

Geotaxis and phototaxis are not determinant factors for white pine weevil (Col., Curculionidae) oviposition location on intact trees and severed treetops

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Ms. received: May 3, 2003; accepted: February 11, 2004

Abstract: The objective of this investigation was to determine if external factors such as phototaxis and geotaxis determine oviposition site location by reproductively active female white pine weevils, *Pissodes strobi* (Peck), on intact trees or cut treetops. In prior studies, light and gravity, both external tree factors, were consistently linked with oviposition location. In this study, the external factors that were varied in whole trees or cut treetops, included two weevil populations and two tree species in upright, inverted and horizontal orientations with thick or thin stems, indoor and outdoor locations, warm and cool, wet and dry, and light and dark conditions. The results show that 100% of the oviposition occurred at or near treetops, regardless of external factors. The results are unequivocal; they are without variance. These findings suggest that the reproductively active female weevil's feeding preference is for primary cortex tissue, an internal tree factor. The primary cortex thickness gradient could account for these weevils' capability to locate treetops, where the thickest primary cortex tissue occurs, even when treetops are not at the highest or brightest locations.

Key words: gravity, light, oviposition location, spruce, weevil

1 Introduction

The white pine weevil [*Pissodes strobi* (Peck)] is a major pest of young spruce and pines in North America. During the early spring, adult weevils emerge from the duff in drier regions (WALLACE and SULLIVAN, 1985), or from the lower stem and branches in warmer and wetter regions of North America (GARA et al., 1971). Adult female weevils become reproductively active after feeding on leaders (GARA and WOOD, 1989; HAMEL et al., 1994) and are commonly observed ovipositing on the terminal leaders of susceptible trees (SULLIVAN, 1959, 1961; SILVER, 1968; GARA et al., 1971; WALLACE and SULLIVAN, 1985).

Oviposition has been observed to commence at the tip of the leader and proceed downward (JOHNSON, 1965). SULLIVAN (1961) reported that thin leaders of *Pinus strobus* L. cause the oviposition to occur on multiple internodes, unlike on open-grown leaders where it was confined to the leader. This phenomenon was also shown for small-diameter young grafts of Sitka spruce [*Picea sitchensis* Bong. (Carr)] (ALFARO, 1996).

According to SULLIVAN (1959), overwintered *P. strobi* adults 'move up the trees in accordance with their photopositive reaction at low temperatures and their negatively geotactic reaction'. GARA et al. (1971) concluded that gravitational stimuli had little influence on the distribution of oviposition punctures on leaders, as caged weevils oviposited on horizontal leaders.

OVERHULSER and GARA (1975) indicated that adult female weevil feeding activity was largely confined to leaders, from which they inferred that leader feeding provided females the necessary nutrition for oviposition activities.

VANDERSAR and BORDEN (1977), based on their experiments with excised leaders, advanced major roles for both positive phototaxis and negative geotaxis in the selection of oviposition sites by reproductively active female weevils. They claimed that either light or gravity mechanism alone or both acting in concert, could account for the oviposition pattern produced by *P. strobi* each spring in the apical zone of intact leaders of spruce trees. WALLACE and SULLIVAN (1985) stated 'the combination of geotactic, phototactic, and photic pattern responses then leads them (weevils) to the uppermost and most vertically oriented parts of the tree'.

Reproductively active female weevils preferentially feed on primary cortex tissue (MANVILLE et al., 2002). They appear to seek thick primary cortex tissue coincident with the onset of their oviposition period and, thus, reach treetops where this tissue is thickest. We believe that this behaviour is of primary importance in the location of oviposition sites by *P. strobi*.

Our findings reported in this paper show that positive phototaxis and negative geotaxis, as shown by VANDERSAR and BORDEN (1977), are secondary factors that come into play only on excised tree leaders which

lack a weevil-discernable primary cortex gradient (MANVILLE et al., 2002).

2 Materials and Methods

2.1 Weevils

Coastal weevils were collected in the fall of 1999 and again in 2000 near Eve River, Vancouver Island, British Columbia (BC) (50°20'N, 126°W); interior specimens were collected in the fall of 1999 at Clearwater, BC (51°40'N, 120°05'W). During storage, weevils were allowed to feed on pieces of freshly cut spruce branches while kept in a controlled environment chamber at 5–7°C. Seventy-four hours before starting an experiment, weevils were sorted by sex, according to the method of LAVALLÉE et al. (1993), and acclimatized at room temperature. Following each experiment, recovered female weevils were dissected to affirm that they were reproductively active.

2.2 Trees

Interior [*Picea glauca* (Moench) Voss (white), *Picea englemannii* Parry (Englemann)] and coastal [*Picea sitchensis* Bong. (Carr.) (Sitka)] spruce were selected for this study. Interior spruce trees were all from weevil-susceptible families obtained from the BC Ministry of Forests' Kalamalka Research Station at Vernon, BC. They were 5–8 years old, grown in 15-cm square pots or 30-cm-diameter round pots. Four-year-old Sitka spruce trees, grown in 30-cm-diameter round pots, were from two families (76.1 and 51) known to be susceptible and early flushing types according to the BC Forest Service. The current year's leader growth on these trees was beginning periderm formation at the start of the experiment. In 2002, Sitka spruce treetops (4 years growth) were obtained from the BC Ministry of Forests, Mesachie Lake, BC. Bark samples were removed from each internode of each tree using a 2-mm internal diameter (i.d.) cork borer. Bark tissue thicknesses were determined using a binocular microscope (Leica Wild M3C) with an ocular micrometer disc (Bausch and Lomb, Rochester, NY, USA) (31-16-02) in the eyepiece.

For the first three experiments, trees of similar leader diameter were selected. Then, trees were randomly allocated to one of two vertical orientations, upright or inverted. In the third experiment, two additional trees were placed in the horizontal position. For the last experiment, six treetops were placed in cardboard boxes fitted with acrylic lids and six in boxes with plywood lids. Treetops were suspended from lids with a single wood screw.

Trees in the first three experiments were individually caged with muslin cloth secured to the stem at or near the soil. Prior to closing the cage a number of reproductively active female weevils were introduced onto laterals at mid-stem locations. In the experiment on severed treetops in opaque boxes, open plastic vials containing female weevils were taped to a lateral close to the lid, i.e. furthest from the treetop. Experiments were terminated after oviposition had occurred, as evidenced by the presence of oviposition plugs.

2.2.1 Large-diameter leaders, interior spruce, potted trees

On 15 June 2000, 6-year-old interior spruce trees with large-diameter leaders were used (mean upper-leader diameter = 10.13 mm (SE = 0.47); for 1999 and 1998 growth, average bark thickness was 1.93 and 2.17 mm, respectively, and

average periderm plus primary cortex thickness was 1.23 and 0.90 mm, respectively). Six previously mated female interior weevils were placed on each tree. Trees were individually caged and oriented upright or inverted, two at each orientation both outdoors and in the greenhouse. The experiments with greenhouse trees were concluded after only 6 days, whereas those outdoors were stopped after 12 days.

2.2.2 Large-diameter leaders, Sitka spruce, potted trees

On 30 June 2000, 4-year-old Sitka spruce trees with thick leaders were used [mean upper leader diameter = 12.08 mm (SE = 0.64), for 1999 and 1998 growth, average bark thickness was 1.53 and 1.60 mm, respectively and average periderm plus primary cortex thickness was 1.18 and 0.72 mm, respectively]. Five previously mated female coastal weevils were placed on each tree. Trees were individually caged, placed outdoors for 15 days, four each in vertical and inverted orientations. Then, maintaining their respective orientations, all trees were moved inside the greenhouse for 5 days to effect oviposition.

2.2.3 Small-diameter leaders, interior spruce, potted trees

On 19 May 2000, 6-year-old interior spruce trees with small-diameter leaders were positioned in three orientations, two each in upright, horizontal (one top facing north and one top facing south), and inverted [mean upper leader diameter = 7.17 mm (SE = 0.27), 1998 growth diameter = 11.21 mm (SE = 0.35), and 1997 growth diameter = 13.32 mm (SE = 0.42); average bark thickness for stem internodes from 1999 to 1997 was 1.36, 1.50, and 1.41 mm, respectively; and average periderm plus primary cortex thickness was 0.93, 0.70, and 0.40 mm, respectively]. Ten female and five male coastal weevils were placed on each tree. Trees were caged separately and kept close together in the greenhouse approximately 1 m from the floor. The experiment was conducted for 8 days.

2.2.4 Large-diameter leaders, Sitka spruce, severed stems

On 25 April, 2002, 12 apical Sitka spruce treetops (4 years growth) with mean leader diameter of 7.8 mm (SE = 1.5) were selected. Average bark thicknesses for stem internodes from 2001 to 1998 were 1.71, 1.66, 1.82 and 1.65 mm, respectively; and average periderm plus primary cortex thickness was 1.33, 1.24, 1.18 and 0.97 mm, respectively). Treetops were randomly selected and six secured to an acrylic and six to a plywood lid with a single screw. These were placed inverted inside cardboard boxes (61 × 51 × 145 cm). Six female weevils were released on each treetop from open plastic vials taped to a lateral branch close to the butt (lid). Box edges were sealed with opaque tape to retain weevils and exclude light. Light intensity, measured with a light meter (General Electric, Cleveland, OH, USA) was >4000 lx at tree butts and <1000 lx beneath treetops for boxes with an acrylic lid.

Statistical analyses (chi-square) of the data were performed with Statistica for Windows (StatSoft, Tulsa, OK, USA).

3 Results

Oviposition occurred only on the main stem of trees in these experiments.

Table 1. Total number of oviposition holes on spruce stems by location and orientation

| Experiment | Orientation | Location | |
|------------|-------------|----------|--------|
| | | Top | Bottom |
| 2.3.1 | U | 180 | 0 |
| | I | 76 | 0 |
| 2.3.2 | U | 236 | 0 |
| | I | 112 | 0 |
| 2.3.3 | U | 132 | 0 |
| | I | 147 | 0 |
| | H | 126 | 0 |
| 2.3.4 | I, l | 12 | 0 |
| | I, d | 8 | 0 |
| Total | | 1029 | 0 |

U, upright; I, inverted; H, horizontal; l, light from above; d, no light.

3.1 Large-diameter leaders, interior spruce, potted trees

One hundred per cent of oviposition on upright and inverted trees occurred in 1999 growth (treetop/leader) (Table 1). No oviposition was observed on older growth (tree base). Location was statistically significant ($\chi^2 = 256$, $P = 0.0000$).

3.2 Large-diameter leaders, Sitka spruce, potted trees

Two trees had no oviposition; these trees were excluded from the results. Except as indicated, all oviposition on upright and inverted trees occurred on treetops (last year's (1999) (leader) and part of current year's (2000) growth) (Table 1). Within the current year's growth only older, brown bark, portions had oviposition. Oviposition was not observed on 1998 or older main stem growth. For the combined data for 1999 and 2000 growth, there was a statistically significant effect for stem position ($\chi^2 = 348$, $P = 0.0000$).

3.3 Small-diameter leaders, interior spruce, potted trees

Oviposition on upright, horizontal and inverted trees was found on 1999 (leader), 1998 and 1997 growth (Table 1). No oviposition occurred on 1996 and older growth. Treating the top three growth segments as a unit, there was a statistically significant stem position effect (for upright and inverted only, $\chi^2 = 279$, $P = 0.0000$).

3.4 Large-diameter leaders, Sitka spruce, inverted severed stems

In boxes receiving light, oviposition holes were found exclusively on stem tops, 2001 growth, at sites located furthest from the source of the point of release and natural light (Table 1). Oviposition holes were observed on four treetops; two treetops had no oviposition. In boxes with opaque lids, oviposition was also found exclusively on 2001 growth (Table 1). Oviposition holes were observed on two of six inverted treetops. There was a statistically significant stem position effect ($\chi^2 = 20$, $P = 0.0000$).

4 Discussion

Oviposition by 220 reproductively active female weevils on 34 trees and treetops occurred 1029 times, all of it occurred at or near treetops, none of it occurred in the lower half of the tree (Table 1). In this study, external factors were varied greatly. These included orientation, two weevil populations; two tree species with thick or thin stems; indoor and outdoor locations; warm and cool, wet and dry, light and dark conditions; whole trees and cut treetops. Trees placed in horizontal, inverted and upright orientations were attacked in the same locations, indicating that external factors were inconsequential. The observation of inconsistent amounts of oviposition between upright and inverted treetops and individual experiments is irrelevant for the purpose of this study, the determination of oviposition location.

Oviposition location is not influenced by external factors it must therefore be determined by internal tree factors. An internal tree factor, the primary cortex thickness gradient, was the only factor consistently available to the weevil throughout this study. Reproductively active female weevils arrive at treetops where the primary cortex tissue, the preferred food for ovarian maturation feeding and oviposition, is most plentiful (MANVILLE et al., 2002). By following this internal gradient to treetops, weevils afford themselves and their offspring the best opportunity for adequate nutrition and survival.

In experiments on inverted and upright trees with thick leaders, oviposition location was normal; no oviposition occurred on growth older than the leader. This result would not be expected if gravity and light were dominant mechanisms governing oviposition location.

Oviposition on small diameter trees was observed to occur on older growth in addition to the leader growth. Nevertheless, oviposition was restricted to the top portion of these trees. These findings agree with those of SULLIVAN (1961) for *P. strobus* and with ALFARO (1996) for Sitka spruce. Again, bark thickness (SULLIVAN, 1961; MANVILLE et al., 2002) provides an appropriate explanation of these 'abnormal' results, not resin canal density (for an in depth discussion, see SAHOTA et al., 2000). Regardless, oviposition did not occur at or near a tree base. Gravitational and light factors could not influence the weevil's choice of oviposition sites on horizontal trees, yet the oviposition pattern matched that found on upright and inverted trees.

Even bright natural light from above did not induce weevils to oviposit at the butt end of inverted treetops enclosed in boxes, even when the weevils were released on a lateral branch close to the butt. Excluding light did not alter the pattern of oviposition.

In the past, geotaxis and phototaxis have often been claimed to be the mechanisms that allowed reproductively active female weevils to locate suitable oviposition sites (DIXON and HOUSEWEART, 1983; PHILLIPS and LANIER, 1986; LAVALLEE et al., 1996; TOMLIN and BORDEN, 1996, 1997; HALLETT et al., 1999). Our findings indicate that positive phototaxis and negative geotaxis, as

shown for excised leaders (VANDERSAR and BORDEN, 1977), are secondary factors that come into play only when a weevil-discernable primary cortex gradient is not present (MANVILLE et al., 2002). In addition, VANDERSAR and BORDEN's (1977) results were never tested on whole trees.

In the light of the current findings, we are unable to substantiate the claim that reproductively active female weevils rely on negative geotaxis and positive phototaxis to locate suitable oviposition sites on whole trees.

Acknowledgements

The authors gratefully acknowledge the assistance of the British Columbia Ministry of Forests for providing the trees and Dr Jason Nault of the Pacific Forestry Centre, Canadian Forest Service, for useful suggestions and statistical analyses.

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