Lodgepole pine seedset increase by mesh bagging is due to exclusion of *Leptoglossus occidentalis* (Hemiptera: Coreidae).

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ABSTRACT

Lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var *latifolia*) seed orchards in British Columbia, Canada, suffer from low seedset problems. Seedset can be improved by installing mesh bags over the second-year cones. One mechanism of improved seedset has been shown to be exclusion of the seed-feeding western conifer seedbug, *Leptoglossus occidentalis*, but the possibility of microclimate alteration leading to improved seedset has not been carefully explored. I measured the internal cone temperatures of cones both inside and outside mesh bags, as well as the relative humidity around cones both inside and outside bags. I also installed time-lapse cameras that, every 5 minutes, photographed unbagged cones situated near bagged cones, and examined the photographs for feeding by *L. occidentalis*. Internal temperatures of cones inside bags were warmer, accumulated more heat units, and had higher peak temperatures than cones outside bags. Humidity was slightly higher inside bags in late season, particularly during rainy days. The evidence did not support the hypothesis that microclimate change is the cause of improved seedset inside bags. On the other hand, the cameras documented extensive feeding by *L. occidentalis* on unbagged cones, and showed a strong correlation between the amount of time a cone was fed upon and the subsequent seed loss. Therefore the increase in seedset due to the mesh bags is not related to microclimate change, but is caused by exclusion of *L. occidentalis*.

INTRODUCTION

Conifer seed orchards produce seed from commercial forestry tree species that have been genetically improved through traditional breeding techniques. In British Columbia (BC), Canada, seed orchards provided seeds in 2012 for 243 million seedlings used in reforestation (Forest Genetics Council of BC 2013a). However, lodgepole pine (*Pinus contorta* Dougl. ex. Loud. Var. *latifolia*) orchards have not been meeting production targets due to low seedset issues (Forest Genetics Council of BC 2013b).

Lodgepole pine seedset, as measured by the number of filled seeds per cone or percent filled seeds, has been below the potential maximum in all BC seed orchards except those at the Prince George Tree Improvement Station. The potential number of filled seeds is between 30 and 40 per cone (Owens 2006), but many orchards experience fewer than 15, even as low as 3 to 5, filled seeds per cone (Stephen Joyce[2], personal communication). One factor influencing seedset is the western conifer seedbug, *Leptoglossus occidentalis* (Heidemann) (Hemiptera: Coreiidae) (Hedlin *et al.* 1980; Koerber 1963), which has been shown to reduce seed crops significantly (Bates *et al.* 2000; Blatt & Borden 1996; Strong 2006).

It was discovered in 2010 that a substantial amount of seed loss occurs from late July through August; this was substantiated in 2011 and 2012 (WBS, unpublished data). Though seasonal profiles of seed loss caused by *L. occidentalis* have been determined previously (Bates *et al.* 2002b; Strong 2006; Strong *et al.* 1998), these studies concluded their research in late July or shortly thereafter. The 2010–2012 research was the first indication of substantial seed loss in August.

One feature of this late-season seed loss is that it is prevented by installing bags of polyester nylon mesh (1 mm mesh size) over the second-year cones. It has been known since 1994 that

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installing insect bags increases seedset in lodgepole pine (Strong *et al.* 1998). One reason mesh bags increase seedset is exclusion of the *L. occidentalis* (e.g., Bates *et al.* 2002a; Strong 2006; Strong *et al.* 2001). The possibility that mesh bags might also influence seedset by altering microclimate has never been rigorously addressed. Strong *et al.* (2001) tried to test microclimate effects by using different types of bags that either excluded or allowed entry of *L. occidentalis*, while varying the effects of temperature and relative humidity within the bag: it appeared that microclimate was not relevant to final seedset, while *L. occidentalis* exclusion was. Furthermore, excluding *L. occidentalis* by pesticides resulted in the same increase in seedset as protecting cones with mesh bags, suggesting that bag microclimate is unimportant (Strong *et al.* 2001).

Mesh-bag induced changes in the microclimate around the developing cone have never been directly measured. It has been theorized that seed orchards in the BC southern Interior are too hot and dry for good seed production (Dr. Michael Carlson[3], personal communication), particularly considering that lodgepole pines typically grow in cooler, higher-elevation biogeoclimatic zones (Meidinger and Pojar 1991). Mesh bags used in these hot seed orchards may cool the cones or increase humidity, or both, thus preventing the observed seed loss. Damage attributed to excess temperature may be the result of a high mean temperature, time spent above a certain threshold temperature, or maximum temperature experienced in the seed-bearing portion of the cones. Increased humidity may reduce water stress inside cones.

Visual counts showed *L. occidentalis* densities to be low from 2010 to 2012 (Kalamalka Seed Orchards monitoring data, unpublished). This suggested that the prevention of August seed loss by mesh bags might be due to microclimate changes rather than *L. occidentalis* exclusion. The current experiment was designed to determine whether mesh bags increased seedset because of changes in temperature or humidity, or because of exclusion of *L. occidentalis*.

It has been found that *Leptoglossus occidentalis* prefers to feed on certain genotypes, termed ‘clonal preference’ (Blatt and Borden 1996, 1999; Richardson 2013). Certain genotypes were strongly favoured by *L. occidentalis*, while others were strongly avoided. Clonal preference was not stable from year to year, possibly because *L. occidentalis* were using host-finding cues that are not strongly genetically determined, and thus change yearly independent of clone. Host-selection cues might include cone size, cone count, or both (Blatt and Borden 1996, 1999; Richardson 2013); cone chemistry (Richardson 2013); or visual cues (Zahradnik 2012).

Some of these earlier studies were conducted in one of the two orchards used in the current study (Kalamalka Seed Orchards #307). Because clonal preference was not completely stable and the other orchard has no clonal-preference profile, I did not use preferred clones in this study. Similarly, we have no information on the influence of bag microclimate on clonal variation. Furthermore, I was interested in maximizing the generalizability of any conclusions. It was possible to use five ramets (individual trees) of one clone in one orchard, and five ramets of another clone in the other orchard (there is no overlap of clones between the two orchards). This would have reduced interplot variation for a more statistically powerful experiment at the expense of generalizability. Furthermore, any clone choice would have a good probability of selecting clones that were non-preferred, resulting in poor *L. occidentalis*-feeding data. So, to maximize generalizability and spread the risk of selecting non-preferred clones, 10 different clones were used in this study.

MATERIALS AND METHODS

In 2013, 10 lodgepole pine trees representing 10 different clones were randomly selected, five of each growing in each of two commercial seed orchards near Vernon, BC. Orchards were Orchard 307 (50° 14' 11" N, 119° 16' 39" W), with trees 30–32 years old and heights up to 8 m; and Orchard 339 (50° 23' 43" N, 119° 12' 31" W), with trees 10–12 years old and heights of 4–6 m. Trees were managed according to standard management of conifer seed orchards in BC,

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Table 1

Response variables measured on each of the four cone clusters selected on each experimental tree.

Cone cluster	Bagged	Response variable	Cones used
1	Yes	Temperature	2
		Humidity	--
2	No	Temperature	2
		Humidity	--
3	Yes	*Leptoglossus* feeding	3–4
4	No	*Leptoglossus* feeding	3–4

including drip irrigation, fertilizing, pruning, pest management, and harvest (Forest Genetics Council of BC 2014).

On each of the 10 trees, four cone clusters were selected, with three to four second-year cones in each. Cone clusters within each tree were of approximately equal aspect and height, and contained cones of approximately equal size. Cones and clusters were assigned to measuring response variables as described below (Table 1).

Internal cone temperatures: On each of the 10 selected trees, a 1-mm hole was drilled into two cones in each of two clusters (four cones per tree). Holes were drilled from near the stem end of the cone into the seed-bearing portion, about 1 cm deep. One K-type thermocouple with 30-guage wires (0.26 mm diameter) was inserted into each hole (Fig. 1). Within one day, pitch had sealed off the hole and fixed the thermocouple wires in place. All four thermocouples on each tree were plugged into a battery-powered 4-channel thermocouple datalogger (model SD947, Reed Instruments, Ste. Anne de Bellevue, Quebec) that was programmed to record thermocouple temperatures every 5 minutes. One cone cluster with two thermocouple-containing cones was enclosed in a white polyester mesh bag (hole size: 0.6 x 0.9 mm); the other cluster was left unbagged. Thus, on each experimental tree, there were two cones inside mesh bags, and two outside, and the internal temperatures of each were measured every 5 minutes.

Mean internal cone temperatures, peak temperatures, and time above putative threshold temperatures of 35 and 40 °C were computed. Time above threshold temperatures was computed as degree-days by subtracting the threshold temperature from the measured temperature for each 5-minute interval, and summing positive differences. The temperature measurement for each 5-minute interval was assumed to be the mean temperature for that interval.

Data were analyzed in R (R Core Team 2013) by one-way RCB ANOVA (blocked by tree) after transformation with log(x+1) to normalize the residuals when applicable, for mean temperatures and cumulative degree-days, and by paired t-tests for peak temperatures and monthly degree-day accumulations.

Relative humidity (RH): To measure RH, weatherproof iButtons (Maxim Integrated, San Jose, CA) were used. These are about 17 mm diameter and 6 mm thick (Fig. 2), and can be preprogrammed to measure temperature and RH at desired intervals, then left in the field to run independently. iButtons were programmed to measure RH every 10 minutes, then one iButton was attached (using fabric first-aid tape) to a third cone in each of the cone clusters used for thermocouple measurements. The iButton was positioned on the lower north side of each cone to avoid sun as much as possible, and the RH-monitoring hole was positioned away from the cone and left exposed by the tape. Thus, on each experimental tree, RH around one bagged cone cluster was measured every 10 minutes, and RH around a non-bagged cone cluster was also measured the same way.

Mean daily RH was computed for the iButton inside and outside bags on each tree. Data were analyzed with a randomized complete block split-plot with trees as blocks, date as main plots, and

Figure 1. Thermocouple wire inserted into a 1-mm hole drilled into the seed-bearing portion of a lodgepole pine cone.

bagging (bagged or unbagged) as sub-plots. Missing data lead to an unbalanced design, so R package lmerTest (Kuznetsova *et al.* 2014) was used, which estimated the degrees of freedom for an unbalanced type III ANOVA.

Leptoglossus occidentalis feeding: The two remaining cone clusters on each tree (those not used for temperature and RH measurements) were used for measuring *L. occidentalis* feeding. On one cluster, a mesh bag was installed to exclude *L. occidentalis* from the cones. Pine needles and small branches surrounding the cone cluster held the bag away from the cones, preventing *L. occidentalis* from feeding through the bag. The second cone cluster was left unbagged. A time-lapse digital camera (Wingscapes Inc, Alabaster, AL; Fig. 3) was installed 1–1.5 m away and aimed at the unbagged cone cluster. Cameras were set to take one photo every 5 minutes from 06:00 through 22:30, starting May 13 and ending September 9. *Leptoglossus occidentalis* is known to be a diurnal insect (Koerber 1963; Hedlin *et al.* 1980), so photos were not taken at night.

All photos were examined for the presence of L occidentalis adults and nymphs. Camera resolution was sufficient to distinguish between adults and nymphs, but not between male or female adults, nor between instars. Insect activity was classed as feeding, walking, or resting. *Leptoglossus occidentalis* feed by inserting their stylets into a developing seed within a cone, injecting salivary enzymes that macerate seed contents, and sucking the resulting liquid out (Koerber 1963). This process takes time, so if the insect —and particularly its head —remained in a similar position for >5 minutes, it was considered to be feeding. If the insect changed positions in consecutive photos, it was considered to be walking. Feeding *L. occidentalis* tend to move their bodies somewhat while holding their heads in approximately the same place: if an insect remained in exactly the same position, it was considered to be resting.

If a photo documented an *L. occidentalis*, the activity of the *L. occidentalis* was considered to have spanned a mean of 5 minutes. The time adults and nymphs spent feeding was summed for early season (May 13–June 30), late season (July 1–Sept 9), all season, and weekly.

After September 9, cones were collected from the bagged clusters and the exposed, photographed clusters. On collection, it was discovered that the exclusion bag for tree Kal 01 had been installed on the wrong tree, so tree Kal 01 was dropped from further analysis. Seeds were extracted at the Kalamalka Forestry Centre, Vernon, BC. Cones were dipped for about 10 s in water heated to between 90 and 96 °C to break any serotinous bonds between cone scales. Cones were then baked for 8 h at 45 °C, then tumbled in a cone tumbling machine to dislodge seeds. Wings were removed by gently rubbing in a moistened cotton bag. Clean seeds were then X-rayed in a digital X-ray machine (Carestream InVivo DXS Pro, Woodbridge, Connecticut), and filled and empty seeds were counted. A seed was considered filled if the megagametophyte, embryo erosion cavity, and embryo were intact and filled at least four-fifths of the inside length of the seed coat (Kolotelo *et al.* 2001; Owens 2006). Most empty seeds were without megagametophytes, though remnants of the nucelli were apparent; occasionally, small, deformed, or eroded megagametophytes were present.

Seedset data were calculated as averages for each cone cluster: total seeds per cone, filled seeds per cone, and percent filled seeds. Seedset between bagged and unbagged cones was compared by paired t-test with bagged/unbagged for each tree, after transformation with log (x+1) to normalize the residuals when appropriate. Seed decline for each tree was computed as the difference in seedset data between the cones exposed to *L. occidentalis* feeding (unbagged cones) and cones on that tree protected from feeding (bagged cones). Seed decline was regressed against the cumulative number of minutes/cone/camera-day the exposed cones were fed upon by *L. occidentalis* for early season, late season, and all season.

RESULTS AND DISCUSSION

Internal cone temperatures: A total of 893,261 cone temperature measurements were taken between May 12 and September 5. Because of equipment malfunctions, about 443,000 potential measurements were missed. Equipment malfunctions were of a nature that missing data were never individual data points or small groups of data points, but whole days or multiple days. Because of this, it is not possible to extrapolate from adjacent data, and these data points were registered as missing data.

During early season (before July 15), mean cone temperatures of bagged cones (20.36 °C) were significantly higher than unbagged cones (20.01 °C; $F_{1,\ 196637} = 54.69$, $P < 0.0001$). During the late-season seed-loss period of July 15–Sept 6, mean bagged cone temperatures were also higher (23.38 °C) than unbagged (23.01 °C; $F_{1,\ 251911} = 56.62$, $P < 0.0001$). These figures represent

Figure 2. iButtons showing the RH-monitoring hole.

Figure 3. Time-lapse camera aimed at an unbagged cone cluster.

the average day and night temperatures. It is expected that the critical high temperatures would occur during daytime. It is possible that bags maintain cone warmth at night and provide cooling during the day, resulting in the observed slight mean warming. Therefore, means were computed for daytime (08:00 to 19:59) and night time (20:00 to 07:59) periods during late season, July 15–Sept 6. Daytime temperatures had an even greater differential in bagged vs. unbagged cones (28.92 and 28.05 °C, respectively; Fig 4A; $F_{1,\ 126089} = 453.9$, $P < 0.0001$). On the other hand, during the night, cone temperatures were slightly cooler inside the bags than outside (17.82 and 17.95 °C, respectively; Fig 4B; $F_{1,\ 125811} = 45.79$, $P < 0.0001$).

Peak internal cone temperatures were generally higher for bagged than unbagged cones (Table 2). Average peak temperature was significantly higher inside bags (43.14 °C) than outside (41.62 °C; t= 2.44, two-tailed P= 0.0245). Accumulated degree-days over 35 °C were significantly higher inside bags than outside (Fig 5A; $F_{1,\ 9}= 11.19$, P= 0.00860), and degree-days above 40 °C occurred almost exclusively in bagged cones (Fig. 5B; $F_{1,\ 9}= 4.82$, P= 0.0557).

It seems clear that the mesh bags did not cool cones as hypothesized, rather they increased cone temperature, especially during daytime. It is unlikely that heating the cones beyond the already hot Okanagan summers would somehow protect seeds, preventing the loss of seedset inside bags. Thus we infer that temperature is not the reason that mesh bags prevent seed loss.

Relative humidity: The iButtons were active for 10 days in late May and early June before they ceased collecting data. They were restarted on July 22, and they worked through August. In early season, there was no significant difference between RHs inside and outside bags, at 37.2% and 37.0%, respectively (Fig. 6; $F_{1,\ 86.9} = 0.2591$, P= 0.612). The later-season measurements, taken from July 22 to August 28, were from the seed-loss period of interest. During this time, the RH was significantly higher inside (53.0%) than outside (51.4%) bags (Fig. 6; $F_{1,\ 151} = 168.39$, $P< 0.0001$).

The late-season differences in RH were largely driven by high-RH (rainy) days. Days on which the bagged RH exceeded 60% (n=13) had a mean increase of 3.27% RH inside the bags, while days on which bagged RH was 59% or less had a mean increase of only 0.98% inside the bags. This could be because the bags retain moisture on foliage and cones longer after a rain event, leading to a longer period of elevated RH than unbagged cones. If moisture stress was a limiting factor to seed development, then these humid days would be unimportant in seed loss; only the low-RH days would be important. But the difference in RH between bagged and unbagged cones during dry spells is less than 1%. It is difficult to envision this small difference being biologically relevant to seed health.

The biological relevance of increased humidity is particularly drawn into question when one considers that the variation in RH between trees is greater than the variation between bagged and unbagged clusters within a tree for any given date. Humidity inside bags is lower on some trees than humidity outside bags on other trees; this occurs for every single date after July 22. Even so, bagging increased seedset in every instance (see seed data below). If an increase of 1% RH were responsible for an increase in seedset, then we would have seen higher seedset in cone clusters with higher RH, regardless of bagging status. This was not the case. Therefore, we infer that relative humidity is not the reason that mesh bags prevent seed loss.

Leptoglossus occidentalis feeding: Over the course of the summer, 185,550 images were taken (e.g., Fig. 7). Feeding of adults and nymphs varied through the season (Fig. 8). Some cameras failed to function on some days, so feeding for each week is a mean of cameras operating during that week, expressed as minutes of feeding per camera-day. From Fig. 8, it is apparent that overwintered adults invaded the orchards through late May and June, and fed on developing cones. They oviposited for an extended period; their nymphs started to feed in late June. Feeding by overwintered adults declined as they died off by early July. Nymph feeding increased to a peak in late July. As nymphs matured, they emerged to the second-generation of adults, which started to feed in mid-July. Nymph and second-generation adult feeding declined through August, as nymphs matured to adults, and as adults left the orchard for overwinter sites. The bulk of feeding occurred during the time of interest, mid-July through August.

Cumulative *L. occidentalis* feeding was divided into early season and late season based on Fig. 8. The last feeding of overwintered adults occurred around June 30; this was also about the time

Table 2

Peak internal cone temperatures achieved (°C). Mean peak temperatures of bagged and unbagged cones were significantly different (T= 2.44, two-tailed P= 0.0245).

	Bagged		**Unbagged**	
Tree	**T1**	**T2**	**T3**	**T4**
ER 1	39.6	39.3	38.7	41.2
ER 2	39.4	41.8	38.7	42.2
ER 3	42.9	42.8	43.5	39.4
ER 4	46.9	43.7	39.2	46.8
ER 5	39.6	40.8	40.2	42
Kal 1	45.4	42.8	42.6	40
Kal 2	41	43.3	40.3	42
Kal 3	43.9	51.9	45.4	42.4
Kal 4	41.9	47	43.4	42.5
Kal 5	43.2	45.5	39.6	42.3
MEANS	43.14		41.62*	

nymphs began to feed. Early season was thus defined as May 15–June 30, late season as July 1–September 1. No feeding was detected after September 1.

In early season, mean daily feeding on each cone ranged from 0.00 to 11.53 minutes for adults, and 0.00 to 1.11 minutes for nymphs (Fig 9A). In late season, mean daily feeding on each cone ranged from 0.06 to 16.53 minutes for adults, and 1.49 to 52.97 minutes for nymphs (Fig 9B). Cumulatively, feeding on each cone ranged up to 7.33 hours in early season, and 27.28 hours in late season. *Leptoglossus occidentalis* are known seed feeders; their presence for so many hours on each cone cluster strongly indicates they are reducing the number of seeds inside those cones. Access to cones is prevented by the insect-exclusion bags, thus preventing *L. occidentalis* from reducing the seedset in cones enclosed by the bags.

Trees varied dramatically in the extent of feeding they suffered (Fig. 9). In early season, two trees (ER 05 and Kal 04) were completely avoided by *L. occidentalis*, while cones from only five trees were fed upon for more than 2 minutes/cone/day. Similar, though less dramatic, differences

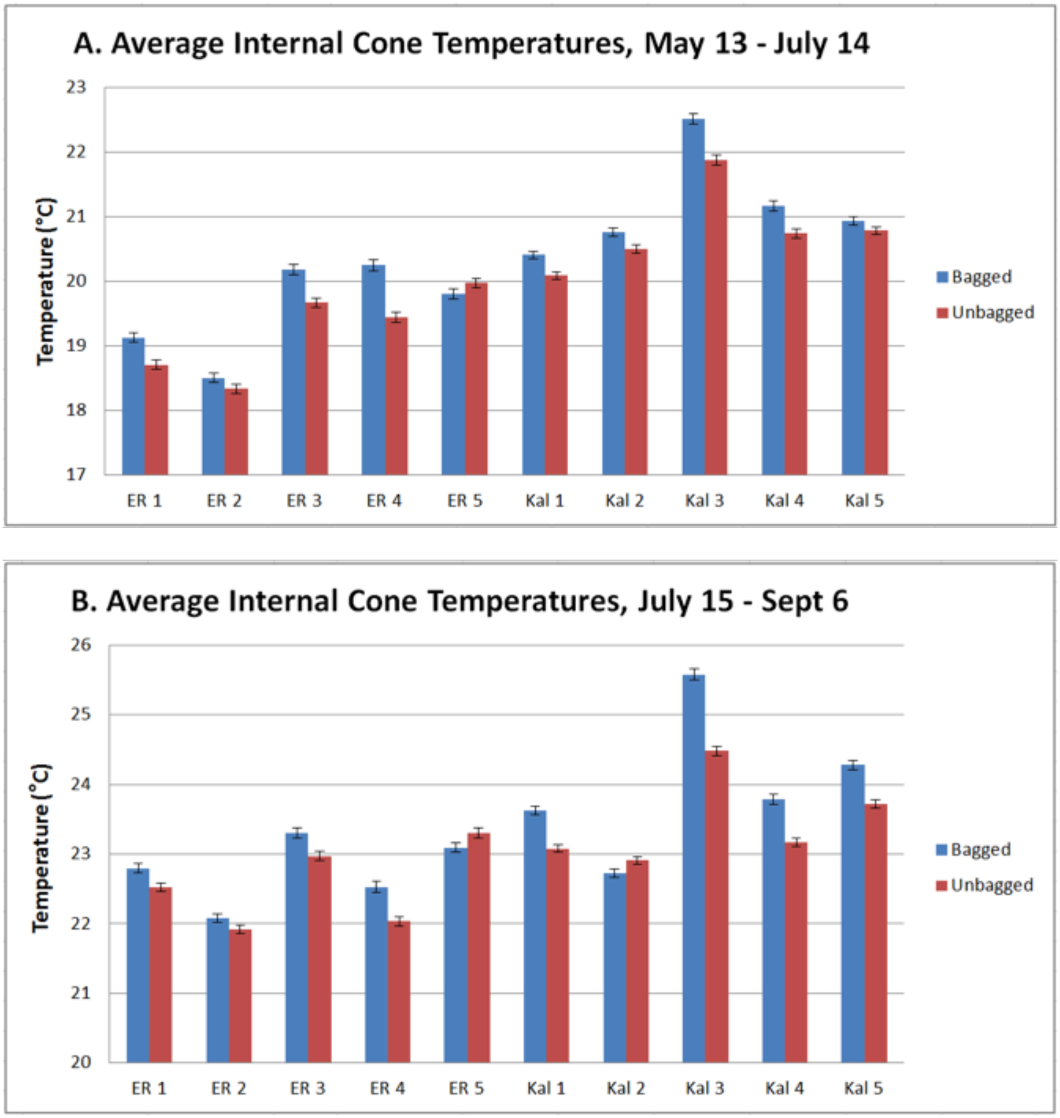

Figure 4. Mean internal cone temperatures (±SE) of bagged and unbagged cones in each of the 10 experimental trees. ER, Eagle Rock seed orchard 339. Kal, Kalamalka Seed Orchard 307.

exist for late-season feeding. These differences could be due to random variation or to preference for or avoidance of specific tree genotypes. The patterns found in this trial are consistent with the clonal preference findings of Blatt and Borden (1996, 1999) and Richardson (2013). Interestingly, the preferred or avoided genotypes changed from early season to late season, with the exception of ER 05, which was avoided in both time periods. It is possible that the host finding cues used by *L. occidentalis* change over time or that overwintered *L. occidentalis* use different foraging cues than second-generation *L. occidentalis*.

These foraging patterns also suggest that overwintered *L. occidentalis* prefer to feed on certain genotypes, while ovipositing on other genotypes. This is because nymphs are less mobile than adults: they are stuck on the trees their parents chose for oviposition. Nymphs were found on a different set of trees than 1st generation adults, so the adults must have oviposited on trees other than those they preferred for feeding. This in turn suggests there may be differences in foraging

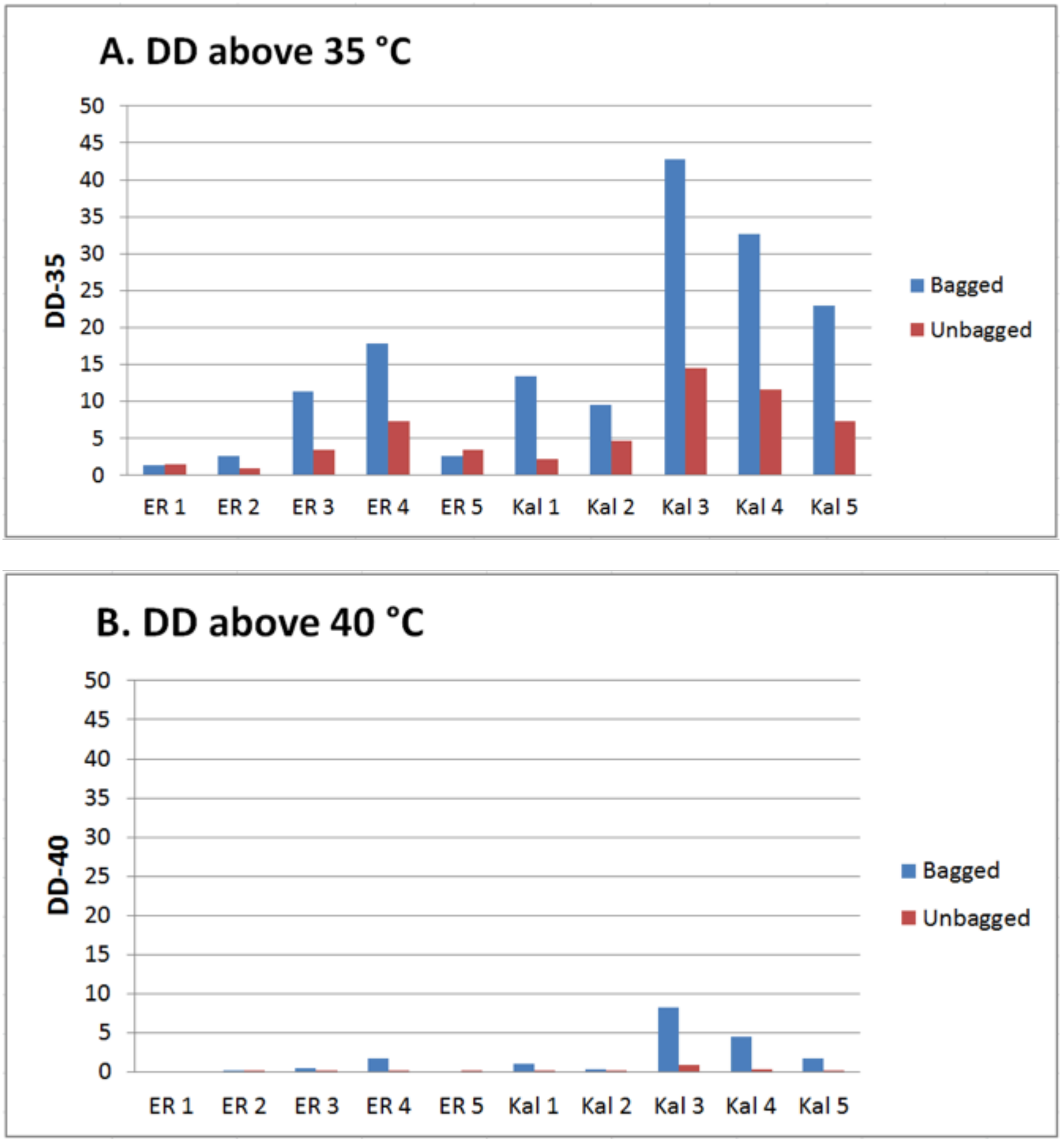

Figure 5. Degree-day sums of internal cone temperatures above a temperature threshold of 35 °C (A) or 40 °C (B).

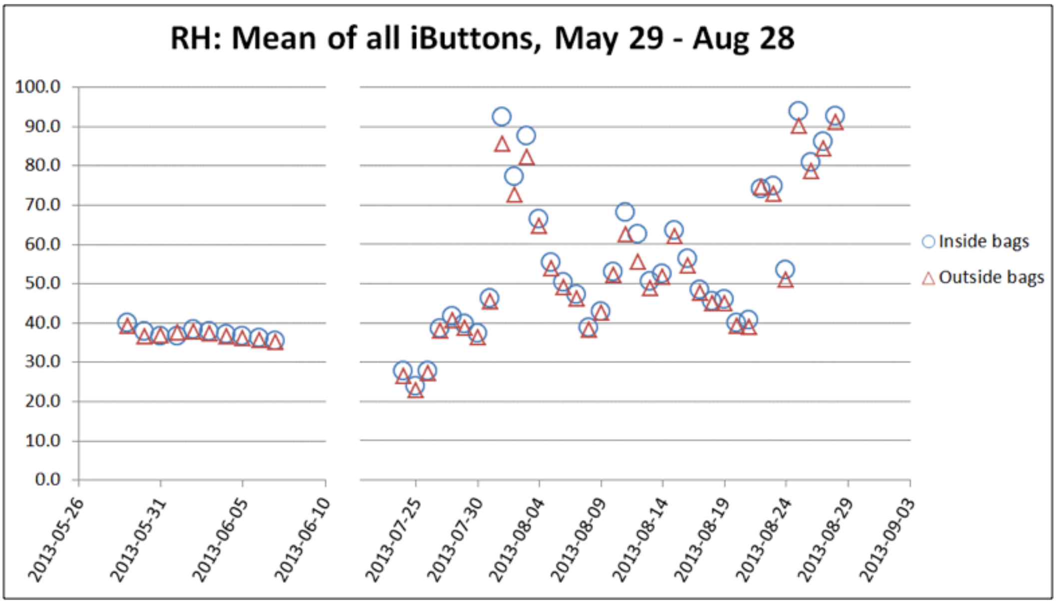

Figure 6. Daily relative humidity of cones inside and outside bags, averaged across all trees for each date.

cues used for feeding and oviposition. Different preferred hosts for adults and nymphs may be an adaptive behaviour, preventing depletion of nymph resources by adults.

Seed extractions. There was a mean of 11.8 filled seeds per cone inside the mesh bags, significantly (P= 0.0017) more than the 2.8 filled seeds per cone found in unbagged cones (Fig. 10). Percent filled seed declined from 58.6% for bagged cones to 20.8% for unbagged (P=0.0013); total seeds per cone declined from 20.3 in bagged to 13.0 in unbagged cones (P=0.018). Preventing *L. occidentalis* access to cones within mesh bags thus appears to have prevented loss of seedset in the enclosed cones.

Figure 7. One image from a time-lapse camera, with a *L. occidentalis* visible on the centre cone.

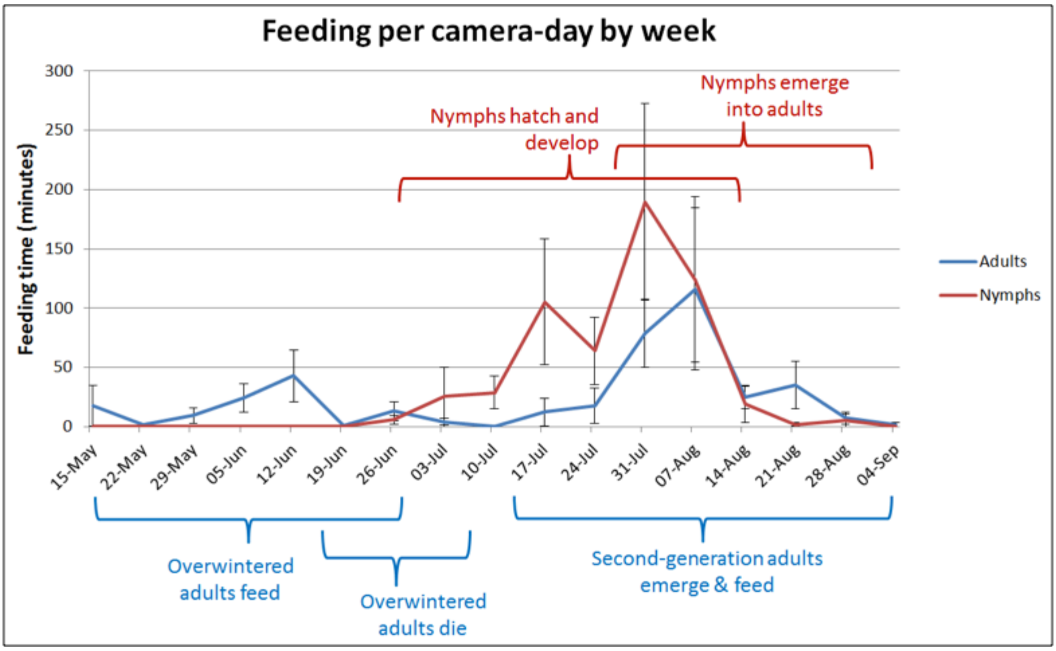

Figure 8. Minutes ± SE of *L. occidentalis* feeding per camera-day for each week of the summer. Dates are mid-point of each calendar week. Insect phenology is demarcated for overwintered adults, nymphs, and second-generation adults. Standard errors reflect variation between trees in cumulative feeding during each week.

If feeding by *L. occidentalis* was responsible for the observed seed loss, then cones which experienced more hours of feeding should have sustained more seed loss. Seed loss was positively correlated to hours spent feeding on each cone cluster (Fig. 11). Regression analyses that were not forced through the origin all had intercepts not significantly different from zero, indicating that the main source of seed loss is *L. occidentalis* feeding. Because of this, and because theoretically there should be no seed loss without *L. occidentalis* feeding, all regressions were subsequently forced through the origin.

During July and August, the relationship between feeding and seed loss was strong (r^2=0.6774, P= 0.0035; Fig 11A). An even closer relationship exists when feeding from May through August is considered (r^2 = 0.8414, P< 0.0001; Fig 11B). These data suggest that *L. occidentalis* causes seed loss not only in late season, but in early season as well. This supports other research that has also found that *L. occidentalis* reduces filled seeds per cone by early-season feeding (Bates *et al.* 2002b; Strong 2006).

Percent filled seeds lost were strongly correlated with amount of feeding by *L. occidentalis* (r^2=0.9306, P< 0.0001; Fig. 11C). Total seeds are included in the calculation for percent filled seeds, and total seeds are affected by early-season feeding (see below). Thus the season-long measurement for percent filled seeds is most relevant.

Total seeds lost was strongly related to amount of feeding in early season (r^2=0.7389, P=0.0014; Fig 11D). Early-season feeding has been shown to reduce total seeds per cone, since seeds fed upon prior to July 1 fuse to the cone scales and are not extracted (Bates *et al.* 2000). This trial confirms that early-season feeding reduces total seeds per cone.

CONCLUSION

This experiment conclusively proves that neither temperature nor relative humidity are the reason that enclosing second-year lodgepole pine cones in mesh bags increases seedset. Rather, the increased seedset is due in large part to protection from feeding by *L. occidentalis*. There may be other minor factors associated with the mesh bags, such as direct insolation on the cones, reduced evaporative water loss from cones or nearby needles, or a combination of local factors that protect against whole-tree stress. However, the physiological mechanisms underlying any of these theories are unclear, and there is no evidence to even build a testable hypothesis based on these mechanisms. However, there is abundant and conclusive evidence that the increase in seed set created by enclosing cones in mesh bags is caused by *L. occidentalis* exclusion.

Leptoglossus occidentalis are not, however, the only cause of seed loss: they are the cause of the losses that are prevented by installing mesh bags. Even in the mesh bags, seed set at the site of this research is typically only 10–15 filled seeds per cone, with many empty seeds. This is much lower than the theoretical maximum of around 35 filled seeds per cone (Owens 2006), and lower than the seed set routinely found in cooler areas of BC, such as Prince George (which also has very few *L. occidentalis*). The poor seed set encountered even when *L. occidentalis* are excluded must be caused by other factors. Factors that have been or are being investigated include self-pollination, lack of pollen, pollination droplet problems, temperature and moisture relationships,

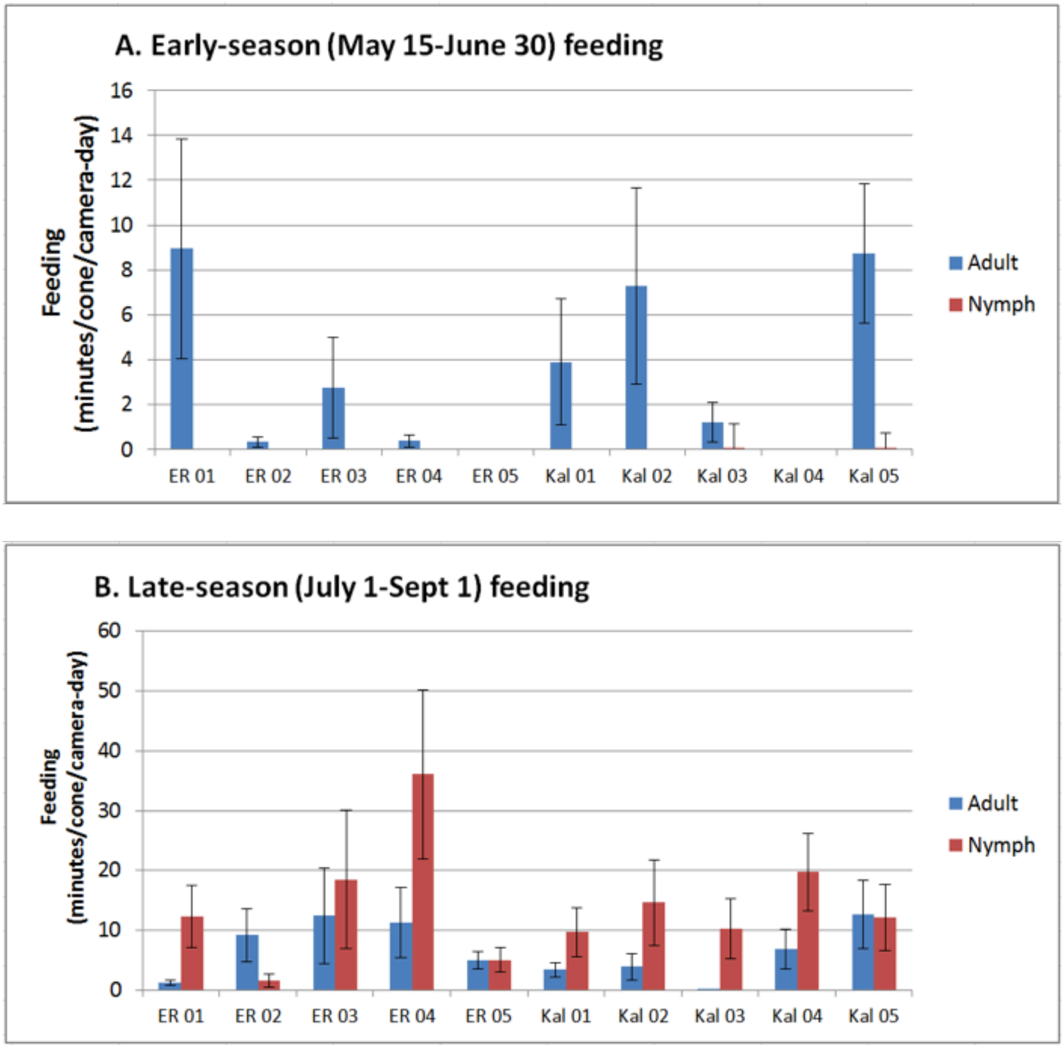

Figure 9. Mean feeding per cone per camera-day (±SE); early (A) and late (B) season for an exposed cluster on each of 10 trees. Standard errors reflect variation in daily feeding for each cone cluster; standard errors are large because no feeding occurred on most days for any given cone cluster.

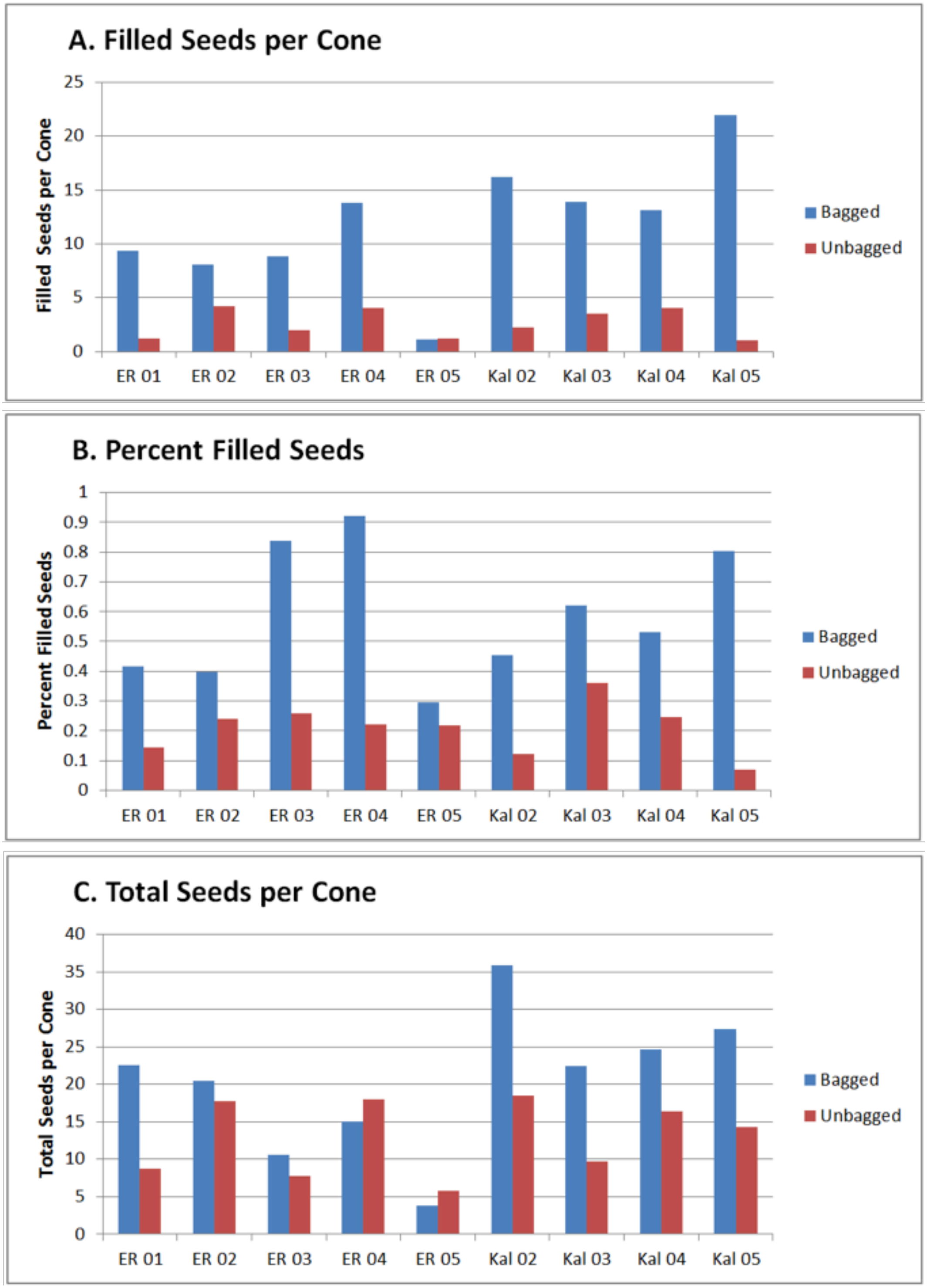

Figure 10. Seed extraction results for bagged and unbagged cones on each of 9 trees. A, mean Filled Seeds per Cone (P= 0.0017); B, mean Percent Filled Seeds (P= 0.0013); C, mean Total Seeds per Cone (P= 0.0180); all tests were 2-tailed paired T-tests.

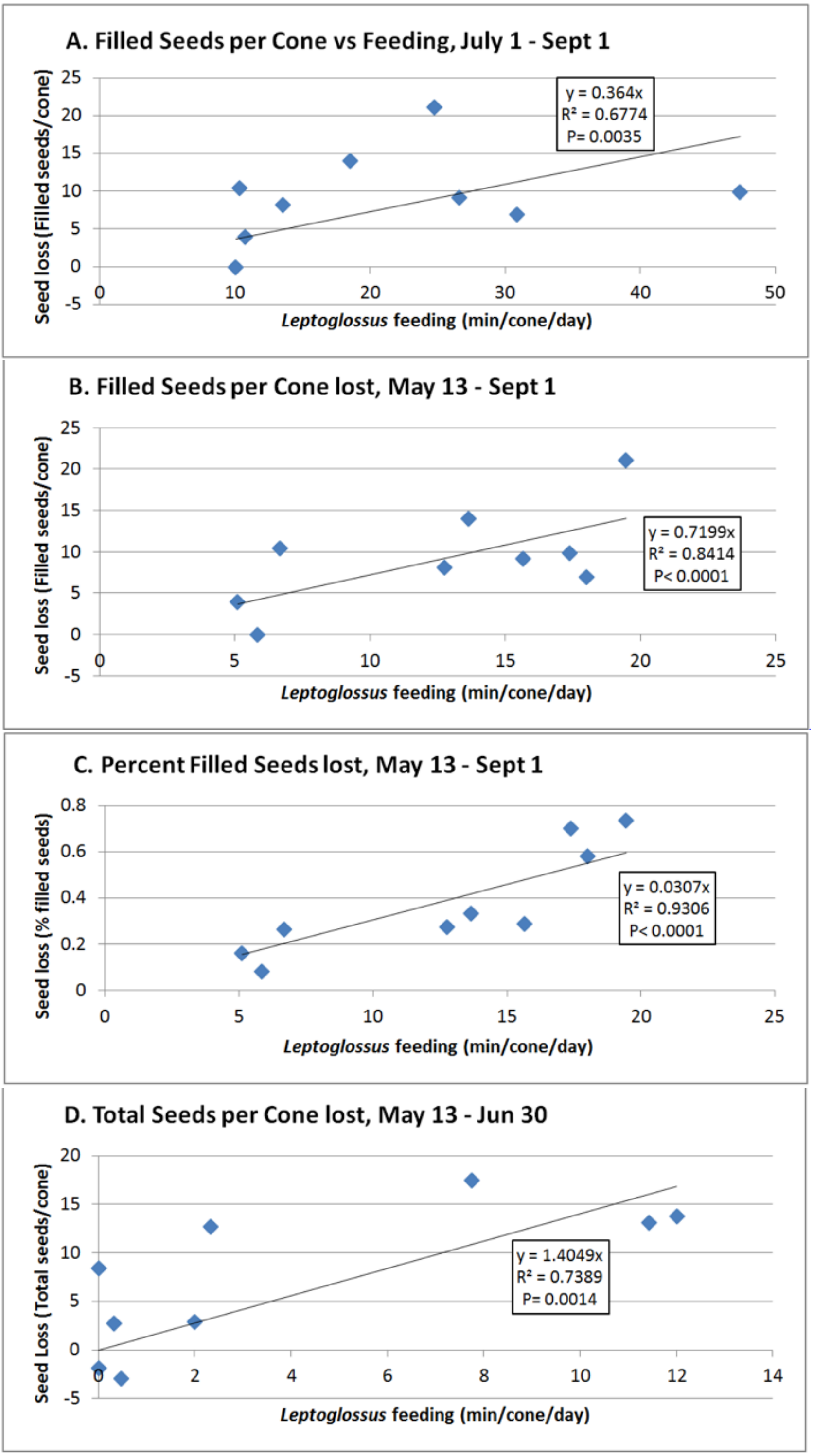

Figure 11. Seeds lost versus daily mean minutes of *L. occidentalis* feeding on each cone cluster. Feeding is combined feeding by adults and nymphs. Seed loss is calculated by subtracting seed values in unbagged cones from seed values in bagged cones.

other orchard culture factors, and seed fungal infections (Webber 2014; von Aderkas 2014). Despite years of research, however, the non-*L. occidentalis* causes of poor seed yield remain unknown.

Finally, despite using chemical control measures against *L. occidentalis*, lodgepole pine seed orchards in BC do still suffer from *L. occidentalis*-related seed loss (WBS, unpublished bagging trials in commercial seed orchards). Continuing research must identify how to manage *L. occidentalis* in order to prevent seed loss. Despite many years of research, we still have no efficient means of monitoring for *L. occidentalis*, no traps, no novel control tactics, and no registered pesticide. The insecticide Sevin XLR® (carbaryl) is registered against mountain pine beetles and pine sawflies, with poorly studied effects on *L. occidentalis*. A new pesticide (Matador®, lambda-cyhalothrin) is currently undergoing registration for *L. occidentalis* control, under the User-Requested Minor-Use Label program of the Pest Management Regulatory Agency (Caroline Bedard[4], personal communication). This and a related pesticide are the main products used to control *L. occidentalis* in the USA; therefore, it may help manage seed loss due to *L. occidentalis* in Canada.

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