage *P. strobi* to remain on this species. Repellent and/or deterrent compounds detected by close-range or contact chemoreception on western red cedar, deter *P. strobi* feeding activity, and prompt the adults to abandon such non-host species. Stroh and Gerhold (1965) concluded that *P. strobi* feeding

5

behaviour is adversely affected by thin host leader bark, in which the inside and outside cortical resin canals lie close to each other and to the periderm. Thin bark, characteristic of suppressed or shaded leaders, permits *P. strobi* limited manoeuvrability in excavating feeding cavities around and between the two concentric rings of cortical resin ducts without rupturing the lining epithelial cells. As a result, first the feeding cavity, and ultimately the host leader, are abandoned. A dense needle distribution, often associated with suppressed host leaders, constitutes an additional impediment to weevil feeding activity.

Whereas the location of feeding sites in the bark of acceptable host leaders is largely determined by chemoreception, additional photic and gravitational stimuli are required to release oviposition behaviour in *P. strobi*. Negative geotaxis and positive phototaxis, acting alone or in concert, can account for the initiation of oviposition at the leader apex, below the terminal bud cluster.

Results of the present study suggest that there are sex-related differences in the host selection behaviour of *P. strobi*. Females responded more sensitively to the presence of feeding repellents and/or deterrents in western red cedar, and also demonstrated a feeding response to Sitka spruce leader bark extract that was concentration dependent. In addition, only female weevils discriminated in favour of the preferred host, Sitka spruce, whereas males fed equally on both Sitka spruce and Douglas-fir. This differential response to chemical repellents and feeding stimulants, may reflect the critical choice females must make in the selection of oviposition sites, as the legless larvae cannot abandon the host leader in which the eggs have hatched.

There is some evidence to suggest that female weevils possess greater visual acuity than males in the selection of potential host leaders following spring dispersal. Females selected only the 3x10 cm vertical rectangle in laboratory orientation experiments, whereas males distributed their orientation response over three silhouettes, the 3x10 cm and 5x6 cm vertical rectangles, and the 7x4.3 cm horizontal rectangle. Both sexes preferred the vertical rectangle and the 15° off-vertical parallelogram over the remaining four leaning silhouettes, but only the females expressed an additional preference for the 30° off-vertical parallelogram over both the 60° off-vertical parallelogram and the horizontal rectangle, to which only a single female oriented in each case. These results suggest that female *P. strobi* are more selective in their choice of acceptable host leaders in the field, a behaviour that is complemented by superior chemoreception following arrival on new hosts.

The present study also offers some practical leads that pertain to *P. strobi* manipulation in the field. The visual orientation of *P. strobi* to vertical, rectangular silhouettes, approximately 3 cm in width, suggests that traps baited with the population aggregation pheromone should be of this approximate design, and deployed at the height of susceptible host leaders in the plantation. The isolation and identification of *P. strobi* feeding stimulants from the bark of preferred host conifers, may allow rapid and accurate laboratory assessment of provenance or hybrid susceptibility to weevilling, and subsequently curtail or eliminate costly field studies that often require years of exposure to natural weevil populations. Similarly, the isolation and identification of naturally-occurring feeding repellents and/or deterrents from western red cedar, may permit their prudent application to host species susceptible to weevil attack during spring and early summer months.

LITERATURE CITED

Anderson, J. M., and Fisher, K. C. 1956. Repellency and host specificity in the white pine weevil *(Pissodes strobi)*. Physiol. Zool. 29: 314-24.

Anderson, J. M., and Fisher, K. C. 1960. The response of the white pine weevil to naturally occurring repellents. Can. J. Zool. 38:547-64.

Barton, G. M., and MacDonald, B. F. 1971. The chemistry and utilization of western red cedar. Dept. Fish. For. Can. For. Serv. Pub. No. 1023, 31 pp.

Beck, S. D. 1965. Resistance of Plants to Insects. Ann. Rev. Ent. 10: 207-32.

Belyea, R. M., and Sullivan, C. R. 1956. The white pine weevil; a review of current knowledge. For. Chron. 32:58-67.

Connola, D. P. 1966. Preliminary studies on resistance in eastern white pine to the white pine weevil, *Pissodes strobi* (Coleoptera: Curculionidae) in New York. Ann. Entomol. Soc. Am. 59:1011-12.

Dethier, V. G. 1954. Evolution of feeding preferences in phytophagous insects. Evolution 8:33-54.

Fowells, H. A. (Ed.). 1965. Silvics of Forest Trees of the United States. U.S. Dept. Agric. Handbook No. 271. 762 pp.

Fowler, D. P., and Heimburger, C. C. 1969. Genetic improvement of red pine and eastern white pine. For. Chron. 45:414-20.

Gara, R. I., Carlson, R. L., and Hrutfiord, B. F. 1971. Influence of some physical and host factors on the behavior of the Sitka spruce weevil, *Pissodes sitchensis,* in Southwestern Washington. Ann. Entomol. Soc. Am. 64:467-71.

Garrett, P. W. 1973. Geographic variation in resistance to white pine weevil *Pissodes strobi* (Coleoptera: Curculionidae) by eastern white pine *Pinus strobus*. Can. Ent. 105:347-50.

Gerhold, H. D. 1966. In quest of insect-resistant forest trees. pp. 305-23. In: H. D. Gerhold, E. J. Schreiner, R. E. McDermott, and S. A. Winieski (Eds.), Breeding Pest-resistant Trees. Pergamon Press, Oxford, 505 pp.

Gilbert, B. L., Baker, J. E., and Norris, D. M. 1967. Juglone (5-hydroxy-1, 4-naphthoquinone) from *Carya ovata,* a deterrent to feeding by *Scolytus multistriatus*. J. Insect. Physiol. 13:1453-59.

Harman, D. M. 1975. Movement of individually marked white pine weevils, *Pissodes strobi*. Env. Entomol. 4:120-24.

Harman, D. M., and Kulman. H. M. 1969. Dispersion of released white pine weevils in intrastand growth types. Ann. Entomol. Soc. Am. 62:835-38.

Harris, R. J. 1975. Primer of Multivariate Statistics. Academic Press, New York, N.Y. 332 pp.

Hopkins, A. D. 1911. Contribution towards a monograph of the bark-weevils of the genus *Pissodes*. U.S. Dept. Agric. Tech. Ser. 20, Pt. 1. 68 pp.

Kriebel, H. B. 1954. Bark thickness as a factor in resistance to white pine weevil injury J. Forest. 52:842-45.

Loschiavo, S. R. 1965. Methods for studying aggregation and feeding behavior of the confused flour beetle, *Tribolium confusum* (Coleoptera: Tenebrionidae). Ann. Entomol. Soc. Am. 58:383-88.

Loschiavo, S. R., Beck, S. D., and Norris, D. M. 1963. Behavioral responses of the smaller European elm bark beetle, *Scolytus multistriatus* (Coleoptera: Scolytidae) to extracts of elm bark. Ann. Entomol. Soc. Am. 56:764-68.

Manna, G. K., and Smith, S. G. 1959. Chromosomal polymorphism and interrelationships among bark beetles of the genus *Pissodes* Germar. Nucleus (Boston) 2:179-208.

McMullen, L. H., and Condrashoff, S. F. 1973. Notes on dispersal, longevity and overwintering of adult *Pissodes strobi* (Peck) (Coleoptera: Curculionidae) on Vancouver Island. J. Ent. Soc. B.C. 70: 22-26.

Mitchell, R. G., Johnson, N. E., and Wright, K. H. 1974. Susceptibility of 10 spruce species and hybrids to the white pine weevil (=Sitka spruce weevil) in the Pacific Northwest. U.S.D.A. For. Serv. Pac. NW. For. and Range Expt. Sta. Res. Note PNW 225.

Morrison, D. F. 1976. Multivariate Statistical Methods. Second Edition, McGraw-Hill, Toronto. 338 pp.

Norris, D. M., and Baker, J. E. 1967. Feeding responses of the beetle *Scolytus* to chemical stimuli in the bark of *Ulmus*. J. Insect. Physiol. 13:955-62.

Norris, D. M., Baker, J. E., Borg, T. K., Ferkovich, S. M., and Rosental, J. M. 1970. An energy-transduction mechanism in chemoreception by the bark beetle, *Scolytus multistriatus*. Contrib. Boyce Thompson Inst. 24:263-74.

Overhulser, D. L. 1973. Flight and seasonal activity of the Sitka spruce weevil, *Pissodes strobi* (Peck) (Coleoptera: Curculionidae), in western Washington. M.Sc. Thesis, Univ. Washington. 71 pp.

Overhulser, D. L., and Gara, R. I. 1975. Spring flight and adult activity of the white pine weevil, *Pissodes strobi* (Coleoptera: Curculionidae), on Sitka spruce in western Washington. Can. Ent. 107:251-56.

Peck, W. D. 1817. On the insects which destroy the young branches of the pear tree, and the leading shoot of the Weymouth pine. Mass. Agri. J. 4:205-11.

Plank, G. H., and Gerhold, H. D. 1965. Evaluating host resistance to the white pine weevil using feeding preference tests. Ann. Entomol. Soc. Am. 58:527-32.

Roche, L. 1969. A genecological study of the genus *Picea* in British Columbia. New Phytol. 68:505-54.

Sampson, P. 1976. Stepwise discriminant analysis. pp. 233-53. In: W. J. Dixon (Ed.), Biomedical Computer Programs. University of California Press, Berkeley.

Silver, G. T. 1968. Studies on the Sitka spruce weevil, *Pissodes sitchensis*, in British Columbia. Can. Ent. 100:93-110.

Smith, S. G. 1962. Cytogenetic pathways in beetle speciation. Can. Ent. 94:941-55.

Smith, S. G., and Sugden, B. A. 1969. Host trees and breeding sites of native North American *Pissodes* bark weevils, with a note on synonymy. Ann. Entomol. Soc. Am. 62:146-48.

Soles, R. L., Gerhold, H. D., and Palpant, E. H. 1970. Resistance of western white pine to white pine weevil. J. For. 68:766-68.

Stevenson, R. E. 1967. Notes on the biology of the Engelmann spruce weevil, *Pissodes engelmanni* (Curculionidae: Coleoptera) and its parasites and predators. Can. Ent. 99:201-13.

Stroh, R. C., and Gerhold, H. D. 1965. Eastern white pine characteristics related to weevil feeding. Silvae Genet. 14:160-69.

Sullivan, C. R. 1959. Effect of light and temperature on the behaviour of adults of the white pine weevil, *Pissodes strobi* Peck. Can. Ent. 91:213-32.

Sullivan, C. R. 1960. The effect of physical factors on the activity and development of adults and larvae of the white pine weevil, *Pissodes strobi* Peck. Can. Ent. 92:732-45.

Sullivan, C. R. 1961. The effect of weather and the physical attributes of white pine leaders on the behavior and survival of the white pine weevil, *Pissodes strobi* Peck., in mixed stands. Can. Ent. 93:721-41.

Wright, J. W., and Gabriel, W. J. 1959. Possibilities of breeding weevil-resistant white pine strains. U.S.D.A. For. Serv. NE. For. Expt. Sta. Paper No. 115.

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Born 26 October 1944 in Haarlem, Holland
Canadian citizenship 1972
32 years old; single; excellent health; 5'11"; 170 lbs.

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EDUCATION

Graduated Port Credit Secondary School, Ontario; 1963

B.Sc. University of Toronto: 1967
Toronto, Ontario
Majors: Animal Physiology, Biochemistry

M.Sc. University of Toronto
Department: Chemistry
Thesis: Elucidation of chemical mechanisms involved in the molecular rearrangement of a silicon stereoisomer

Ph.D. Simon Fraser University; 1977
Burnaby, British Columbia
Department: Biological Sciences
Thesis: Role of vision, chemoreception, geotaxis, and phototaxis in the host-selection behaviour of a conifer weevil, *Pissodes strobi*

PUBLICATIONS

Borden, J. H., VanderSar, T. J. D., and Stokkink, E. 1975. Secondary Attraction in the Scolytidae: An Annotated Bibliography. S.F.U. Pest Management Paper No. 4. 102 pp.

VanderSar, T. J. D. 1977. Overwintering Survival of *Pissodes strobi* Peck (Coleoptera: Curculionidae) in Sitka Spruce Leaders. J. Ent. Soc. B.C. (accepted for publication).

VanderSar, T. J. D., and Borden, J. H. 1977. Aspects of Host Selection Behaviour of *Pissodes strobi* Peck (Coleoptera: Curculionidae) as Revealed in Laboratory Feeding Bioassays. Can. J. Zool. 55:405-14.

VanderSar, T. J. D., Borden, J. H., and McLean, J. A. 1977. Host Preferences of *Pissodes strobi* Peck (Coleoptera: Curculionidae) Reared from Three Native Hosts. J. Chem. Ecol. (accepted for publication).

VanderSar, T. J. D., and Borden, J. H. Visual Orientation of *Pissodes strobi* Peck (Coleoptera: Curculionidae) in relation to Host Selection Behaviour. (submitted for publication).

VanderSar, T. J. D., and Borden, J. H. Role of Geotaxis and Phototaxis in the Feeding and Oviposition Behaviour of Overwintered *Pissodes strobi*. (submitted for publication).

HONOURS AND SCHOLARSHIPS

University of Toronto Bursaries; 1963-1967
National Research Council (Canada) Postgraduate Scholarship; 1967-1968; University of Toronto
Ontario Graduate Fellowship; 1968-1969; University of Toronto

PROFESSIONAL MEMBERSHIPS

Association for the Study of Animal Behaviour; 1975-1977
Entomological Society of Canada; 1974-1977
Entomological Society of British Columbia; 1974-1977

CREATIVE INTERESTS

Freelance Writer and Photographer: Illustrated articles on natural history topics for publication in international magazines

Sports: skiing, hiking, scuba-diving, squash, handball

WORK EXPERIENCE

Greenhouse Labourer: Lorne Park Florists
Mississauga, Ontario; 1958-1964
Duties: Greenhouse maintenance and repair; crop planting, cutting, shipping

Supervisor: Port Credit Florists
Mississauga, Ontario; 1964-1965
Duties: Greenhouse maintenance and repair; crop rotation

Research Chemist: Empire Chemical Company
Toronto, Ontario; 1966
Duties: Organic synthesis of insect repellents, sugar substitutes, fine pharmaceuticals

Technical Sales Representative: Rohm and Haas Canada
Toronto, Ontario; 1969-1973
Duties: Sales and technical service in acrylic polymer coatings; transferred to Vancouver, British Columbia in 1972. Expanded duties included sales and technical service to coatings, agricultural, plastics, mining, and construction industries throughout Western Canada

TEACHING EXPERIENCE

Demonstrator: University of Toronto

Introductory Botany; 1966-1967
Organic Chemistry; 1967-1969

Teaching Assistant: Simon Fraser University

Introductory Biology; 1973-1974
Biology of Vascular Plants; 1975
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