Feeding by *Leptoglossus occidentalis* (Hemiptera: Coreidae) reduces seed set in lodgepole pine (Pinaceae)

Ward B Strong[1]

British Columbia Ministry of Forests, Kalamalka Forestry Centre, 3401 Reservoir Road, Vernon, British Columbia, Canada V1B 2C7

Sarah L Bates

Department of Biological Sciences, Simon Fraser University, 8888 University Way, Burnaby, British Columbia, Canada V5A 1S6

Michael U Stoehr

British Columbia Ministry of Forests, Research Branch, 712 Yates Street, Victoria, British Columbia, Canada V8W 1L4

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Abstract—Low seed set is a serious problem in seed orchards of lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann) in the southern interior of British Columbia. We tested the hypothesis that *Leptoglossus occidentalis* Heidemann is responsible for the low seed set. Cones enclosed in insect exclusion bags as part of a pollination experiment produced significantly more filled seeds per cone than cones that were not bagged. In a separate bagging experiment, cones that were enclosed with a *L. occidentalis* female and her progeny produced only about one filled seed per cone, compared with about 28 seeds in bagged control cones. Changes in microclimate associated with the use of bags did not appear to be responsible for the observed increase in seed set in bagged cones. *Leptoglossus occidentalis* was also excluded from trees using the insecticide fenvalerate. Cones on fenvalerate-treated trees produced >11 filled seeds per cone, whereas water-treated (control) cones produced <1.7 filled seeds. These data suggest that *L. occidentalis* should be considered a serious pest in lodgepole pine seed orchards.

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Résumé—La faible grenaison est un problème sérieux dans les plantations de production de graines du pin de Murray (*Pinus contorta* var. *latifolia* Engelmann) dans la région intérieure du sud de la Colombie-Britannique. Nous avons éprouvé l'hypothèse selon laquelle le responsable de cette réduction est *Leptoglossus occidentalis* Heidemann. Au cours d'une expérience sur la pollinisation, des cônes enfermés dans des sacs à l'épreuve des insectes ont produit plus de graines pleines par cône que les cônes non protégés. Dans une autre expérience d'ensachage, les cônes qui ont été enfermés en présence d'une femelle de *L. occidentalis* avec sa progéniture n'ont produit grosso modo qu'une graine pleine par cône, alors que les cônes témoins non ensachés produisent environ 28 graines pleines par cône. Les changements de microclimat associés à l'ensachage ne semblent pas responsables de l'augmentation de la grenaison observée dans les cônes mis en sac. *Leptoglossus occidentalis* a également été exclus des arbres par un traitement à l'insecticide fenvalerate. Les cônes des arbres traités au fenvalerate ont produit plus de 11 graines

[1] Author to whom all correspondence should be sent (E-mail: Ward.Strong@gems7.gov.bc.ca).

pleines par cône, alors que les cônes des arbres témoins traités à l'eau ont donné moins de 1,7 graine pleine par cône. Ces données indiquent que *L. occidentalis* doit être considéré comme une espèce très nuisible dans les plantations de production de graines du pin de Murray.

[Traduit par la Rédaction]

Introduction

High quality seeds of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann (Pinaceae), produced in seed orchards are used extensively in tree improvement and reforestation programs in British Columbia (Carlson 2001). Between 1984 and 1992, several lodgepole pine seed orchards were established in the Okanagan Valley, in the southern interior of British Columbia. These orchards have suffered from chronically low seed set, averaging from four to nine filled seeds per cone (WBS, unpublished data), compared with 18–26 seeds per cone in natural stands and lodgepole pine seed orchards located north of the Okanagan Valley. These figures compare with the natural stand maximum of about 25 found by Carlson (1985) and a theoretical maximum of 35–50 (Owens and Molder 1984; Owens *et al.* 2000). Among the possible causes of low seed set are climatic factors, lack of pollination, unsuccessful fertilization of ovules, seed abortion, and damage by cone- and seed-feeding insects (Owens *et al.* 1991). Interior lodgepole pine seed orchards often harbour large populations of *Leptoglossus occidentalis* Heidemann, which is known to feed on seeds of several pine species, suggesting that these insects may impact seed set.

Leptoglossus occidentalis is distributed throughout most of western North America (Hedlin *et al.* 1981; Katovich and Kulman 1987). Adults and nymphs feed on developing seeds, leaving no obvious external signs of cone or seed damage. At harvest, seeds that have been completely emptied by seed bug feeding are indistinguishable from seeds that have aborted owing to environmental or genetic causes (Schowalter and Sexton 1990; Bates *et al.* 2000). Past estimates of damage range from <5 to 70% for Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae) (Schowalter and Sexton 1990; Blatt and Borden 1996; Bates *et al.* 2000), from 70 to 80% for western white pine, *Pinus monticola* Dougl. ex D. Don (Connelly and Schowalter 1991), up to 55% for ponderosa pine, *Pinus ponderosa* Lawson (Krugman and Koerber 1969; Pasek and Dix 1988), and up to 2.1% for whitebark pine, *Pinus albicaulis* Engelmann (Anderton and Jenkins 2001).

By caging seed bugs on developing cones and excluding them from others, we tested the hypothesis that *L. occidentalis* causes low seed set in lodgepole pine.

Materials and methods

All experiments were conducted in lodgepole pine seed orchards near Vernon, British Columbia, Canada (50.3°N, 119.3°W). Orchard trees were 13–15 years old, with a stem diameter of 10–12 cm at a height of 0.5 m, and topped to a maximum height of 3 m. Tree spacing was 4 × 5 m and all trees were drip irrigated.

Pollination experiment

In 1996 and 1997, two ramets of each of six clones were selected in one orchard. Pollen was applied manually to 2–4 clusters of first-year conelets on each tree. The following years (1997 and 1998, respectively), insect exclusion bags (30 × 60 cm nylon bags, 1-mm mesh) were placed around pollinated second-year cones of one ramet of each clone. Cones were harvested in August 1997 (1252 cones) and 1998 (670 cones), respectively, air-dried for at least 30 d, and every seed removed by manual dissection. All seeds were X-rayed (Hewlett-Packard Faxitron at 12 kV and 2.0 mA for 60 s), to determine the number of filled seeds per cone. Untransformed data were analyzed by ANCOVA (α = 0.05), with clones treated as blocks and total seeds per cone as the covariate.

Bagging experiment

In 1997, on each of 10 randomly selected trees, six south-facing branches at heights of 1.5–2.5 m, each with 3–5 second-year cones, were selected. On each branch, one of six treatments was applied on 5 May, when *L. occidentalis* first appeared in the orchard. **(1) Control (no bag).** The cones were left exposed. **(2) Insect exclusion bag.** Cones and associated foliage were enclosed in 30 × 60 cm bags similar to those used in 1996, to determine the level of seed set in the absence of insect feeding pressure. **(3) Insect inclusion bag.** A single female *L. occidentalis* was enclosed in a bag as in treatment 2. Up to 14 nymphs were produced from the eggs laid by each female, creating an artificially high feeding pressure. Nymphs or adults that died were replaced. **(4) Open bag.** An insect bag with several slits and right-angle tears was installed as in treatment 2, but not tied off tightly. By allowing wild insects to enter the bag, this treatment was designed to distinguish between the effects of insect exclusion and microclimate change. **(5) Sun bag.** An insect bag with a 20 × 40 cm clear-plastic window on the upper side was placed as in treatment 2, excluding insects but allowing full sunlight to shine on the cones. This treatment was designed to determine if cone shading within the bags was responsible for any changes in seed set. On 26 May, 1-mm holes were punched into the plastic panes about 10 mm apart, to reduce condensation. **(6) Parasol.** A 25 × 50 cm brown-paper bag with one side removed was tied over the branch, forming a hood that shaded the cones but allowed free access by insects. A cone-feeding cercopid, *Aphrophora canadensis* Walley (Hemiptera: Cercopidae), was removed from cones in all treatments where necessary.

Four temperature probes, 2 × 10 mm, were placed in one randomly selected tree, to determine internal cone temperatures related to each treatment. One probe was inserted into the ovule-bearing portion of a single cone in each of the following: (*a*) inside an insect exclusion bag; (*b*) inside a parasol; (*c*) in an unbagged cone exposed to sunlight for most of the day; and (*d*) in an unbagged cone in the shade of other branches most of the day. Probes were attached to Hobo data recorders (Onset Computer Corporation, Escondido, California), and internal cone temperatures were recorded at 15-min intervals. Bag condition and *L. occidentalis* survival in inclusion bags were checked once or twice weekly until the trial ended. Untransformed daily maximum and minimum temperatures were analyzed by complete-block ANOVA, with day as the block, and the means separated by Fisher's least significant difference (LSD), α = 0.05.

Cones were harvested 12–14 August 1997 and air-dried in mesh bags for ≥30 d. Cones were submerged in boiling water for 15 s, oven-dried for 10 h at 55°C, and shaken in a closed plastic container to dislodge the seeds. Cones were resoaked in cold water for 2 h, oven-dried as before, and shaken again. Seeds were X-rayed to distinguish between filled and empty seeds. Untransformed data on the number of seeds per cone were analyzed by ANOVA with trees as blocks. Data on full seeds per cone were transformed by $\log(x + 1)$, to stabilize the variances, and analyzed by ANCOVA, with trees as blocks and total seeds per cone as the covariate. Means were compared with Fisher's LSD, α = 0.05.

Insecticide exclusion experiment

In 1998, two ramets of each of 10 clones were randomly selected. Each tree had at least 50 second-year cones. One tree of each pair was sprayed twice with fenvalerate (Belmark 300 EC, Ciba-Geigy Canada Ltd) at 0.05% a.i. (active ingredient) in water, using a backpack sprayer (Solo Equipment Corporation, Sindelfingen, Germany) at 45–50 psi (310–345 kPa), until all foliage was wetted, about 2.7 L per tree. Fenvalerate at 0.075% a.i. was 90% lethal to a related species, *Leptoglossus corculus* (Say), for up to 3 weeks, despite 16 cm of rainfall (Nord and DeBarr 1992). The corresponding control tree in each pair was treated with water. Application dates were 7 May and 14 July, coinciding with first sightings of overwintered and first-generation adult *L. occidentalis*, respectively, in the orchard. After the first treatment, three or four insect exclusion bags (as above) were installed over 19–25 cones on the fenvalerate-treated trees.

All cones on each tree were visually examined for seed bugs eight times between 13 May and 24 July, without disturbing the tree or any insects on it. Cones were harvested on 3–5 August, and the seeds extracted and X-rayed as above, to distinguish filled from empty seeds. Data on filled seeds per cone were analyzed by ANOVA of untransformed data, $\alpha = 0.05$, and the means separated by Fisher's LSD, $\alpha = 0.05$.

All results were analyzed statistically using SAS version 8.02 for Windows NT (SAS Institute Inc, Cary, North Carolina 27513).

Results and discussion

Pollination experiment

In both 1997 and 1998, cones from which insects were excluded produced more filled seeds per cone than unbagged cones (Fig. 1) (1997: $F_{1,5} = 7.589$, $P = 0.04$; 1998: $F_{1,5} = 12.64$, $P = 0.016$). More seeds were produced in 1997 than in 1998, whereas the percent increase in seed set due to bagging was greater in 1998 than in 1997. Our results suggest that the bag effect is robust, producing significant results regardless of weather patterns, pollination success, or other natural factors that could affect seed set.

Although the bags excluded insects larger than 1 mm, it is unclear which insect, if any, was responsible for the seed-set reduction in unprotected cones. Several pine-cone and seed-feeding insects are present in the interior of British Columbia (Hedlin *et al.* 1981). We observed no obvious cone damage by lepidopterans, such as western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae), or *Dioryctria* Zeller spp. (Lepidoptera: Pyralidae). *Leptoglossus occidentalis* and *A. canadensis* were present in the orchard but were never observed or recovered on the experimental cones. It is possible that the increase in seed set in bagged cones was the result of a change in microclimate, such as increased humidity or cooler temperatures, leading to empty seeds for physiological reasons (Owens and Molder 1984).

Bagging experiment

The highest maximum internal cone temperature, 44°C, was recorded in the cone under the parasol and the lowest maximum, 36.0°C, in the unbagged cone in shade (Fig. 2A). The order was slightly different for mean temperatures, the highest being 38.3°C for the exposed cone in sunlight (Fig. 2B). Lowest cone temperatures ranged between 7 and 8°C, with mean lows between 11.8 and 12.5°C. It is unlikely that the differences in mean or highest maximum temperatures were sufficient to affect ovule development, especially in lodgepole pine, which is adapted to high summer temperatures

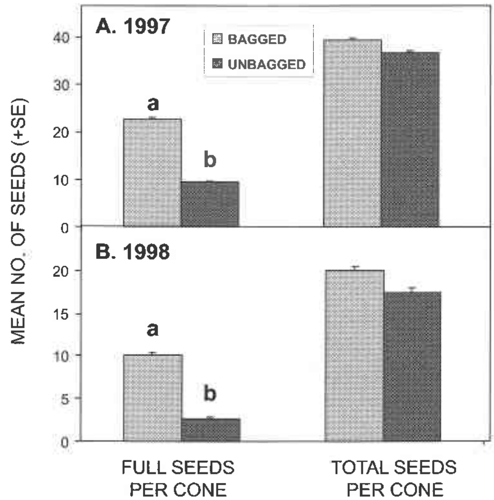

FIGURE 1. **Comparison of total seeds per cone and filled seeds per cone from bagged or unbagged *Pinus contorta* cones in 1997 (A) and 1998 (B). Paired bars with the same letter are not significantly different (ANCOVA, $P > 0.05$, $n = 6$).**

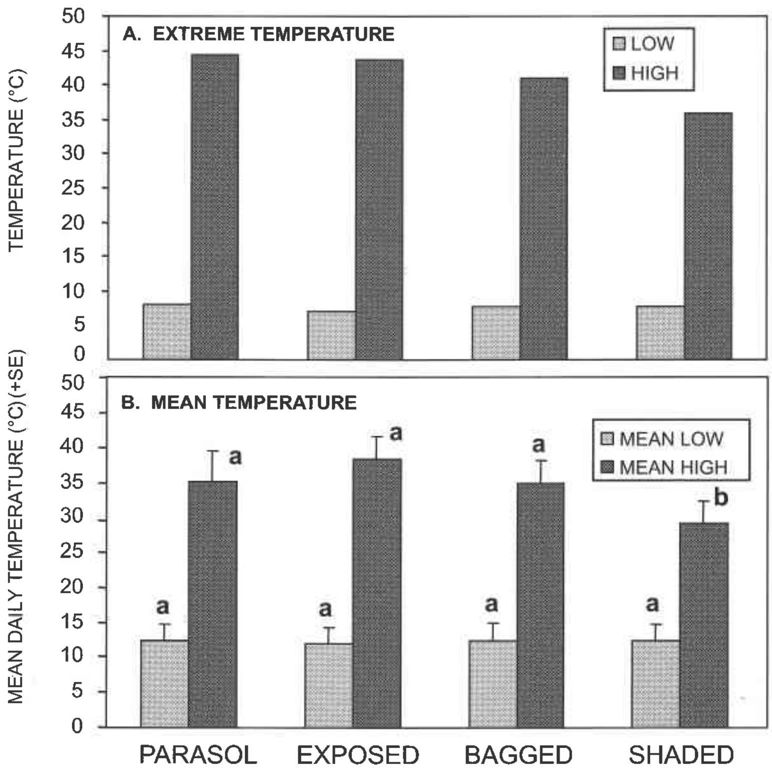

FIGURE 2. **Comparison of extreme (A) and mean (B) daily maximum and minimum temperatures recorded from probes inserted into *Pinus contorta* cones in four positions. Mean daily maximum or minimum temperature bars with the same letter are not significantly different (Fisher's LSD, $P > 0.05$, $n = 36$).**

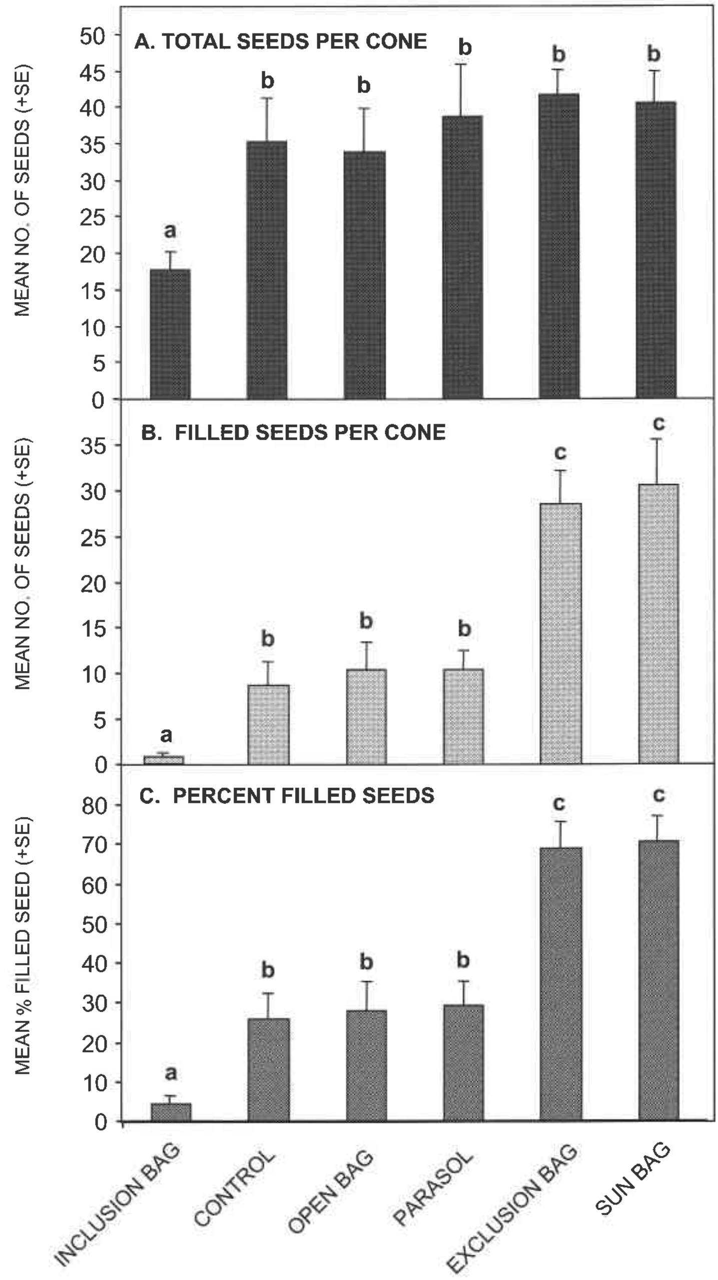

FIGURE 3. Comparison of total seeds per cone (A), filled seeds per cone (B), and percent filled seeds (C) in *Pinus contorta* cones exposed to six bagging treatments. Bars with the same letter within each graph are not significantly different (Fisher's LSD, $P > 0.05$, $n = 10$).

(Fowells 1965). This hypothesis is supported by the high seed set observed in bagged cones (Fig. 3).

There were fewer total seeds harvested per cone in the *L. occidentalis* inclusion treatment than in the other treatments (Fig. 3A) ($F_{5,48} = 2.93$, $P = 0.022$). Feeding

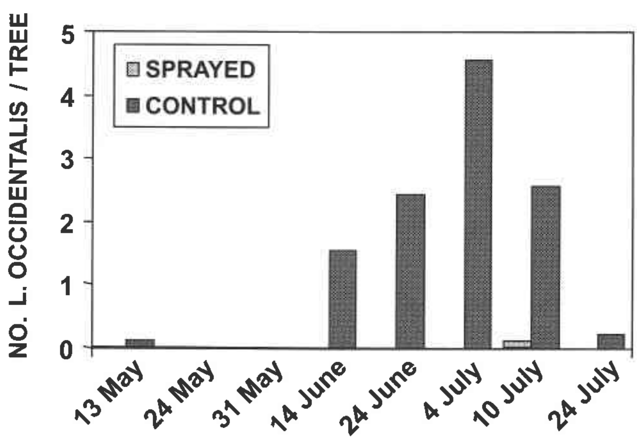

Figure 4. Number of *Leptoglossus occidentalis* observed on fenvalerate-treated and water-treated (control) *Pinus contorta* trees on eight sampling dates.

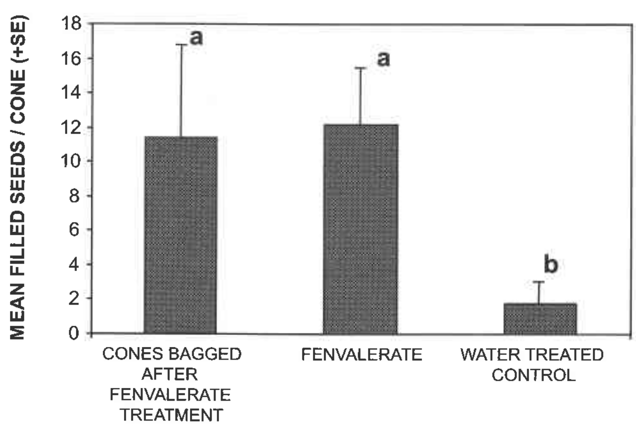

Figure 5. Comparison of number of filled seeds in cones from *Pinus contorta* trees treated with fenvalerate or water or treated with fenvalerate and bagged. Bars with the same letter are not significantly different (Fisher's LSD, $P > 0.05$, $n = 10$).

damage that occurs early in the season before the seed coat has hardened can result in adhesion of seeds to the cone scale, making the seeds unextractable. This type of damage has been observed in ponderosa pine and Douglas-fir (Krugman and Koerber 1969; Bates *et al.* 2000). Our data suggest that this type of early damage would have occurred under maximum *L. occidentalis* feeding pressure in the inclusion bag, but not in exposed cones (control, open-bag, and parasol treatments) that would not have been subjected to high feeding pressure until after the seed coat had hardened.

The data for filled seeds per cone (Fig. 3B) ($F_{5,48} = 23.99$, $P < 0.0001$) and percent filled seeds (Fig. 3C) ($F_{5,48} = 21.35$, $P < 0.0001$) fell into three groupings. The inclusion bag had almost no filled seeds, indicating the potential effect of high *L. occidentalis* infestations. Cones in exclusion bags (including the sun bag) produced 28–31 filled seeds per cone, close to the theoretical maximum of about 35 and within the desired target for seed production. Because differences in microclimate between the two exclusion bags apparently had no effect on seed set, we conclude that exclusion of insects is responsible for the high level of seed set. Cones exposed to naturally occurring densities of *L. occidentalis* (control, open bag, and parasol) had levels of filled seeds per cone typical of orchard seed set.

Insecticide exclusion experiment

Fenvalerate-treated trees harbored fewer *L. occidentalis* than water-treated (control) trees (Fig. 4); only one *L. occidentalis* adult was found on the sprayed trees, on 10 July. The apparent efficacy of fenvalerate is consistent with the results of Nord and DeBarr (1992). Cones protected by fenvalerate alone or fenvalerate plus exclusion bags had similar seed set, >11 filled seeds per cone, higher than the <1.7 filled seeds per cone on water-treated control trees (Fig. 5) ($F_{2,15} = 24.85$, $P < 0.0001$). These data suggest that the fenvalerate treatment was effective because it excluded *L. occidentalis* from the treated trees, although other insects could also have been excluded. The low seed set in the treated cones compared with the insect exclusion treatments in other experiments could have been due to a number of factors, including the use of a different seed orchard, with different tree genotype, vigour, and pollen production; weather during pollination; and phytotoxicity caused by the insecticide.

Conclusion

We have demonstrated conclusively in the bagging experiment that *L. occidentalis* can cause low seed set in lodgepole pine. Data from the other two experiments strongly support this conclusion. Our data suggest that *L. occidentalis* should be considered a serious pest in British Columbia seed orchards, causing up to 70% reduction in filled seeds at the natural population densities experienced in these experiments and over 95% reduction in filled seeds at the artificially high densities inside our inclusion bags. This magnitude of loss easily warrants the cost of control measures.

No system has yet been developed to quantitatively monitor *L. occidentalis* densities, and the damage potential of monitored densities is unknown. One means of assessing damage potential may be to use the antibody assay developed by Lait *et al.* (2001) as a tool to detect residual *L. occidentalis* saliva left in lodgepole pine seeds. This assay would separate damage caused by *L. occidentalis* from that caused by other insects, and would also allow feeding damage to be distinguished from naturally aborted seeds.

Although a quantitative monitoring system is not available, visual observations and anecdotal evidence suggest that *L. occidentalis* densities vary greatly between years. Because of the high price of lodgepole pine seed ($1000–$5000/kg), it is likely that an economic density threshold for *L. occidentalis* is exceeded at fairly low levels, perhaps justifying prophylactic insecticidal sprays in most years, as occurs in southern pine seed orchards for *L. corculus* (Nord 1990). Knowledgeable, economically based recommendations regarding such insecticidal treatments cannot be made to orchard managers in British Columbia until quantitative monitoring methods are developed, damage assessments are reliable, and action thresholds are determined.

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