Seasonal changes in seed reduction in lodgepole pine cones caused by feeding of *Leptoglossus occidentalis* (Hemiptera: Coreidae)

Ward B. Strong

British Columbia Ministry of Forests and Range, Kalamalka Forestry Centre,
3401 Reservoir Road, Vernon, British Columbia, Canada V1B 2C7
(e-mail: Ward.Strong@gov.bc.ca)

Abstract—Management of *Leptoglossus occidentalis* Heidemann in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) seed orchards of British Columbia, Canada, would be improved with knowledge of its damage potential at different times of the growing season. Mesh insect-exclusion bags were placed over cones, and adults or nymphs of *L. occidentalis* were enclosed in different bags for 9 periods of 10 to 38 days between 6 May and 17 September 2004. Feeding by adult females between 6 May and 28 May reduced total extractable seeds, a result of ovule damage before fertilization. Reduction in the number of filled seeds per cone was highest between 6 May and 29 June, with each adult female reducing yield by approximately 1.7 seeds per day. Between 29 June and 10 August, each adult female reduced the number of filled seeds per cone (seed set) by 1.0 to 1.25 per day. Seed set reduction declined to approximately 0.25 filled seeds per adult female per day after 10 August. Third to fifth instars caused seed set reduction between 0.6 and 1.2 filled seeds per cone per nymph feeding day from 29 June to 10 August. Utilizing these findings would improve management of *L. occidentalis* in a commercial seed orchard setting.

Résumé—La gestion des *Leptoglossus occidentalis* Heidemann dans les pépinières à graines du pin vrillé (*Pinus contorta* var. *latifolia* Engelm.) en Colombie-Britannique serait améliorée si on connaissait leur potentiel de dommage à différents moments dans la saison de croissance. Des sacs d'exclusion en filet ont été placés sur les cônes; des adultes ou des larves de *L. occidentalis* ont été introduits dans des sacs différents durant 9 périodes de 10 à 38 jours entre le 6 mai et le 17 septembre 2004. L'alimentation par les femelles adultes entre le 6 mai et le 28 mai a réduit le nombre total de graines récupérables, à cause du dommage fait aux ovules avant la fécondation. La réduction du nombre de graines pleines par cône est maximale entre le 6 mai et le 29 juin, alors que chaque femelle adulte réduit le rendement par environ 1,7 graine par jour. Entre le 29 juin et le 10 août, chaque femelle adulte réduit les graines pleines de 1,0 à 1,25 graine par jour. La réduction des ensembles de graines diminue à 0,25 graine pleine par adulte femelle par jour après de 10 août. Les larves de troisième à cinquième stades causent une réduction des ensembles de graines de 0,6 à 1,2 graines pleines par jour d'alimentation de larve entre le 29 juin et le 10 août. L'utilisation de ces résultats dans le contexte d'une pépinière à graines commerciale pourrait améliorer la gestion de *L. occidentalis.*

[Traduit par la Rédaction]

Introduction

Conifers in western North America are subject to seed loss by feeding of the western conifer seed bug, *Leptoglossus occidentalis* Heidemann (Koerber 1963). This polyphagous pest is known to feed on several conifer species and has been shown to reduce seed production in seed orchards (Krugman and Koerber 1969; Schowalter and Sexton 1990; Connelly and Schowalter 1991). In British Columbia, Canada, seed orchards of several species are impacted (Blatt and Borden 1996); low seed yields in seed orchards of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann (Pinaceae), have largely been attributed to *L. occidentalis* feeding (Strong *et al.* 2001; Bates *et al.* 2002*a*).

Critical to effective management of this pest is knowledge of its damage potential at different times of the season. In spring, overwintered

Received 26 October 2005. Accepted 10 May 2006.

Can. Entomol. **138**: 888–896 (2006)

adults are the only stage present. Females are the most damaging sex of *L. occidentalis* (Hanson 1984; Bates and Borden 2005); in early spring, females feed on soft, easily penetrated cones, and many of the small undeveloped ovules may be required to satisfy their appetite. However, the cool weather and attendant slower metabolism may limit their feeding. Later in summer, nymphs become abundant. Third to fifth instars, while being the most damaging nymphal stages, consume fewer seeds than females (Hanson 1984). Further, cones and seed coats are harder in summer than in early spring, and fewer of the larger seeds may satiate *L. occidentalis*, thus possibly limiting consumption. However, the higher temperatures and increased metabolic demands may sharpen their appetite.

Damage potential at different times of the season has been studied to some degree. Connelly and Schowalter (1991) found that adult *L. occidentalis* bagged on second-year cones of western white pine (*Pinus monticola* Dougl. ex D. Don) for a 3-week period in May increased seed abortion and reduced the total number of extractable seeds, while feeding for a 3-week period in July did not result in seed abortion or a decrease in total seeds but did increase the number of empty seeds, thus reducing harvestable yields of filled seeds. Schowalter and Sexton (1990) demonstrated that *L. occidentalis* nymphs increased seed abortion when enclosed over cones of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) for 2 weeks in mid-June, while nymphs enclosed over cones in early or late July increased the number of partially filled seeds. Bates *et al.* (2000) found that nymph feeding on Douglas-fir in June, but not July or August, reduced the number of filled seeds and increased the number of "fused" seeds, which were flattened and fused to the cone scale. Fused seeds caused by *L. occidentalis* feeding were differentiated from naturally occurring sterile seeds attached to sterile ovuliferous scales. Bates *et al.* (2002*a*) examined the effect of *L. occidentalis* feeding on lodgepole pine with an antibody-based method (Lait *et al.* 2001). Feeding in May–June increased the number of fused seeds, while feeding in June–July or July–August resulted in up to two seeds per insect per day being fed upon.

Though these studies indicated that there are differences in the type and extent of damage caused by *L. occidentalis* feeding at different times of the season, the time scales used were too coarse to be useful for management decisions. A maximum of three periods during the season were examined, with each feeding period lasting up to 6 weeks. Early-spring and late-summer feeding effects were not examined at all, though damaging densities of *L. occidentalis* are often found in early May or during harvest (unpublished data). Finally, the effects of feeding by late-instar nymphs, which become abundant from late June through August, were poorly quantified.

This study examines in greater detail the influence of season on feeding damage during periods when *L. occidentalis* adults and nymphs are present in lodgepole pine seed orchards in British Columbia.

Materials and methods

A lodgepole pine seed orchard near Vernon, British Columbia, (50°15′N, 119°16′W) was used for this study. The orchard was established in 1988, planted on 4 m × 5 m spacing, and drip irrigated, and tree height was kept below 3 m. It has been in full cone production since 1995. In the year of this study, 2004, insecticide sprays were not applied within 50 m of the experimental area of this orchard.

Ten trees of different genotypes were randomly selected from the central portion of the orchard. Fourteen shoots bearing three second-year cones were selected on each tree. Any older cones were removed from the shoots. On 23 April 2004, one shoot was randomly selected for an unbagged control; insect-exclusion bags were placed over the other 13 shoots and fastened tightly in place with zip-ties. Exclusion bags were made of white flexible nylon screening with a 1 mm mesh size, measured 25 cm × 50 cm, and had one 25 cm edge open. Shoots were inspected and cleared of visible arthropods before bags were put in place. All bags were opened on 28 May, 19 June, and 12 July to remove any *Cinara* aphids (Hemiptera: Aphididae) or *Aphrophora* spittlebugs (Hemiptera: Cercopidae) that may have developed within the bags. Shoots were randomly assigned to one of the following 14 treatments.

Treatments 1 to 9. Two field-collected female *L. occidentalis* were placed in each bag for periods of 10 to 18 days, except in treatment 9, in which bags contained females for 38 days. Two females per three cones represents a very high field density. In treatments 1–7, overwintered adult females were used. In treatment 8, one overwintered female and one newly emerged female were placed in each bag, since new adults were frequently found in the field at this time. In treatment 9, only newly emerged adult females were used, since overwintered adults were difficult to find in the field. At the end of each period, females were removed and the bags were resealed. Bags were occupied sequentially from 6 May (first detection of *L. occidentalis* in the field) through 17 September (Table 1). All visible *L. occidentalis* eggs were removed from the bags at the end of the feeding period. Bags that had harboured females were also opened 2 and 4 weeks after female removal and any *L. occidentalis* nymphs that had hatched from undetected eggs were removed.

Treatments 10 to 12. Two third or fourth instars were placed in each bag for periods of 11 to 18 days. Third and fourth instars were selected so that they would be mostly fourth and fifth instars by the end of the feeding period. At the end of each period, nymphs or adults were removed and the bags were resealed. Bags were occupied sequentially from 29 June (first detection of third and fourth instars in the field) through 10 August (Table 1).

Treatment 13. No females were introduced into the bags (insect-exclusion control).

Treatment 14. No bags were installed (control for level of feeding at naturally occurring field densities). Because no trapping methods or quantitative monitoring schemes exist for *L. occidentalis* (Bates and Borden 2005), it was not possible to quantitatively assess field densities.

All bags were removed and cones collected on 17 September. Seeds were extracted by dipping cones in boiling water for 15 s, baking in an oven at 52 °C for 8 h, shaking in a tumbler for 3 min, rubbing gently to dewing, screening to remove small debris, and rolling down an inclined plane to separate large debris. Cleaned seeds were X-rayed (Hewlett-Packard Faxitron at 12 kV and 2.0 mA for 60 s) and filled and empty seeds were counted. Raw data were expressed as total seeds per cone (TSPC) and filled seeds per cone (FSPC). Filled seeds per cone is a generally accepted measure of seed set in conifer seed orchards (Portlock 1996). *Leptoglossus occidentalis* feeding can result in completely or partially emptied seeds (Connelly and Schowalter 1991; Bates *et al.* 2000). Only 14% to 18% of partially filled seeds are capable of germination (Blatt and Borden 1998; Bates 1999). Therefore, in this study I considered any seeds that did not look completely filled on the X-ray sheets to be empty.

To account for differences in the duration of insect enclosure among treatments, as well as different mortality among bags, "feeding days" were calculated for each experimental unit (*i.e.*, individual insect-exclusion bag). This is the number of *L. occidentalis* in the bag times the number of days for that bag's treatment. *Leptoglossus occidentalis* that were dead at the end of the treatment period were considered to have died halfway through. To assess the impact of *L. occidentalis* feeding, the mean FSPC for treatment 13 (the insect-exclusion control) was assumed to be the potential value for every cone in the absence of *L. occidentalis* feeding. For treatments 1–12, the FSPC for each bag was subtracted from the mean for treatment 13 to arrive at "seeds lost" for each experimental unit. Seeds lost was divided by feeding days for each observation to arrive at a standardized number of seeds lost per feeding day, with which the different treatments could be compared on an even footing.

Untransformed data (TSPC, FSPC, and seeds lost per feeding day) were analyzed by two-way ANOVA without interaction, and treatment means were separated with Duncan's new multiple range test (Steel and Torrie 1960). Interpretation and discussion of the results of the means separation are complex, so I simplified matters by further separating treatment means into groupings based on the Duncan's new multiple range test. Group 1 consisted of those means not different from the smallest mean. Group 2 consisted of those means different from both the smallest and the largest mean. Group 3 comprised those means not different from the largest mean.

Results

Between 0 and 12 adults died in treatments 1 through 9, and 2–5 nymphs died in treatments 10 through 12 (Table 1). Few adult deaths occurred from 6 May through 29 June; the maximum mortality occurred from 12 to 23 July, when 67% of adults died, or an average of 6.1% per day. From 23 July to 10 August, half of the introduced adults were overwintered; of these, 70% died, or an average of 3.9% per day. All of the newly emerged adults introduced on 23 July

Table 1. Introduction schedule of *L. occidentalis* into insect bags, duration of each bagging period, and number of dead individuals at the end of the period.

Treatment	*n*	Female IN	Female OUT	Nymph IN	Nymph OUT	Time period (days)	Total no. dead	Mean no. of feeding days
1	10	6 May	18 May	—	—	12	0	24.0
2	10	18 May	28 May	—	—	10	1	19.5
3	10	28 May	8 June	—	—	11	0	22.0
4	10	8 June	19 June	—	—	11	2	20.9
5	8	19 June	29 June	—	—	10	0	20.0
6	9	29 June	12 July	—	—	13	5	22.4
7	9	12 July	23 July	—	—	11	12	14.7
8	10	23 July	10 Aug.	—	—	18	7	29.7
9	9	10 Aug.	17 Sept.	—	—	38	8	59.1
10	10	—	—	29 June	12 July	13	2	24.7
11	10	—	—	12 July	23 July	11	4	19.8
12	10	—	—	23 July	10 Aug.	18	5	31.5
13	10	Insect-exclusion (bagged) control						0
14	9	Unbagged control						Field levels

Note: Feeding days for each bag were calculated using the formula (2 – no. dead × 0.5) × time period, and averaged for each treatment.

were alive on 10 August. Of the 18 new adults introduced on 10 August, 8 had died by 17 September, or an average of 1.2% per day.

Eggs were found in five replicates of treatment 3, all replicates of treatments 4, 5, and 6, and five replicates of treatment 7.

Feeding by *L. occidentalis* significantly reduced TSPC ($F_{13,111} = 10.13$, $P < 0.0001$). Adult feeding in May (treatments 1 and 2) significantly reduced TSPC compared with the insect-exclusion control (Fig. 1). Early May feeding (treatment 1) reduced TSPC to 23% of the bagged control level. TSPC during late May feeding (treatment 2) was not different from the unbagged control, treatment 14 (field densities of *L. occidentalis*).

Filled seeds per cone was also reduced by *L. occidentalis* feeding ($F_{13,111} = 13.40$, $P < 0.0001$). All treatments had significantly fewer filled seeds per cone than the insect-exclusion control (Fig. 2). Adult feeding from 6 May through 29 June caused the greatest reduction in FSPC (group 1); these levels were not different from the unbagged control. Adult feeding after 29 June, and feeding by nymphs, caused less damage than early adult feeding (group 2).

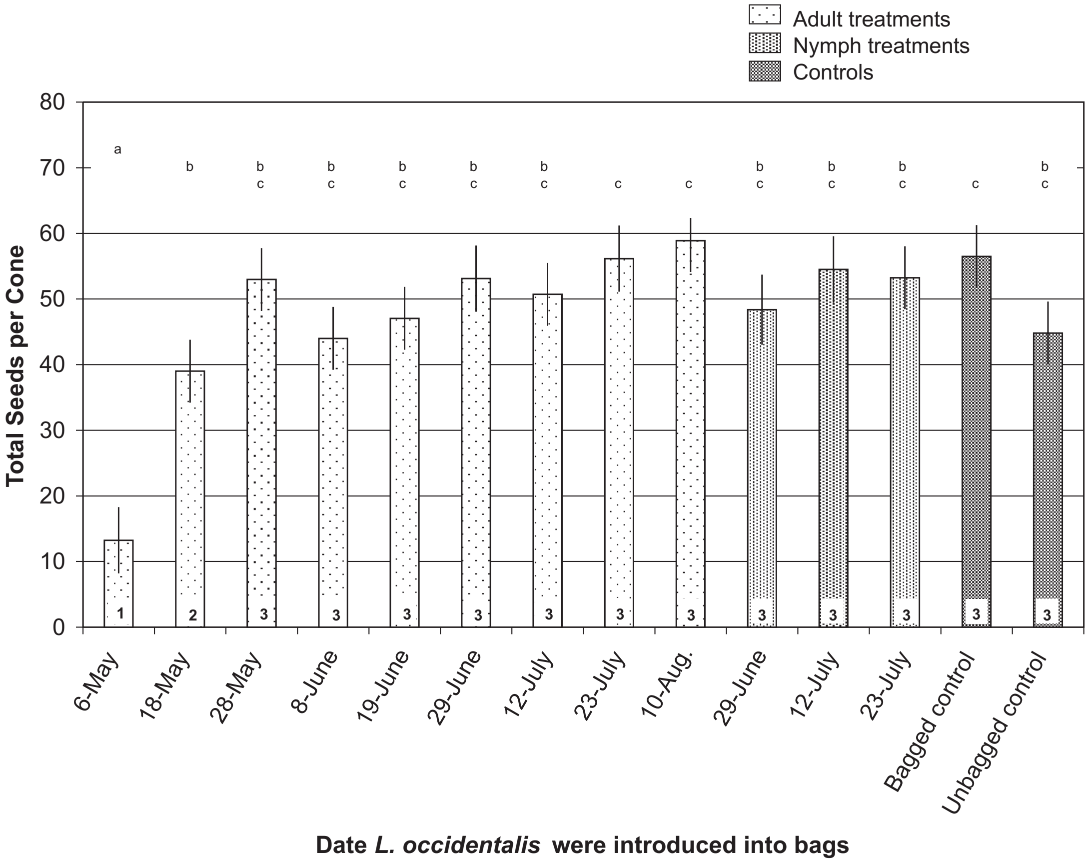
There were significant differences in seeds lost per feeding day among the bagging treatments ($F_{11,94} = 9.78$, $P < 0.0001$). Adult feeding from 6 May through 29 June resulted in the most seeds lost per feeding day (Fig. 3), between 1.6 and 1.8 (group 3). Intermediate losses occurred for adult feeding between 29 June and 10 August, and for nymphs in mid and late (but not early) July (group 2), with losses between 0.75 and 1.25 seeds per feeding day. The lowest losses were from adult feeding after 10 August and nymph feeding in early July (group 1).

Discussion

The mortality and oviposition data provide information on the life history of *L. occidentalis*. Overwintered adults displayed good survival through to the end of June, and mortality increased thereafter. Presumably all wild overwintered adults die before the following winter. New adults showed much better survivorship: no mortality from 23 July to 10 August, and a low mortality rate compared with overwintered adults from 12 July through 10 August.

The presence of bags containing eggs suggests an oviposition period sometime between 28 May and 23 July, peaking between 8 June and 12 July. This corresponds well with the findings of Koerber (1963) and Bates and Borden (2005), who determined that *L. occidentalis* oviposition occurs between 23 May

Fig. 1. Total seeds per cone (filled, partially emptied, and empty) extracted from cones that had been exposed to *L. occidentalis* feeding. Feeding for each time period started at the date under the column and ended at the date under the next column. Vertical bars represent SE. Letters above columns are Duncan's new multiple range test rankings: columns with the same letter are not significantly different, $P = 0.05$. Numbers in columns represent biologically significant groupings: 1, means not significantly different from the smallest mean; 2, means significantly different from both the smallest and the largest mean; and 3, means not significantly different from the largest mean.

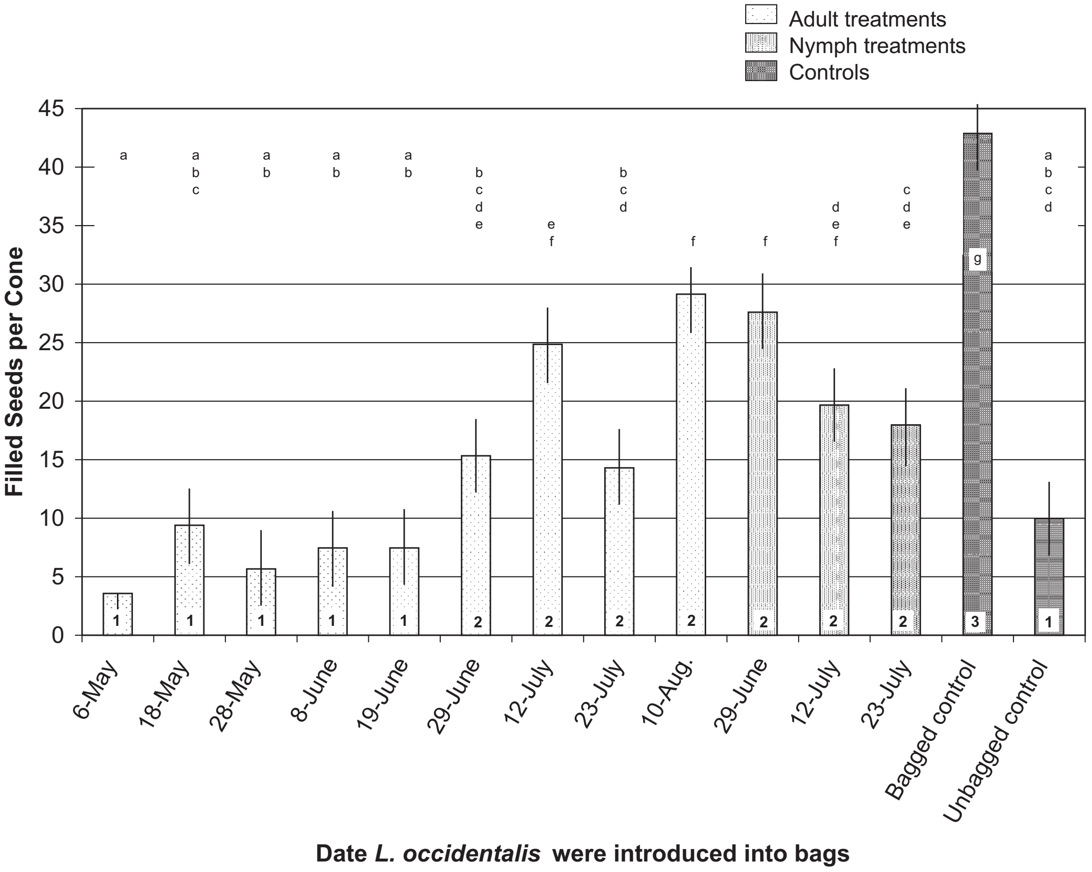


and 17 July. No eggs were found in treatments using newly emerged adults only (treatments 8 and 9). Nymphs have been found in seed orchards into September (author's unpublished data; Bates *et al.* 2002*b*). Thus, these nymphs are likely the offspring of old, surviving overwintered adults. Since only adults overwinter (Koerber 1963), the evolutionary implications of these late-surviving overwintered adults and their offspring is unclear.

The total number of seeds per cone was reduced only in the earliest feeding periods. This period is prior to ovule fertilization, which occurs at the end of May or in early June (Owens and Molder 1984) in the interior of British Columbia. Ovules fed upon (or deteriorated for other reasons) before fertilization do not abscise from the cone scale and become "fused" seeds. This therefore reduces the total amount of extractable seeds, or TSPC. Such damage has been associated with *L. occidentalis* feeding in the past (Schowalter and Sexton 1990; Bates *et al.* 2000). Bates *et al.* (2002*a*) were unable to demonstrate with the antibody method that fused seeds were a result of *L. occidentalis* feeding, but comparison with controls leads to that conclusion anyway. I found that this damage, as measured by a reduction in TSPC from control levels, was most prevalent in early May, less prevalent in late May, and nonexistent after the beginning of June.

Fertilization stimulates the development of a seed coat even if the embryo subsequently dies (Owens and Molder 1984). Thus, *L. occidentalis*

Fig. 2. Filled seeds per cone extracted from cones that had been exposed to *L. occidentalis* feeding. Feeding for each time period started at the date under the column and ended at the date under the next column. Vertical bars represent SE. Numbers and letters above and in columns are as described in Fig. 1.

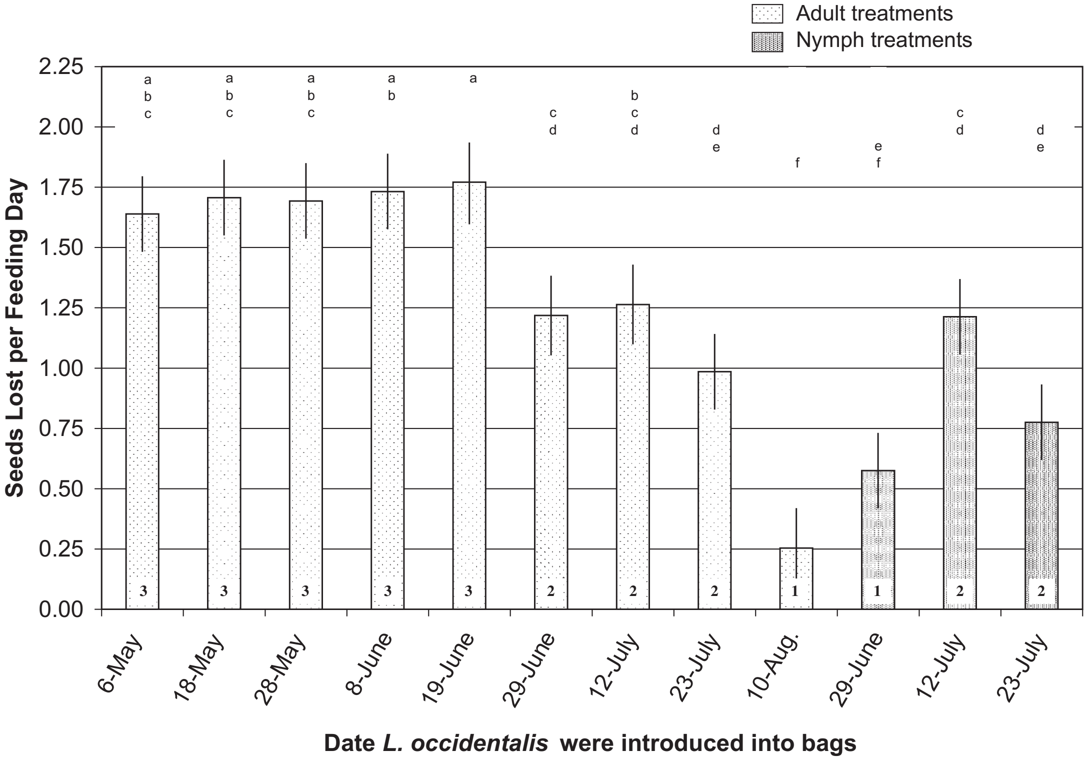


feeding (as well as other factors) after fertilization can produce an empty or partially filled seed. If feeding occurs before the seed coat hardens, the seed will appear collapsed, while feeding after seed-coat hardening will result in seeds of normal appearance (Krugman and Koerber 1969; Strong *et al.* 2001). Total extractable seeds per cone will not be affected, but FSPC will be reduced. I found that TSPC was not reduced after fertilization occurred, but FSPC was.

Leptoglossus occidentalis reduced FSPC most dramatically early in the season, as a result of feeding by overwintered adults prior to 29 June. Feeding in early May reduced FSPC to 8.3% of levels in the insect-exclusion control. Adult feeding from 29 June through 27 September reduced FSPC to a similar degree as nymph feeding from 29 June through 10 August. This level was not different from that in the unbagged control, which measured reduction in FSPC due to field densities of *L. occidentalis*. Unfortunately it is not possible at this point to relate field densities to densities in the bags, since no reliable monitoring protocol has been developed (Strong *et al.* 2001; Bates 2002).

The duration of insect enclosure in these treatments varied, as did the mortality of insects during enclosure. The seeds lost per feeding day are standardized across treatments with respect to enclosure period and mortality. Again, feeding prior to 29 June caused the most damage, with between 1.5 and 2 filled seeds lost per insect per day. This figure is higher than the 0.5 seeds fed on per day determined by Bates *et al.* (2002*a*) for "early-season" feeding. However, their study did not examine the reduction in FSPC, but rather used an antibody-based method to determine which seeds had been fed upon. The authors admit that the antibody method is increasingly inaccurate for seeds fed on earlier in the season, for a variety of reasons.

Fig. 3. Filled seeds lost per feeding day. Feeding for each time period started at the date under the column and ended at the date under the next column. Vertical bars represent SE. Numbers and letters above and in columns are as described in Fig. 1.



The present study suggests that the estimate of Bates *et al.* (2002*a*) is low.

Seed loss caused by adults from 29 June through 10 August fell to intermediate levels, between 0.75 and 1.25 filled seeds lost per feeding day. This level of seed reduction by adults agrees with the "mid-season" data of Bates *et al.* (2002*a*), who found that feeding between 6 June and 15 July resulted in about 1.0 seed fed on per insect per day. However, these authors found that "late-season" feeding, between 10 July and 15 August, resulted in nearly 2.0 seeds fed on per day, considerably more than the levels found in this study. It is possible that the antibody technique detected seeds that were probed but not fed on, or fed on for short periods of time; such seeds would have been determined as filled by the radiographic examination used in this study. Minor amounts of feeding result in a seed that can still germinate and produce a viable seedling (Bates *et al.* 2001). Thus, while the antibody technique might be superior at detecting precisely which seeds have been fed upon, the radiographic method may be more relevant from a practical pest management perspective. The antibody method would still be useful for determination of *L. occidentalis* feeding damage in the absence of insect-exclusion controls.

The reduced seed losses after 29 June are likely related to normal phenological events. *Leptoglossus occidentalis* mortality increased after 29 June, and oviposition tapered off in mid-July. Apparently the overwintered insects were aging; as oviposition drew to a close, nutritional demands abated as vigour and survivorship declined. At the same time (June–July), embryos in the seeds were developing and the female gametophyte (endosperm) of the seed was accumulating proteins and lipids (Owens and Molder 1984). As a result, fewer seeds might have satisfied the nutritional requirements of the adults. Thus, the decline in seed loss during June and July would appear to be the result of predictable physiological processes in both insects and seeds.

Feeding by new adults from 10 August through 17 September resulted in the least damage, with about 0.25 seeds lost per feeding day. Cone harvest usually starts in early August in central British Columbia and extends through early September. Populations of *L. occidentalis* can persist or accumulate in orchards being harvested (unpublished data), but the damage potential is unknown. It appears that these late-season adults are preparing for winter rather than producing eggs; thus, their nutritional demands are reduced. They are therefore of less concern from a pest management point of view than populations feeding earlier in the season.

Feeding by nymphs resulted in intermediate levels of seed loss not different from levels resulting from feeding by adults from 29 June through 10 August. Although seed loss during nymph feeding from 29 June to 12 July was not different from the minimum, and therefore fell into group 1 (Fig. 3), it was also not different from that during the late nymph feeding period, from 23 July to 10 August. I found higher seed loss due to nymphs than did Bates *et al.* (2002*a*), who found that 0.3 to 0.4 seeds per insect per day were fed upon. However, they enclosed first instars and kept them until nymphal development was complete. First and second instars feed minimally, while older instars feed much more (Hanson 1984). Therefore, the data of Bates *et al.* (2002*a*) underestimate the seed loss caused by the most damaging stages. Data from this study show that third and older instars should be considered as important as adults during the same time of the season in pest management protocols.

Feeding by late-season nymphs, after 23 July, was not tested in this experiment because they are known to not feed on mature cones (Bates *et al.* 2002*b*). Nymphal feeding during this period can, however, reduce seed set and increase conelet abortion of first-year cones, which will mature the following year, and thus must be considered in management practices.

Conclusions

The results of this study are relevant to pest management decisions regarding *L. occidentalis*. Adults in May and June are the most damaging stage, causing more seed loss than formerly known. Previously used action thresholds need to be lowered during this time of the season. Also, the impact of nymphs was previously poorly quantified. This study shows that the damage potential of third to fifth instars should be considered equal to that of adult females in July and August. The exact timing of these seasonal changes is likely to be phenologically driven, and thus will change from year to year. However, the basic principle will likely hold true regardless of phenological timing.

My results show that newly emerged adults during harvest cause less seed loss than previously estimated. Thus, action thresholds at this time of the season can be raised. The only currently available tactic for controlling *L. occidentalis* is application of broad-spectrum insecticides. Raised action thresholds translate to reduced sprays during harvest, which has important implications for worker safety and the integration of control measures into harvest activities. Whether late-summer new adults reinvade the same orchard the following spring is not known, so killing them in autumn to prevent subsequent infestations is not a viable tactic.

Unfortunately, it is difficult to use these data directly for pest management decisions because a quantitative monitoring system is still under development. Therefore, the relation of *L. occidentalis* densities in this study to actual or monitored field densities is unknown. However, the general principles are applicable, and when a quantitative monitoring system is developed, these data can be used to establish economic thresholds.

Acknowledgements

The author thanks Kate Pieper for field assistance; Chris Walsh and Gary Giampa for access to an unsprayed lodgepole pine seed orchard at Kalamalka Seed Orchards, Vernon, British Columbia; Chris Walsh and Dave Kolotelo for helpful comments on the manuscript; and Sarah Bates and Robb Bennett for many insightful discussions on the subject. This project was partially funded by the Forest Genetics Council of BC Operational Tree Improvement Program, grant No. SPU0716.

References

Bates, S.L. 1999. Impact of the western conifer seed bug, *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae), on yield, seed storage reserves and seedling vigour in Douglas-fir. Master of Pest Management thesis, Simon Fraser University, Burnaby, British Columbia.

Bates, S.L. 2002. Detection, impact and management of the western conifer seed bug, *Leptoglossus occidentalis* (Heteroptera: Coreidae), in lodgepole pine seed orchards. Ph.D. thesis, Simon Fraser University, Burnaby, British Columbia.

Bates, S.L., and Borden, J.H. 2005. Life table for *Leptoglossus occidentalis* Heidemann (Heteroptera: Coreidae) and prediction of damage in lodgepole pine seed orchards. Agricultural and Forest Entomology, **7**: 145–151.

Bates, S.L., Borden, J.H., Kermode, A.R., and Bennett, R.G. 2000. Impact of *Leptoglossus occidentalis* (Hemiptera: Coreidae) on Douglas-fir seed production. Journal of Economic Entomology, **95**: 1444–1451.

Bates, S.L., Lait, C.G., Borden, J.H., and Kermode, A.R. 2001. Effect of feeding by the western conifer seed bug, *Leptoglossus occidentalis*, on the major storage reserves of developing seeds and on seedling vigor of Douglas-fir. Tree Physiology, **21**: 481–487.

Bates, S.L., Lait, C.G., Borden, J.H., and Kermode, A.R. 2002*a*. Measuring the impact of *Leptoglossus occidentalis* (Heteroptera: Coreidae) on seed production in lodgepole pine using an antibody-based assay. Journal of Economic Entomology, **95**: 770–777.

Bates, S.L., Strong, W.B., and Borden, J.H. 2002*b*. Abortion and seed set in lodgepole and western white pine conelets following feeding by *Leptoglossus occidentalis* (Heteroptera: Coreidae). Environmental Entomology, **31**: 1023–1029.

Blatt, S.E., and Borden, J.H. 1996. Distribution and impact of *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae) in seed orchards in British Columbia. The Canadian Entomologist, **128**: 1065–1076.

Blatt, S.E., and Borden, J.H. 1998. Interactions between the Douglas-fir seed chalcid, *Megastigmus spermotrophus* (Hymenoptera: Torymidae), and the western conifer seed bug, *Leptoglossus occidentalis* (Hemiptera: Coreidae). The Canadian Entomologist, **130**: 775–782.

Connelly, A.E., and Schowalter, T.D. 1991. Seed losses to feeding by *Leptoglossus occidentalis* (Heteroptera: Coreidae) during two periods of second-year cone development in western white pine. Journal of Economic Entomology, **84**: 215–217.

Hanson, P.D. 1984. Comparison of damage to douglas-fir (*Pseudotsugae menziesii* (Mirb.) Franco) seed, by each life stage of *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae). B.Sc. (Forestry) thesis, University of British Columbia, Vancouver, British Columbia.

Koerber, T.W. 1963. *Leptoglossus occidentalis* (Hemiptera: Coreidae), a newly discovered pest of coniferous seed. Annals of the Entomological Society of America, **56**: 229–234.

Krugman, S.L., and Koerber, T.W. 1969. Effect of cone feeding by *Leptoglossus occidentalis* on ponderosa pine seed development. Forest Science, **15**: 104–110.

Lait, C.G., Bates, S.L., Morrissette, K.K., Borden, J.H., and Kermode, A.R. 2001. Biochemical assays for identifying seeds of lodgepole pine and other conifers fed on by *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae). Canadian Journal of Botany, **79**: 1349–1357.

Owens, J.N., and Molder, M. 1984. The reproductive biology of lodgepole pine. British Columbia Ministry of Forests, Information Services Branch, Victoria, British Columbia.

Portlock, F.T. 1996. A field guide to collecting cones of British Columbia conifers. Canadian Forest Service, Victoria, British Columbia.

Schowalter, T.D., and Sexton, J.M. 1990. Effect of *Leptoglossus occidentalis* (Heteroptera: Coreidae) on seed development of Douglas-fir at different times during the growing season in western Oregon. Journal of Economic Entomology, **83**: 1485–1486.

Steel, R.G.D., and Torrie, J.H. 1960. Principles and procedures of statistics. McGraw-Hill, Toronto, Ontario.

Strong, W.B., Bates, S.L., and Stoehr, M.U. 2001. Feeding by *Leptoglossus occidentalis* (Hemiptera: Coreidae) reduces seed set in lodgepole pine (Pinaceae). The Canadian Entomologist, **133**: 857–865.