AN INVESTIGATION OF THE CONE AND SEED INSECTS OF WHITEBARK PINE AND ALPINE LARCH EMPHASIZING THE WESTERN CONIFER SEED BUG (HEMIPTERA: COREIDAE) AND THE LARCH CONE FLY (DIPTERA: ANTHOMYIIDAE)

by

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ABSTRACT

An Investigation of the Cone and Seed Insects of Whitebark Pine and Alpine Larch Emphasizing the Western Conifer Seed Bug (Hemiptera: Coreidae) and the Larch Cone Fly (Diptera: Anthomyiidae)

by

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Utah State University, 2000

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Laboratory and field feeding tests with *Leptoglossus occidentalis* Heidemann proved that both immature and mature seed bugs can use cones and foliage of whitebark pine, *Pinus albicaulis* Engelmann, as a food source for 1- to 2-week periods. Damage to unprotected whitebark pine cones by seed bugs ranged from 0.3 to 2.1% of seeds per cone, and for bagged cones averaged 0.7% of seeds per cone. Total insect damage ranged from 0.4 to 7.2% of seeds per cone. A seed chalcid, *Megastigmus* sp., was documented for the first time on whitebark pine and damaged 4.7% of examined seeds at one site. Four out of five upper elevation subsites had an average of 24.9% fewer filled seeds per cone than lower elevation subsites. Within-site elevation differences had no significant effect on cone length, number of seeds per cone,
percentage of potential seeds per cone, or percentages of seed bug and insect-damaged seeds per cone.

The larch cone fly *Strobilomyia macalpinei* Michelsen was found in cones of alpine larch, *Larix lyallii* Parl., in the Bitterroot Range of Montana. This is the first record of this species in the United States and the first since its description in 1988. Ninety-four percent of a sample of alpine larch cones were damaged by cone fly larvae, and 64% contained larvae or puparia. Colored traps did not succeed in trapping adult cone flies in an alpine larch stand with no cone crop.
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CHAPTER I
INTRODUCTION

There are approximately 400 species of conifer seed and cone insects worldwide which are found in the orders Coleoptera, Diptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, and Thysanoptera (Turgeon et al. 1994). Insects are important seed predators and can cause seed losses in almost all species of North American conifers (Hedlin et al. 1980) and in some years and localities they are capable of destroying virtually all the seeds of a given species (Furniss and Carolin 1977). Traditionally, foresters have considered cone and seed insects to be less serious pests than those that directly inhibit conifer growth such as defoliators and cambial miners (Michelsen 1988). However, with the advent of intensified artificial reforestation and breeding programs to improve tree quality, plantations and seed orchards have arisen for which knowledge of cone and seed insects is valuable (Amirault and Brown 1986; Michelsen 1988; Turgeon 1989). Consequently, most of the published work on cone and seed insects is concerned primarily with the economically important tree species of the genera Abies, Picea, Pinus, or Pseudotsuga (Hedlin et al. 1980; Amirault and Brown 1986), and more recently of Larix (Turgeon et al. 1994).

Two high-elevation conifers for which cone and seed insects have received little attention are whitebark pine, Pinus albicaulis Engelm., and alpine larch, Larix lyallii Parl. Although these trees are not significant economically and are logistically
inconvenient to study, their cone and seed insects are still of interest and may play integral roles in high-altitude tree ecology. Cone and seed insect damage can be severe in the lower-elevation seed orchards where most studies of these insects have been done, but they have also been shown to considerably limit tree reproduction near timberline as well. A survey of cone insects of Swiss stone pine, *Pinus cembra* L., a European pine related to whitebark pine, found overall cone crop damage of up to 40% (Dormont and Roques 1999). Similarly, Jenkins and Roques (1997) found cone damage of between 46 and 74% in high elevation European larch, *Larix decidua* Miller, a species similar to alpine larch. If cone and seed insects were routinely capable of similar damage in whitebark pine, they could seriously impact not only the survival of a tree already threatened by white pine blister rust, *Cronartium ribicola* Fisher, and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Scolytidae), but also that of wildlife such as the Clark's nutcracker, *Nucifraga columbiana* Wilson, that depends so heavily on the tree's nutritious seeds. Although alpine larch is not as threatened and is not known to be as vital to its ecosystem as whitebark pine, documentation of its cone insects, particularly of the larch cone fly (*Strobilomyia* sp.) (Diptera: Anthomyiidae), could expand our knowledge of little-known species and possibly result in the discovery of new ones.

The same environmental factors that make life challenging for conifers at high altitudes can also be problematic for insects. Cold temperatures, high winds, a short growing season, abundant snow, and high rates of evaporation, insolation, and radiation are all conditions commonly found at higher elevations that can affect the
vigor and reproduction of trees and insects. Investigating how cone and seed insect incidence and damage may differ from low to high elevations may lead to the discovery of previously unknown adaptive strategies for a given insect species, such as prolonged diapause or the production of antifreeze compounds to better enable overwintering in severe conditions. The interplay of insect populations with cone crop size should also be instructive at high altitudes where cone crops are likely to be less regular and trees have relatively more to lose from a failed crop than at lower elevations.

Increased knowledge of the cone and seed insects of whitebark pine and alpine larch may therefore prove helpful to the trees themselves and to the field of high-altitude tree-insect interaction ecology.
CHAPTER II
LITERATURE REVIEW

Whitebark Pine Ecology

Taxonomy and Distribution. Whitebark pine is grouped with the white or soft pines in the subgenus *Strobus*, section *Strobus*, and it is one of the five stone pines of subsection *Cembrae* Loud. (Little and Critchfield 1969). The other four are the Swiss stone pine, *P. cembra* L., found in Europe, the Siberian stone pine, *P. sibirica* Du Tour, of Siberia and Mongolia, and two far eastern species, the Japanese stone pine, *P. pumila* Regel, and the Korean stone pine, *P. koraiensis* Sieb. and Zucc. All stone pines have five-needled fascicles, wingless seeds, and cones that remain totally or partially closed even once seeds have matured (Lanner 1990).

The distribution of whitebark pine in North America is roughly divided into two populations (Critchfield and Little 1966). The western population starts in southern British Columbia along the lower Fraser River and extends south through the Cascades of Washington and Oregon, skips discontinuously through northern California but then becomes prevalent in the Sierra Nevada. The eastern population begins in the Rocky Mountains of British Columbia and Alberta and continues south through the higher mountains of western Montana and central Idaho and into the Yellowstone region and Wind River Mountains of Wyoming. Some isolated stands also occur between the two major distributions (McCaughey and Schmidt 1990). Typical elevations for whitebark pine are lower in the northern latitudes (1980 to 2290 m in the Canadian Rockies) and
the more maritime areas (1170 to 2130 m on the west slope of the Cascades) than in
the southern or continental parts of its range (2440 to 3200 m in Wyoming and 3050 to
3510 m in the Sierra Nevada) (Arno and Hoff 1989).

Reproductive Life History and Relationships with Wildlife. Whitebark pine
is a monoecious tree with a flowering cycle that encompasses three consecutive
growing seasons (Weaver and Forcella 1986). Reproductive and vegetative buds are
initiated late in the summer of the first year and pollination occurs from June to
mid-July of the second year, depending on elevation (Arno and Hoff 1989). Ovulate
cones occur in groups of two to five near the tips of branches in the upper crown.
They grow to mature size (about 4 to 9 cm) by August of the third summer when they
turn a deep purplish-brown color (McCaughey and Schmidt 1990). Seeds numbering
about 75 per cone make up between 30 and 50% of cone mass and continue to mature
through September and into October (Weaver and Forcella 1986).

Large cone crops are produced every 3 to 5 years (Krugman and Jenkinson
1974) with years of sparse to no crop in between (Arno and Hoff 1989). Weaver and
Forcella (1986) found that high cone crop years were most often preceded by poor
crop years in a study of 29 stands of whitebark pine in Montana. They hypothesized
that poor crop years are due to weather rather than factors within the tree, but were
unable to correlate weather conditions with cone crop production in a way that would
allow straightforward prediction of future cone crops.

Dissemination of whitebark pine seed is intimately tied to foraging by the
Clark’s nutcracker, *Nucifraga columbiana*, which is dependent on these seeds for most
of the year. Its coevolution with this tree has led to a remarkable and intricate interdependence (Hutchins and Lanner 1982). The nutcracker begins harvesting seeds in August even before cones are mature and continues well into October. Its caching behavior makes the nutcracker the most efficient and dependable agent for both the dispersal and establishment of whitebark pine (Hutchins 1990). It is possible that nutcracker behavior can be influenced indirectly by cone insects, since the bird can discriminate between good versus aborted or insect-infested seeds by shaking each one in its bill before taking it into its pouch (Tomback 1978). Christensen et al. (1991) have shown that nutcrackers foraging on pinyon pine, *P. edulis* Engelm., prefer longer cones with more seeds as well as cones with a greater proportion of viable seeds, and these characteristics can be affected by cone insect infestation (Hedlin et al. 1980). Nutcrackers also harvest a greater number and a greater percentage of seeds from trees with the most available cones. As Christensen and Whitham (1991) demonstrated, stem- and cone-boring insects such as *Dioryctria albovittella* (Hulst) (Lepidoptera: Pyralidae) can significantly reduce cone abundance and thereby restrict nutcracker visits to those trees and stands with the heaviest infestations.

The red squirrel, *Tamiasciurus hudsonicus*, is another important whitebark pine seed harvester, although its midden-building activities are probably more important to the black bear, *Ursus americanos*, and the grizzly bear, *U. arctos horribilis*, than they are to the pine, since squirrels usually bury seeds too deep for successful germination and establishment (Hutchins and Lanner 1982). The bears can obtain cones by scavenging or by directly removing them from small trees, but more often they simply
raid squirrel caches. In fact, Mattson and Reinhart (1994) hypothesized that bear use of pine seeds is more closely related to squirrel density in a given area than to the abundance of whitebark pine. The availability of the lipid-rich seeds may affect the fecundity of female bears as well as the survivorship of young males and adult females due to increased interaction between bears and humans in poor cone years (Mattson and Reinhart 1994). Whitebark pine cones and seeds thus have far-reaching influences on many species.

**Cone and Seed Insects of Whitebark Pine and their Occurrence in Other Pines.** The pines of North America are subject to attack by many different cone and seed insects, and since insects of the same genus tend to colonize the cones of congeneric trees (Turgeon et al. 1994), it is not surprising that some of the insects found on whitebark pine are also found on other pines that are similar evolutionarily or ecologically.

Kegley et al. (in prep.) found the seed bug (*Leptoglossus occidentalis* Heidemann) (Hemiptera: Coreidae) to be a significant seed predator on whitebark pine. It damaged up to 17% of the seeds collected, and damage was more frequent at the higher elevation sites, possibly due to less competition from other insects or superior adaptation to altitude. Western white pine, *P. monticola* Doug., another five-needled pine in section *Strobus*, can also host the seed bug, which can feed on both first-year conelets and on maturing second-year cones (Hedlin et al. 1980). Connelly and Schowalter (1991) reported a reduction in filled seed of 70 - 80% caused by *L. occidentalis* in an Oregon western white pine seed orchard, along with a 40% abortion
rate of second-year cones. Reports of seed bug impacts on other hosts include a 41% damage rate on initial ovules in ponderosa pine, *P. ponderosa* Dougl. ex Laws. (Pasek and Dix 1988), and a seed abortion rate in Douglas-fir, *Pseudotsuga menziesii* Mirb., of more than 50% over controls (Schowalter and Sexton 1990).

*L. occidentalis* mates in the spring, oviposits from late May to early July, and goes through five instars before reaching maturity in August (Koerber 1963). The adult overwinters in protected sites and emerges in mid-May. It feeds by inserting the stylets of its proboscis through the cone scales until they reach the seed or developing ovule. The seed's endosperm then shrinks and becomes spongy but the only external evidence of feeding is a minute puncture hole in the cone (Koerber 1963). Although originally described as a western species, the adaptable *L. occidentalis* appears to be actively expanding its range eastward, finding new host trees as it goes. It has now been found as far east as New York (Gall 1992).

Another insect that caused appreciable damage in the study by Kegley *et al.* (in prep.) was the cone worm [*Dioryctria abietivorella* (Grote)] (Lepidoptera: Pyralidae), which infested up to 39% of collected cones and destroyed up to 5% of extracted seed. The three lowest elevation sites received the most damage. *D. abietivorella* is a transcontinental species with a large number of potential hosts and an imperfectly known life history (Hedlin *et al.* 1980). Larvae mine inside the cones and can feed on shoots and buds as well. This insect is also found in western white pine as well as limber pine, *P. flexilis* James, another five-needled pine with corvid-dispersed seeds in section *Strobus*. Haverty and Shea (1986) found that *D. abietivorella* attacked nearly
half (46%) of the cones of western white pines not treated with insecticide and reduced seed yield by 44%.

Another species of cone worm, *D. albovittella* (Hulst), is commonly found in singleleaf pinyon, *P. monophylla* Torrey and Fremont (Jenkins 1984b), and Colorado pinyon (Whitham and Mopper 1985; Christensen and Whitham 1991). Like whitebark pine, both of these pinyons have large wingless seeds that are corvid-dispersed. Not only does the cone worm have the potential to affect cone production directly by increasing cone mortality (an average of 57%, Christensen and Whitham 1991), but it can also indirectly curtail seed dispersal due to its preference for feeding in and destroying terminal cone-producing shoots. If this occurs repeatedly it stimulates the growth of lateral buds and results in a tree with a bushy growth form that is functionally male because of its loss of female cone-bearing ability (Whitham and Mopper 1985). Even if it manages to produce a few cones, such a tree will likely not be visited by seed-dispersing birds, which prefer trees with many cones (Christensen and Whitham 1991). A twig-boring *Dioryctria* sp. was mentioned by Kegley *et al.* (in prep.) but its impact was not quantified.

A third cone insect of whitebark pine is the cone beetle, *Conophthorus ponderosae* Hopkins (Coleoptera: Scolytidae). Kegley *et al.* (in prep.) found it in only one of their study sites where it caused minimal damage, but they noted its presence on cones in several other locations. The cone beetle has the potential to destroy many seeds since the female severs the conducting tissues at the bases of second-year cones and kills the whole cone even if no young are produced (Hedlin *et al.* 1980). Larvae
feed inside the cones and can overwinter there or in shoots or conelets. *C. ponderosae* also infests the cones of western white pine, limber pine, and lodgepole pine, *P. contorta* Dougl., although it is relatively rare in the latter (Furniss 1997). Several studies of cone beetles have revealed that beetle populations are intimately regulated by cone crop size and variability. Jenkins (1984a) monitored cone crops for five consecutive years in a western white pine seed orchard in Idaho and found that a high cone beetle population was able to attack 90% of the cones in a very low cone crop year. However, the paucity of food then reduced the beetle population such that it was able to attack less than one percent of the bumper cone crop the following year. Forcella (1980) noted a similar dynamic with *C. edulis* Hopkins on Colorado pinyon pine, and suggested that stands with the most consistent annual cone production will be subject to greater cone losses to beetles. Little variation in the food source allows the beetles to maintain higher average populations than would be possible with fluctuating cone crops. A similar phenomenon may occur in whitebark pine but has so far been undocumented.

Other cone insects of whitebark pine have been noted but no details are available. Kegley *et al.* (in prep.) found an incidence of adelgid (*Pineus* sp.) (Homoptera: Phylloxeridae) of up to 16% but did not specify damage. They also found damage by a seedworm, *Cydia* sp. (Lepidoptera: Olethreutidae), of less than 1%. Hoff and McDonald (1977) showed that whitebark pine seedlings in a greenhouse were more susceptible to the woolly aphid, *P. coloradensis* Gillette, than the other stone pines. Bartos and Gibson (1990) list cone worms (*Eucosma* sp.) (Lepidoptera:...
Olethreutidae), and seed chalcids (*Megastigmus* sp.) (Hymenoptera: Torymidae), among whitebark pine cone insects but give no further information. All of these insects are probably of minor importance to whitebark pine seed production.

**Other Insects and Diseases.** Whitebark pine cone production can suffer indirectly from many factors other than cone insects. Another type of insect that is the most damaging overall in whitebark pine stands is the mountain pine beetle, which can feed on and kill mature trees (Bartos and Gibson 1990). It prefers larger diameter trees with thicker phloem, which are more prevalent since the advent of fire suppression (Arno 1986). Extensive mortality of whitebark pine in the Northern Rockies between 1910 and 1940 and in the Flathead National Forest of northwestern Montana in the 1970's is attributed to pine beetle epidemics that began in adjacent lodgepole pine stands and then spread upwards into the whitebark pine (Arno 1986). However, the beetle can cause mortality in whitebark pine even where lodgepole pine is absent (Bartos and Gibson 1990). Although under endemic conditions the beetle tends to infest the same tree species in which it completed larval development (Baker *et al.* 1971), it is evidently able to attack any available host during epidemic conditions (Amman 1982).

Other insects found on whitebark pine are far less damaging, including several secondary beetles of the genera *Ips*, *Pityogenes*, and *Pityophthusor* (Arno and Hoff 1989). There are also two species of mealybug [*Puto cupressi* (Coleman)] (Homoptera: Pseudococcidae) and *P. pricei* McKenzie that feed on trunks and branches, as well as the foliage-eating aphid (*Essigella gillettei* Hottes) (Homoptera:
Aphididae) and the lodgepole needletier (*Argyrotaenia tabulana* Freeman) (Lepidoptera: Tortricidae) (Furniss and Carolin 1977).

Because disease can increase tree susceptibility to insect attack as well as lessen cone production (Furniss and Carolin 1977), the diseases of whitebark pine are also worthy of note. A discussion of whitebark pine could hardly be complete without mention of white pine blister rust, a stem rust fungus specific to white pines which was introduced from Eurasia in 1910 and has been responsible for heavy losses of whitebark pine throughout the northern portion of its range (Hoff and Hagle 1990). Blister rust requires *Ribes* sp. as an alternate host, and it is especially prevalent in areas with sufficient moisture to allow infection of *Ribes* leaves in early summer and prevent their drying in late summer (Arno and Hoff 1989). One such area is the Selkirk Range in northern Idaho where blister rust killed more than 90% of the whitebark pine in the early 1980's (Kendall and Arno 1990). In this area as well as in the Mission Range and the Whitefish Range of Montana, observations in the 1960's or before revealed many squirrel caches and whitebark pine seeds in bear scats, but subsequent investigations in the 1980's showed little evidence of either squirrels or bears using whitebark pine seeds. However, whitebark pine still has a chance in drier and more southerly areas such as Yellowstone National Park, which have so far escaped major infection from blister rust (Hoff and Hagle 1990). Also, despite the extreme susceptibility of whitebark pine to blister rust when compared with other white pines (Bingham 1972), some individuals do exhibit genetic resistance and thus have the potential to be used in plantation and reforestation efforts (Arno and Hoff 1989).
Fortunately, the threats whitebark pine faces from endemic diseases are nowhere near as serious as that from white pine blister rust. Several varieties of stem and branch cankers, needlecasts and blights, stem and root decays, and dwarf mistletoes can be locally damaging in whitebark pine stands, but none are reported to reach epidemic status (Hoff and Hagle 1990).

**Cone Insects of Alpine Larch**

**The Larch Cone Fly (Strobilomyia spp.).** Studies of the cone and seed insects of *Larix* worldwide reveal cone flies of the genus *Strobilomyia* to be among the most damaging (Roques 1988; Turgeon 1989; Yao *et al.* 1991). There are 18 recognized species of cone flies, all of which have similar life cycles (Michelsen 1988). The adult emerges in early spring and the female lays her eggs on developing cones. There are three instars, the first of which remains in the egg. Four to 15 days after the eggs are laid, the second instar emerges and begins tunneling into the cone in a characteristic spiral around the cone axis, devouring seeds as it goes. The third instar begins after 6 to 15 days. It will spend 2 to 4 more weeks in the cone before dropping to the duff under the tree to form a puparium in the litter where it will overwinter in obligatory diapause. Some adults will emerge the following spring, but a portion will remain in diapause for an additional 1 to 3 years.

Although most species of *Strobilomyia* are found only on larch, several are found only on spruce or fir. These include the Palearctic *S. anthracina* (Czerny) and the Nearctic *S. neanthracina* Michelsen on spruce, and the Holarctic *S. carbonaria*. 
(Ringdahl) and the Nearctic S. abietis (Huckett) on fir (Michelsen 1988). One species, S. svenssoni Michelsen, was thought to occur only on spruce in Sweden until it was discovered on cones of Dahurian larch, L. gmelinii (Rupr.) Kuzen., in China (Roques et al. 1996). The larch-specific species tend to occur in complexes on hosts in the same area. In Europe, cones of European larch, L. decidua Mill., are colonized by S. melania (Ackland), S. laricicola (Karl), and S. infrequens (Ackland), and cone damage ranges from 30 to 75% (Roques 1988). In Siberia and China, nine species have been recorded on cones of Dahurian larch, Siberian larch, L. sibirica Ledeb., and other larch varieties and hybrids of the area. These species include S. laricicola, S. infrequens, S. svenssoni, S. baicalensis (Elberg), S. melaniola (Fan), S. luteoforceps (Fan and Fang), S. sibirica Michelsen, S. viaria (Huckett), and a new species S. lijiangensis (Roques and Sun) on Himalayan larch, L. potaninii Batalin var. mastersiana Law (Roques et al. 1996). In Northern China, the percentage of damaged larch cones can range from 50 to 90% (Yao et al. 1991). In North America, only one species, S. laricis Michelsen, has been definitively identified on western larch, L. occidentalis Nutt. (Miller and Ruth 1989). This species is also one of the most important cone flies on tamarack, L. laricina (Du Roi) K. Koch, and along with S. viaria can damage up to 90% of potential seed (McClure et al. 1996). S. macalpinei Michelsen is a species known only from the type material reared from seed cones of tamarack and alpine larch (Michelsen 1988), and it may be a high-altitude species of special interest to this study.

A technique that has contributed significantly to the knowledge of Strobilomyia species complexes and life histories is that of visual trapping. Roques (1986) found
that adults of *S. melanica* in the French Alps are attracted to horizontal yellow traps which symbolize nutritional stimuli and to vertical yellow traps with purple stripes which simulate the natural cone-foliage reflectance contrast. Jenkins and Roques (1993) found in addition that fluorescent yellow traps were more attractive to the cone flies than nonfluorescent traps and both kinds of traps caught significantly more males than females. Another study by Roques *et al.* (1995) on *Strobilomyia* spp. in northeastern China also included blue traps and found distinct species-specific and sex-specific responses to trap orientation and color. More flies alighted on blue traps hung in the tree canopy than on yellow traps placed in front of trees, and sexually immature female flies preferred blue traps.

**Cone and Seed Insects of *Larix* spp.** Because cone and seed insects of a given genus tend to colonize the cones of congeneric trees (Turgeon *et al.* 1994), it is reasonable to suppose that the insects of the North American larches, tamarack and western larch, are the most likely to be found on alpine larch. Western larch may be especially likely to share insect pests with alpine larch because although they are usually separated elevationally by 150 - 300 m (Arno and Habeck 1972), they grow together in certain locations in the Bitterroot Range of Montana and produce hybrids (Carlson and Theroux 1993). These species are also closely related phylogenetically as they both have exserted cone bracts, as opposed to tamarack, which is grouped with the larches with non-exserted bracts (LePage and Basinger 1992).

Western larch is tolerant to most insects and diseases in the northern Rocky Mountains, and the insects that cause occasional problems are mostly defoliators rather
than cone and seed insects (Carlson et al. 1992). One exception is the western spruce budworm (*Choristoneura occidentalis* Freeman) (Lepidoptera: Tortricidae), which can seriously deplete the cone and seed production of western larch (Fellin and Shearer 1968; Fellin and Dewey 1982; Carlson et al. 1992). Although the budworm can complete its life cycle on western larch, its survival and pupal weight are less than when it is able to feed on Douglas-fir, subalpine fir, or Engelmann spruce (Beckwith 1983).

Other insects that have been found in western larch cones but which cause minimal damage include the fir coneworm, *Dioryctria abietivorella*, the cone moth *Henricus fuscodorsana* (Kearfott) (Lepidoptera: Cochylidae) (Hedlin et al. 1980), a scale midge (*Resseliella* sp.) (Diptera: Cecidomyiidae), and a woolly aphid (*Adelges viridis* = *A. strobilobius* Ratzeburg) (Homoptera: Phylloxeridae) (Jenkins and Shearer 1989). Of the defoliators of western larch, the larch casebearer [*Coleophora laricella* (Hübner)] (Lepidoptera: Coleophoridae) is the most serious and can reduce growth by as much as 95% (Tunnock and Ryan 1985). However, since the casebearer is most successful below 1500 m (Carlson et al. 1992), it is unlikely to spread to stands of high elevation alpine larch (Arno and Habeck 1972). Another defoliator that has been found on all three North American larches is the larch sawfly [*Pristiphora erichsonii* (Hartig)] (Hymenoptera: Tenthredinidae), and although occasional outbreaks have been recorded for tamarack and western larch, none are on record for alpine larch (Drooz 1971).

Tamarack is a host for many of the same insects that are found on western larch, including the larch sawfly and the larch casebearer (Fowells 1965). A species of
Resseliella also affects tamarack cones (Amirault 1989), as does the spruce budworm, Choristoneura fumiferana (Clemens). In addition, tamarack provides host cones for a seed chalcid, Megastigmus laricis Marc. (Hedlin et al. 1980), and is a secondary host for an aphid, Adelges lariciatus (Patch), which has also been found on alpine larch (Cumming 1968). Prevost (1992) found several species of Lepidoptera mining tamarack cones, collectively causing considerable damage.

**Diseases of Alpine Larch.** Because insect attacks can predispose trees to certain diseases and vice versa (Furniss and Carolin 1977), the diseases of alpine larch are also worthy of note. Ziller (1969) found needle blight, Sarcotrochila alpina (Fuckel) Hoehn., and cast fungi, Lophodermium laricinaum Duby, to be the cause of severe browning of alpine larch in Manning Park in the British Columbia Cascades. Another needle blight, Meria laricis Vuill., was found on alpine larch in Alberta and British Columbia (Maruyama 1984). Arno and Habeck (1972) found Fomes officinalis [= Fomes laricis (Jack.) Murr.] conks on alpine larch trunks, as well as the canker of an unidentified fungus resembling the European larch canker, Dasyscypha willkommii (Hart.) Rehm, neither of which appeared to cause significant damage. Although it was believed until recently that larch dwarf mistletoe, Arceuthobium laricis (Piper) St. John, was a parasite on alpine larch as well as western larch, Mathiasen et al. (1995) showed that a previous report was mistaken and surmised that this mistletoe may be unable to successfully reproduce at the high elevations of alpine larch.

**Effects of Cone Crop Size on Cone Insect Populations.** Many studies of cone and seed insects discuss the correlation between the size and distribution of the
cone crop and the amount of insect damage observed. Findings from throughout the
distribution of *Larix* indicate that the number of larvae per cone and/or the percentage
of attacked cones goes down as the cone crop size or cone abundance per tree goes up
(Rauf and Benjamin 1983; Roques 1988; Yao *et al.* 1991; Turgeon *et al.* 1994; Koziol
1997). Some studies show that the percentage of cones attacked is not related to the
total number of cones per tree (Turgeon 1989; Prevost 1992; Gourov *et al.* 1997), but
these are either short term or use a small sample of trees. It is also common to find that
the distribution of damaged cones follows the distribution of the cone crop in general,
i.e., more damage will occur in those portions of the tree crown with the most cones.
In particular, the number of cones attacked was found in several cases to be highest on
the southern aspect of the middle crown, which corresponds to the most sun-exposed
and cone-laden part of the crown (Rauf and Benjamin 1983; Roques 1988; Turgeon
1989; Prevost 1992). However, Roques (1988) and Turgeon (1989) showed that the
position of a cone on a branch does not appear to affect its potential for insect damage.

If it is true that the most important factor regulating insect population
fluctuations is larval food availability (Turgeon *et al.* 1994), then certain phenomena of
larval abundance are more readily explained. Gourov *et al.* (1997) found a general
trend of cone insect attraction to dominant, border, and isolated trees of four different
species, and hypothesized that this could be due in part to the ability of these trees to
consistently produce a greater number of cones. Roques (1988) also noted that even in
years of low cone production, some cones are usually available on trees at stand edges.
Gourov *et al.* (1997) further speculated that edge trees can produce larger cones with
more seeds than interior trees, thus providing a reliable food source for larvae. However, Jenkins and Roques (1997) found that although the percentage of damage was greater in high-altitude pioneer trees of European larch, these trees actually had fewer mean seeds per cone.

Consistency of cone and seed production could also explain Koziol's (1997) findings of greater larval abundance of *Cydia strobilella* (L.) at higher altitudes the year following a heavy cone crop of *Picea abies* (L.) Karst. In this study in the Tatra Mountains of Poland, trees at higher altitudes were more consistent in their cone production, and it was hypothesized that in the year of sparse cone production following an abundant year, these were the only trees able to provide a constant food supply, and thus they were able to support a greater number of larvae. Conflicting results come from Roques (1988) in which a 10-year survey of *Strobilomyia* larvae in European larch cones in the French Alps showed less overall abundance of larvae at the high altitude site at 2200 m, possibly due to the frequent occurrence of late frosts, which can decimate cone crops but not affect insect emergence. In another study concerning the same species, Jenkins and Roques (1997) found no consistent trend between cone damage and elevation and concluded that the insects are distributed throughout the altitudinal range of larch.

**Cone Insect Diapause.** Research on cone insect life histories is concerned mainly with the timing of life stage transitions and with factors that may affect diapause. It has been found repeatedly that events such as oviposition and adult emergence coincide with the phenology of cone development (Yao *et al.* 1991;
McClure et al. 1996; Koziol 1997). Olenici (1997) was able to estimate degree-day requirements for various stages of both insect and cone development on European larch in Romania. Cone insect diapause is still poorly understood, and it is not certain exactly which factors trigger initiation and termination of prolonged diapause (Turgeon et al. 1994). Roques (1988) found that the incidence of prolonged diapause among Strobilomyia spp. can vary between about 5 and 50%, and it appears to be inversely correlated with the rate of change in cone yield from the current year to the next, and also with the size of the cone crop the following year. Induction of diapause is hypothesized to result from a combination of factors such as the chemical composition of the cones during larval development and abiotic factors such as temperature, rainfall, and solar radiation (Roques 1989). Termination of diapause is probably due to climatic factors such as temperatures at the time of female bud differentiation, or possibly to current cone production of the host tree (Turgeon et al. 1994).
Whitebark pine, *Pinus albicaulis* Engelmannii, is a high-elevation conifer that grows in the mountains of the western United States and southwestern Canada. Until a couple of decades ago, relatively little was known about it due to its remote habitat and limited commercial value. However, in recent years whitebark pine has been the subject of numerous studies due to a growing awareness of its role as a keystone species as well as its uncertain future.

Whitebark pine is valuable for watershed protection and slope stabilization as well as esthetic appeal, but its greatest value is as a food source for the wildlife that shares its high mountain environment (Arno and Hoff 1989). The seeds of whitebark pine are highly nutritious due to their large size (175 mg average weight) (Krugman and Jenkinson 1974), and significant lipid content (52 percent) (Lanner and Gilbert 1994). Normally, almost all the viable seeds produced are harvested by birds and mammals, but those seeds that are cached for later use will have an opportunity to germinate (Kendall and Arno 1990). The species that rely most heavily on whitebark pine seeds and therefore have the most to lose when seeds are not available are Clark's nutcracker, *Nucifraga columbiana*, red squirrel, *Tamiasciurus hudsonicus*, black bear, *Ursus americanos*, and grizzly bear, *U. arctos horribilis* (Hutchins and Lanner 1982).
Unfortunately, the availability of whitebark pine seeds is becoming an issue of some concern given the well-documented decline of this species in many parts of its native range (Arno 1986; Kendall and Arno 1990; Keane and Arno 1993; Keane and Morgan 1994). Mountain pine beetle, *Dendroctonus ponderosae*, and introduced white pine blister rust, *Cronartium ribicola*, have been responsible for mortality as high as 100% in the Whitefish Range of Montana and 90% in Glacier National Park (Kendall and Arno 1990). Successional replacement of whitebark pine by shade-tolerant trees such as subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., and Engelmann spruce, *Picea engelmannii* Parry, has been hastened by beetle and rust damage, as well as by the lack of fire that would open new sites for whitebark pine regeneration (Arno 1986).

Given the uncertainty of whitebark pine's future, any factor that could limit cone and seed production is worth investigating. Insects are important seed predators and can cause seed losses in almost all species of North American conifers (Hedlin *et al.* 1980). In some years and localities they are capable of destroying virtually all the seeds of a given species (Furniss and Carolin 1977). Cone and seed insects could, therefore, have a significant impact on the whitebark pine seed crop and the wildlife that depends on it. Efforts to develop rust-resistant strains of whitebark pine could also be hampered by cone and seed insects feeding on genetically desirable seed, as has occurred with western white pine (Shea *et al.* 1984; Shea 1986). The few references to whitebark pine cone and seed insects in the literature lack detail and rely largely on anecdotal information (Arno and Hoff 1989; Bartos and Gibson 1990). Kegley *et al.*
(in prep.) have begun the task of quantifying the impact of these insects in their study of whitebark pine in seven sites across the northwestern United States, but they indicate the need for further work that would track insect damage levels in years of varying cone crop size. The western conifer seed bug, *Leptoglossus occidentalis*, in particular caused significant seed damage in their study and is known to be a seed predator in a wide variety of other conifers (Hedlin *et al.* 1980). More information on its feeding habits in whitebark pine would be of value.

The objectives of this study were the following: (1) quantify cone and seed insect damage to whitebark pine cones and determine the effect of elevation; and (2) assess whether *L. occidentalis* can survive on whitebark pine cones and the potential damage such feeding may produce.

**Materials and Methods**

Five sites were selected for the field study based on accessibility and the presence of cone-bearing trees. Two of the sites, Seven Devils and Snowbank Mtn., were previously used by Kegley *et al.* (in prep.), and although some trees showed evidence of blister rust infection, the cone crop did not appear to be affected. Each site included an upper and a lower subsite that were separated by at least 120 m of elevation (Table 1). At each subsite, 10 trees were chosen based on their climbability and the presence of at least 10 cone clusters.

**Field Seed Bug Feeding Experiments.** Galena Summit and Togwotee Pass were chosen for the seed bug feeding experiments because they were accessible in late
TABLE 1. Whitebark pine study site characteristics.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation, lower and upper (m)</th>
<th>Aspect</th>
<th>Average slope (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carlton Ridge, MT</td>
<td>46°41' N</td>
<td>114°12' W</td>
<td>2,370</td>
<td>S-SW</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2,490</td>
<td>W-SW</td>
<td>14</td>
</tr>
<tr>
<td>Galena Summit, ID</td>
<td>43°52' N</td>
<td>114°42' W</td>
<td>2,600</td>
<td>S</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2,930</td>
<td>E-SE</td>
<td>11</td>
</tr>
<tr>
<td>Seven Devils, ID</td>
<td>45°20' N</td>
<td>116°30' W</td>
<td>2,260</td>
<td>E</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2,480</td>
<td>SE</td>
<td>30</td>
</tr>
<tr>
<td>Snowbank Mtn., ID</td>
<td>44°26' N</td>
<td>116°07' W</td>
<td>2,170</td>
<td>N-NE</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2,520</td>
<td>E-SE</td>
<td>30</td>
</tr>
<tr>
<td>Togwotee Pass, WY</td>
<td>43°45' N</td>
<td>110°04' W</td>
<td>2,670</td>
<td>SW</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3,030</td>
<td>S-SE</td>
<td>48</td>
</tr>
</tbody>
</table>

May when bagging and caging of cones took place. The trees at these two sites were subjected to three different cone treatments. Six cone clusters per tree were each enclosed in a wire mesh cage approximately 40 x 30 cm (mesh size 7 mm) and a cotton rice bag that was big enough to cover the cage and be securely wired to the branch below. The cages served not only to protect the cones from predation by Clark's nutcrackers and squirrels, but also to hold the bags out away from the cones and help prevent insect feeding on cones through the bags from the outside. Two of the six clusters on each tree served as controls and were not disturbed until cone collection in late August (the "bagged" treatment). In late June, about 170 seed bug nymphs ranging from second to fourth instar were collected from the Bureau of Land Management Russell Bar Ponderosa Pine Seed Orchard near White Bird, Idaho, and were maintained in 11-liter ice cream containers. In early July, two second or third
instar seed bug nymphs each were introduced into two of the bagged clusters on each tree (73 total bugs at Togwotee, 80 at Galena). This was the "seed bug" treatment. They were left in the bags for 7 days at Galena and for 8 days at Togwotee. The branches with these bagged cone clusters were then cut and lowered to the ground, where both cones and remaining live bugs were collected. At this time, at least 10 additional cones per tree were caged (the "caged" treatment) in anticipation of cone collection in late August. Cone caging was then completed at the other three sites. The feeding experiment was repeated at Galena in early August, using three adult seed bugs per bag (118 bugs total) and allowing them to remain for 16 days. All cones were collected from all sites between 19 August and 1 September.

**Laboratory Seed Bug Feeding Experiments. Survival experiments.** Ten 11-liter ice cream containers were used to isolate seed bugs with different food sources for 7 days. Six containers had whitebark pine cones and foliage, two had cones alone (which had been bagged in May to prevent insect feeding), one had conelets and foliage, and one had foliage alone. Ten to 12 seed bugs (mostly fourth or fifth instar nymphs) were introduced into each container with a small water-soaked sponge and were left undisturbed except for water replenishment. After 7 days, the remaining live bugs in each container were counted.

**Feeding observations.** Three four-liter glass jars containing cones and foliage were used to observe seed bug feeding. Two jars were used to observe nymphs and adults, respectively, on whitebark pine cones and foliage. The third jar contained both nymphs and adults on both whitebark and ponderosa cones. In total, 28 bugs were
observed in each jar, but some may have been used more than once since observed bugs were returned to a common container without being marked. Two bugs at a time were placed in each jar and were observed for three 15-minute intervals that were 15 minutes apart. A total of 126 15-minute observations was made. The time each bug spent in each of three basic behaviors (walking or resting, mouthparts probing, and feeding) was recorded, along with whether the behavior occurred on cones, needles, or the jar. Because the two bugs in each jar could influence each other's behavior, they were not considered to be independent and the feeding times used in the analysis represented the average time spent feeding by the two bugs in each observation. To compare the proportion of time spent feeding by nymphs versus adults on whitebark pine (none, a portion of the time, or all of the time), a chi-square test of homogeneity of proportions was run. To detect any differences among the bugs that fed, an analysis of variance of a two-way factorial in a completely randomized design was also done. There were too few observations of nymphs and adults together on whitebark and ponderosa pine cones and too few instances of feeding to support any inferential statistics.

**Cone and Seed Analysis. Cone dissection and seed x-rays.** Eight cones per tree or per treatment type per tree (a total of 1139) were randomly selected for dissection. Cone lengths were measured and cones were dissected by removing and counting all scales. Two times the number of scales gave the potential seeds per cone. Insects found inside the cones were noted and preserved or put into rearing containers with the remaining undissected cones. Extractable seeds were counted and classified as
fully developed or underdeveloped. Both of these categories were used in determining the percent of potential seeds per cone.

The developed seeds from each tree were placed in an envelope and one quarter were randomly selected for x-ray analysis. In total, 21,585 seeds were x-rayed on a Hewlett Packard 43804N Faxitron series machine (25 KV, 2.9 mA, 45 s) using IX50 Fuji film and were developed using a Fuji FPM 4200 processor. Three dissected cones that were small and hard yielded only desiccated seeds, which were not x-rayed. Seed x-rays were analyzed using criteria developed at the Institute of Forest Genetics in Placerville, CA, and used by Kegley et al (in prep.). Categories were normally filled, shrunken endosperm, shriveled endosperm, empty, "other" abnormality such as missing embryo or opaque endosperm, seed bug damaged, Dioryctria damaged, and Megastigmus damaged. A seed was classified as filled only if the endosperm completely filled its cavity and touched the seed coat walls. The shrunken endosperm category applied to seeds with slight to extreme endosperm shrinkage but in which an embryo was still visible. If no embryo could be seen, it was classified as shrunken. Seeds with nothing but a pale membrane inside were classified as empty, while those with normal-sized endosperms that were opaque or missing an embryo were put in the "other" category. Seed bug damage was not always obvious, since it could appear as a slightly shrunken, opaque, or otherwise abnormal endosperm if the bug fed for only a short time, or it could show up more obviously as an endosperm with a sizeable chunk missing. Damage was therefore assigned to seed bugs only when it was of the latter sort. Dioryctria sp. damage was identifiable by holes in the seed coat and/or the
presence of frass inside the seed, and any seeds containing *Megastigmus* sp. larvae were quite apparent.

No analysis was made on cones from the first field seed bug feeding experiment, or on those from the laboratory tests, because the early developmental stage of these cones made seed extraction very difficult, and those seeds that were extractable were uniformly dried and shriveled. An attempt was made to locate seed bug feeding holes on some of these cones and seeds by treating them with ruthenium red dye as suggested by Campbell and Shea (1990). However, the cones were too similar in color to the magenta dye to allow feeding holes to be distinguished, and dying the seeds proved equally unsuccessful.

**Statistical analysis.** An analysis of variance of a two-way factorial in a completely randomized design with subsamples was used to test the effects of site and elevation within site on the following measures: (1) cone length, (2) number of fully developed seeds per cone, (3) percentage of potential seeds present per cone, and (4) percentages of filled, seedbug-damaged, total insect-damaged, and total non-insect damaged seeds per cone. Insect damage included that due to seed bugs, *Dioryctria* sp., and *Megastigmus* sp., while non-insect damage included the shrunken, shriveled, empty, opaque, and no-embryo categories. In this statistical model, site and elevation were fixed-effects factors that used an individual tree as the experimental unit and multiple cones collected from each tree as subsamples. The random-effects factors were trees and cones within trees.
The effects of elevation and cone treatment on the above measures were tested separately for Galena and Togwotee (because they had three and two treatments, respectively) using analysis of variance of a two-way factorial in a split-plot design with subsamples. Here, elevation and treatment were the fixed-effects factors, while trees and cones within trees remained the random-effects factors. The whole plot factor was elevation and the whole plot unit was an individual tree. The subplot factor was treatment, and the subplot unit was a set of (generally) eight cones on a tree. Individual cones were subsamples.

Because two of the treatments (bagged and caged) were common to both sites, the effect of these two treatments overall was also tested using analysis of variance of a three-way factorial in a split-plot design with subsamples. The changes from the separate site analyses were that site was added as a fixed-effects factor and also as a whole-plot factor.

Percentage data were adjusted using the arcsine square root transformation prior to analysis to better meet the assumptions of normality and homogeneity of variance, but improvement was minimal and the original percentage data were therefore used for the analysis. As needed, pairwise comparisons among means were adjusted for experimentwise Type I error using Tukey multiple comparisons. When significant interactions were found between main effects, the simple effect of elevation at each site was examined. All computations were done using PROC MIXED in SAS (SAS Institute Inc. 1996).
Results

Field Seed Bug Feeding Experiments. Average survival of seed bug nymphs placed in bags was 81% for the first test, of which 78% were healthy (Table 2). There was no difference in survival at the upper and lower elevations at Galena, and at Togwotee survival was 9% less at the upper site. Mortality ranged from 6 to 13%, and 7 to 13% could not be located. Adult survival in the second test averaged 90%, with 85% healthy, and 4% greater survival at the lower elevation. There was 7 to 8% mortality and 2 to 5% were missing.

Laboratory Seed Bug Feeding Experiments. Survival experiments.

Survival of seed bugs in the containers with cones, conelets, and/or foliage averaged 92.5% and ranged from 70 to 100% (Table 3). Of the 100 nymphs put into the

<table>
<thead>
<tr>
<th>TABLE 2. Percentages of healthy, injured, dead, and missing seed bugs from bags in field feeding experiments.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
</tr>
<tr>
<td>--------------------------------</td>
</tr>
<tr>
<td><strong>1st test (nymphs):</strong></td>
</tr>
<tr>
<td>Togwotee - lower</td>
</tr>
<tr>
<td>Togwotee - upper</td>
</tr>
<tr>
<td>Galena - lower</td>
</tr>
<tr>
<td>Galena - upper</td>
</tr>
<tr>
<td>Average</td>
</tr>
<tr>
<td><strong>2nd test (adults):</strong></td>
</tr>
<tr>
<td>Galena - lower</td>
</tr>
<tr>
<td>Galena - upper</td>
</tr>
<tr>
<td>Average</td>
</tr>
</tbody>
</table>
containers, 58 had become adults by the time they were removed.

**Feeding observations.** A chi-square test demonstrated that there was no difference in the proportion of time spent feeding between adults and nymphs on whitebark pine ($G^2 = 1.952, df = 2, \text{exact } P = 0.359$). This was also true for cone feeding alone ($G^2 = 1.726, df = 2, \text{exact } P = 0.484$) and for needle feeding alone ($G^2 = 0.164, df = 1, \text{exact } P = 1.000$). For the adults, feeding was observed in seven of the 14 observations of two bugs each. Of these, two were feeding on cones, two were on needles, and three were on both. For the nymphs, eight of the 14 observations included feeding, with four on cones, three on needles, and one on both. When just the observations where feeding took place were considered, average total adult feeding time per 45-min period ($26.4 \pm 4.9 \text{ min}$) was not significantly different from average total nymph feeding time ($12.1 \pm 4.9 \text{ min}$) ($F_{1,13} = 4.27, P = 0.0612$). There was also no difference between the time adults spent feeding on cones ($24.14 \pm 4.4 \text{ min}$) and the time nymphs spent feeding on cones ($12.77 \pm 4.4 \text{ min}$) ($t = 1.66, P = 0.1180$).

**TABLE 3. Average percent survival of seed bugs on whitebark pine food sources after 7 days in containers in the laboratory.**

<table>
<thead>
<tr>
<th>Food source</th>
<th>n</th>
<th>Age</th>
<th>Average percent survival (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cones</td>
<td>20</td>
<td>Nymph</td>
<td>85 (70-100)</td>
</tr>
<tr>
<td>Foliage</td>
<td>10</td>
<td>Nymph</td>
<td>80 (80)</td>
</tr>
<tr>
<td>Conelets and foliage</td>
<td>10</td>
<td>Nymph</td>
<td>100 (100)</td>
</tr>
<tr>
<td>Cones and foliage</td>
<td>60</td>
<td>Nymph</td>
<td>96 (83-100)</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>Adult</td>
<td></td>
</tr>
</tbody>
</table>
The observations on the jar in which both an adult and a nymph were placed with whitebark and ponderosa pine cones are summarized in Table 4.

**Cone and Seed Analysis. Insects found in cones.** Definitive identification of insects found in or on dissected cones was difficult in many cases due to the lack of adults. Larvae and pupal cases that were tentatively identified as *Dioryctria* sp. were found in cones from Seven Devils, Carlton, and Snowbank, but never damaged more than 5% of seeds. One dead adult moth was found in a cone from Snowbank, but it was too deteriorated to identify. One beetle larva was found in a cone from Galena, and three scale insects were found at the base of cones from Seven Devils. Cecidomyiid larvae were found on cones from all sites except Galena. Anywhere from one to 28 of these whitish or bright orange larvae could be found on a single cone under the scales but appeared not to cause damage apart from giving nearby seeds a resinous coating. *Megastigmus* sp. larvae appeared in 4.7% of the x-rayed seeds from Carlton Ridge. These were placed in rearing containers but no adults emerged.

At the time of cone collection, adelgids were not observed on cones, but they

<table>
<thead>
<tr>
<th>Food source</th>
<th>Observations in which feeding observed*</th>
<th>Average time spent feeding (min) per 45 min of observation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa cones</td>
<td>4</td>
<td>20</td>
</tr>
<tr>
<td>Ponderosa needles</td>
<td>8</td>
<td>12</td>
</tr>
<tr>
<td>Whitebark cones</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>Whitebark needles</td>
<td>4</td>
<td>8</td>
</tr>
</tbody>
</table>

* Fourteen total observations were made.
were sometimes present in large numbers around the wires which secured the bags to the branches. Two species of mirid bugs (*Deraeocoris* sp. and *Pilophorus* sp.) were found on cones at Galena, Snowbank, and Seven Devils, and a pentatomid bug was found on a cone at Snowbank.

**Cone and seed statistical analysis.** Mean values for all cone and seed measures are given by site in Table 5, and are broken down into elevational subsites in Table 6. Table 7 contains mean values for treated cones at Galena and Togwotee, and Table 8 subdivides these by elevation.

Caged cones varied in length from 5.5 cm (± 0.1) at Carlton to 6.6 cm (± 0.1) at Togwotee (Table 5). There was a significant interaction between site and elevation ($F_{4,89} = 3.48, P = 0.0108$) in which mean cone length increased with increasing elevation at Seven Devils and Galena, decreased at Snowbank and Carlton, and remained the same at Togwotee (Table 6). Cones were significantly shorter at the upper subsites at Carlton ($F_{1,89} = 5.20, P = 0.0250$) and Snowbank ($F_{1,89} = 8.51, P = 0.0045$) than at their lower subsites. Overall the bagged cones at Galena and Togwotee were shorter than the caged cones at both sites ($t = -5.56, df = 34, P < 0.0001$) and at Galena the bagged cones were also shorter than the seed bug cones ($t = -2.42, df = 36, P = 0.0532$) (Table 7).

The average number of fully developed seeds per cone for caged cones ranged from 47.9 (± 3.7) at Snowbank to 91.2 (± 3.7) at Galena. It varied significantly between sites overall ($F_{4,89} = 31.41, P < 0.0001$), and between elevational subsites only at Seven Devils, where the upper site had more seeds per cone ($F_{1,89} = 8.46$, P = 0.005).
TABLE 5. Site means for caged cone length, number of seeds per cone, percent potential seeds, and percentage of seeds in various damage categories.

<table>
<thead>
<tr>
<th>Site</th>
<th>Mean ± S.E</th>
<th>Percentage of seeds per cone in each category:</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of cones dissected</td>
<td>Cone length (cm)</td>
<td>Number of fully developed seeds per cone</td>
</tr>
<tr>
<td>Carlton Ridge</td>
<td>160</td>
<td>5.5 ± 0.1†</td>
<td>51.5 ± 3.7a*</td>
</tr>
<tr>
<td>Galena Summit</td>
<td>159</td>
<td>6.4 ± 0.1</td>
<td>91.2 ± 3.7b</td>
</tr>
<tr>
<td>Seven Devils</td>
<td>160</td>
<td>5.7 ± 0.1</td>
<td>59.5 ± 3.7a</td>
</tr>
<tr>
<td>Snowbank Mtn.</td>
<td>160</td>
<td>5.7 ± 0.1</td>
<td>47.9 ± 3.7a</td>
</tr>
<tr>
<td>Togwotee Pass</td>
<td>152</td>
<td>6.6 ± 0.1</td>
<td>88.4 ± 3.8b</td>
</tr>
</tbody>
</table>

* Values in the same column followed by at least one of the same letters are not significantly different ($P > 0.05$).
† Columns without letters following means had a significant interaction between site and elevation.
TABLE 6. Upper and lower subsite means for caged cone length, number of seeds per cone, percent potential seeds, and percentage of seeds in various damage categories.

<table>
<thead>
<tr>
<th>Site</th>
<th>Elevation</th>
<th>Cone length (cm)</th>
<th>Number of fully developed seeds per cone</th>
<th>Percentage of potential seeds present per cone</th>
<th>Filled</th>
<th>Seed bug-damaged</th>
<th>Total insect-damaged</th>
<th>Total non-insect-damaged</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carlton</td>
<td>Lower</td>
<td>5.9 ± 0.2*</td>
<td>49.8 ± 5.2</td>
<td>40.9 ± 3.3</td>
<td>22.6 ± 4.1*</td>
<td>0.9 ± 0.4</td>
<td>5.6 ± 1.5</td>
<td>71.7 ± 4.0*</td>
</tr>
<tr>
<td>Ridge</td>
<td>Upper</td>
<td>5.2 ± 0.2*</td>
<td>53.2 ± 5.2</td>
<td>46.1 ± 3.3</td>
<td>1.9 ± 4.1*</td>
<td>0.9 ± 0.4</td>
<td>8.8 ± 1.5</td>
<td>89.3 ± 4.0*</td>
</tr>
<tr>
<td>Galena</td>
<td>Lower</td>
<td>6.3 ± 0.2</td>
<td>87.3 ± 5.2</td>
<td>71.1 ± 3.3</td>
<td>44.5 ± 4.1*</td>
<td>0.4 ± 0.4</td>
<td>0.8 ± 1.5</td>
<td>54.7 ± 4.0*</td>
</tr>
<tr>
<td>Summit</td>
<td>Upper</td>
<td>6.5 ± 0.2</td>
<td>95.0 ± 5.2</td>
<td>67.7 ± 3.3</td>
<td>6.0 ± 4.1*</td>
<td>0.2 ± 0.4</td>
<td>0.2 ± 1.5</td>
<td>93.8 ± 4.0*</td>
</tr>
<tr>
<td>Seven</td>
<td>Lower</td>
<td>5.5 ± 0.2</td>
<td>48.9 ± 5.2*</td>
<td>42.9 ± 3.3*</td>
<td>36.9 ± 4.1*</td>
<td>2.4 ± 0.4</td>
<td>5.1 ± 1.5</td>
<td>58.0 ± 4.0*</td>
</tr>
<tr>
<td>Devils</td>
<td>Upper</td>
<td>5.9 ± 0.2</td>
<td>70.2 ± 5.2*</td>
<td>55.7 ± 3.3*</td>
<td>19.7 ± 4.1*</td>
<td>1.8 ± 0.4</td>
<td>2.0 ± 1.5</td>
<td>78.2 ± 4.0*</td>
</tr>
<tr>
<td>Snowbank</td>
<td>Lower</td>
<td>6.1 ± 0.2*</td>
<td>46.9 ± 5.2</td>
<td>37.3 ± 3.3</td>
<td>37.5 ± 4.1*</td>
<td>1.4 ± 0.4*</td>
<td>6.8 ± 1.5</td>
<td>55.6 ± 4.0*</td>
</tr>
<tr>
<td>Mtn.</td>
<td>Upper</td>
<td>5.3 ± 0.2*</td>
<td>49.0 ± 5.2</td>
<td>43.8 ± 3.3</td>
<td>14.3 ± 4.1*</td>
<td>2.7 ± 0.4*</td>
<td>5.7 ± 1.5</td>
<td>80.0 ± 4.0*</td>
</tr>
<tr>
<td>Togwotee</td>
<td>Lower</td>
<td>6.6 ± 0.2</td>
<td>85.7 ± 5.4</td>
<td>58.8 ± 3.5</td>
<td>5.0 ± 4.3</td>
<td>0.4 ± 0.5</td>
<td>0.5 ± 1.5</td>
<td>94.5 ± 4.3</td>
</tr>
<tr>
<td>Pass</td>
<td>Upper</td>
<td>6.6 ± 0.2</td>
<td>91.1 ± 5.2</td>
<td>60.5 ± 3.3</td>
<td>0.2 ± 4.1</td>
<td>0.3 ± 0.4</td>
<td>0.3 ± 1.5</td>
<td>99.4 ± 4.0</td>
</tr>
</tbody>
</table>

* Values for upper and lower elevation subsites were significantly different ($P < 0.05$).
TABLE 7. Treatment means for cone length, number of seeds per cone, percent potential seeds, and percentage of seeds in various damage categories at Galena Summit, ID, and Togwotee Pass, WY.

<table>
<thead>
<tr>
<th>Site and treatment *</th>
<th>Number of cones dissected</th>
<th>Cone length (cm)</th>
<th>Number of fully developed seeds per cone</th>
<th>Percentage of potential seeds per cone</th>
<th>Filled</th>
<th>Seed bug-damaged</th>
<th>Total insect-damaged</th>
<th>Total non-insect damaged</th>
</tr>
</thead>
<tbody>
<tr>
<td>Galena Summit</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>101</td>
<td>5.8 ± 0.2a&lt;sup&gt;t&lt;/sup&gt;</td>
<td>82.4 ± 4.0a</td>
<td>63.5 ± 2.3a</td>
<td>41.8 ± 3.5</td>
<td>0.81 ± 0.8b</td>
<td>0.81 ± 0.8a</td>
<td>57.3 ± 3.4</td>
</tr>
<tr>
<td>C</td>
<td>159</td>
<td>6.4 ± 0.2b</td>
<td>91.1 ± 3.8b</td>
<td>69.4 ± 2.2b</td>
<td>25.2 ± 3.4</td>
<td>0.34 ± 0.8a</td>
<td>0.53 ± 0.8b</td>
<td>74.3 ± 3.3</td>
</tr>
<tr>
<td>S</td>
<td>95</td>
<td>6.2 ± 0.2b</td>
<td>85.2 ± 4.0ab</td>
<td>67.5 ± 2.3ab</td>
<td>18.2 ± 3.5</td>
<td>11.85 ± 0.8c</td>
<td>11.82 ± 0.9c</td>
<td>70.8 ± 3.5</td>
</tr>
<tr>
<td>Togwotee Pass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>152</td>
<td>6.3 ± 0.1&lt;sup&gt;t&lt;/sup&gt;</td>
<td>84.2 ± 3.9</td>
<td>54.3 ± 2.0&lt;sup&gt;t&lt;/sup&gt;</td>
<td>24.8 ± 1.8</td>
<td>0.69 ± 0.1</td>
<td>0.69 ± 0.2</td>
<td>74.9 ± 1.8</td>
</tr>
<tr>
<td>C</td>
<td>152</td>
<td>6.6 ± 0.1&lt;sup&gt;t&lt;/sup&gt;</td>
<td>88.2 ± 3.9</td>
<td>59.6 ± 2.0&lt;sup&gt;t&lt;/sup&gt;</td>
<td>2.6 ± 1.8</td>
<td>0.38 ± 0.1</td>
<td>0.41 ± 0.2</td>
<td>97.0 ± 1.8</td>
</tr>
<tr>
<td>Galena and Togwotee</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>253</td>
<td>6.0 ± 0.1&lt;sup&gt;t&lt;/sup&gt;</td>
<td>83.3 ± 2.8&lt;sup&gt;t&lt;/sup&gt;</td>
<td>58.9 ± 1.5&lt;sup&gt;t&lt;/sup&gt;</td>
<td>33.3 ± 2.0</td>
<td>0.73 ± 0.1</td>
<td>0.73 ± 0.1</td>
<td>66.1 ± 2.0</td>
</tr>
<tr>
<td>C</td>
<td>311</td>
<td>6.5 ± 0.1&lt;sup&gt;t&lt;/sup&gt;</td>
<td>89.6 ± 2.7&lt;sup&gt;t&lt;/sup&gt;</td>
<td>64.5 ± 1.5&lt;sup&gt;t&lt;/sup&gt;</td>
<td>13.9 ± 2.0</td>
<td>0.36 ± 0.1</td>
<td>0.47 ± 0.1</td>
<td>85.7 ± 1.9</td>
</tr>
</tbody>
</table>

* B = cones caged and bagged, C = cones caged only, S = cones caged and bagged and seed bugs introduced.
† Values in the same column followed by at least one of the same letters are not significantly different (P > 0.05).
* Values for the two treatments are significantly different (P < 0.05).
TABLE 8. Upper and lower subsite treatment means for cone length, number of seeds per cone, percent potential seeds, and percentage of seeds in various damage categories at Galena Summit, ID, and Togwotee Pass, WY.

<table>
<thead>
<tr>
<th>Site and treatment *</th>
<th>Elevation</th>
<th>Cone length (cm)</th>
<th>Number of fully developed seeds per cone</th>
<th>Percentage of potential seeds present per cone</th>
<th>Filled</th>
<th>Seed bug-damaged</th>
<th>Total insect-damaged</th>
<th>Total non-insect-damaged</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Galena Summit</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>Lower</td>
<td>5.8 ± 0.2</td>
<td>83.3 ± 5.6</td>
<td>66.0 ± 3.2</td>
<td>36.2 ± 4.9</td>
<td>0.93 ± 1.2</td>
<td>0.92 ± 1.2</td>
<td>62.8 ± 4.8</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>5.8 ± 0.2</td>
<td>81.4 ± 5.7</td>
<td>60.9 ± 3.2</td>
<td>47.4 ± 5.0</td>
<td>0.69 ± 1.2</td>
<td>0.69 ± 1.2</td>
<td>51.9 ± 4.9</td>
</tr>
<tr>
<td>C</td>
<td>Lower</td>
<td>6.3 ± 0.2</td>
<td>87.3 ± 5.2</td>
<td>71.1 ± 3.3</td>
<td>44.5 ± 4.8</td>
<td>0.43 ± 1.1</td>
<td>0.82 ± 1.1</td>
<td>54.7 ± 4.7</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>6.5 ± 0.2</td>
<td>95.0 ± 5.2</td>
<td>67.7 ± 3.3</td>
<td>6.0 ± 4.8</td>
<td>0.25 ± 1.1</td>
<td>0.25 ± 1.1</td>
<td>93.8 ± 4.7</td>
</tr>
<tr>
<td>S</td>
<td>Lower</td>
<td>5.8 ± 0.2</td>
<td>81.3 ± 5.7</td>
<td>69.6 ± 3.3</td>
<td>15.4 ± 5.0</td>
<td>11.57 ± 1.2</td>
<td>11.54 ± 1.2</td>
<td>75.0 ± 5.0</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>6.5 ± 0.2</td>
<td>89.1 ± 5.7</td>
<td>65.3 ± 3.2</td>
<td>21.0 ± 4.9</td>
<td>12.12 ± 1.2</td>
<td>12.10 ± 1.2</td>
<td>66.6 ± 4.9</td>
</tr>
<tr>
<td><strong>Togwotee Pass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>Lower</td>
<td>6.1 ± 0.2</td>
<td>81.3 ± 5.7</td>
<td>53.7 ± 2.9</td>
<td>38.2 ± 2.7</td>
<td>0.74 ± 0.2</td>
<td>0.74 ± 0.2</td>
<td>61.7 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>6.4 ± 0.2</td>
<td>87.2 ± 5.3</td>
<td>55.1 ± 2.7</td>
<td>11.3 ± 2.5</td>
<td>0.64 ± 0.2</td>
<td>0.64 ± 0.2</td>
<td>88.1 ± 2.5</td>
</tr>
<tr>
<td>C</td>
<td>Lower</td>
<td>6.6 ± 0.2</td>
<td>85.7 ± 5.4</td>
<td>58.8 ± 3.5</td>
<td>5.0 ± 2.7</td>
<td>0.44 ± 0.2</td>
<td>0.50 ± 0.2</td>
<td>94.4 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>6.6 ± 0.2</td>
<td>91.1 ± 5.2</td>
<td>60.5 ± 3.3</td>
<td>0.1 ± 2.5</td>
<td>0.33 ± 0.2</td>
<td>0.33 ± 0.2</td>
<td>99.5 ± 2.5</td>
</tr>
<tr>
<td><strong>Galena and Togwotee</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>Lower</td>
<td>6.0 ± 0.1</td>
<td>82.3 ± 3.9</td>
<td>59.9 ± 2.1</td>
<td>37.2 ± 2.9</td>
<td>0.81 ± 0.2</td>
<td>0.81 ± 0.2</td>
<td>62.3 ± 2.8</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>6.1 ± 0.1</td>
<td>84.4 ± 3.8</td>
<td>58.0 ± 2.1</td>
<td>29.3 ± 2.8</td>
<td>0.65 ± 0.2</td>
<td>0.65 ± 0.2</td>
<td>70.0 ± 2.8</td>
</tr>
<tr>
<td>C</td>
<td>Lower</td>
<td>6.5 ± 0.1</td>
<td>86.5 ± 3.9</td>
<td>64.9 ± 2.1</td>
<td>24.7 ± 2.8</td>
<td>0.44 ± 0.2</td>
<td>0.66 ± 0.2</td>
<td>74.6 ± 2.8</td>
</tr>
<tr>
<td></td>
<td>Upper</td>
<td>6.6 ± 0.1</td>
<td>92.8 ± 3.7</td>
<td>64.0 ± 2.0</td>
<td>3.0 ± 2.7</td>
<td>0.29 ± 0.2</td>
<td>0.29 ± 0.2</td>
<td>96.7 ± 2.7</td>
</tr>
</tbody>
</table>

* B = cones caged and bagged, C = cones caged only, S = cones caged and bagged and seed bugs introduced.

† Values for upper and lower elevations within the treatment are significantly different (P < 0.05).
The bagged cones overall contained fewer seeds per cone than the caged cones \((t = -2.73, df = 34, P = 0.0100)\), but the seed bug cones did not differ from either caged or bagged cones in this respect.

The percentage of potential seed present varied from 40.6 (± 2.4) at Snowbank to 69.4 (± 2.4) at Galena for caged cones and varied significantly between sites \((F_{4,89} = 25.52, P < 0.0001)\) but not between elevations within sites, except once again at Seven Devils \((F_{1,89} = 7.42, P = 0.0078)\) where the upper elevation had the higher percentage of potential seeds. Bagged cones had a lower percentage than caged cones \((t = -4.03, df = 34, P = 0.0003)\), but once again the seed bug cones did not differ from the others.

The caged cones at Togwotee contained the lowest percentage of filled seeds per cone (2.6 ± 3.0) and the highest percentage of seeds with non-insect damage (97.0 ± 2.9). There was a significant site-by-elevation interaction for both of these seed categories (filled: \(F_{4,89} = 4.33, P = 0.0030\); non-insect: \(F_{4,89} = 4.57, P = 0.0021\)). The trend was consistently in the direction of fewer filled seeds (and more seeds with non-insect damage) at the upper elevations, but the magnitude of the difference depended on the site, and was most marked at Galena. Differences between upper and lower subsites existed for all sites except Togwotee. The results among the bagged cones were complicated by a three-way interaction among site, elevation, and treatment (filled: \(F_{1,34} = 65.60, P < 0.0001\); non-insect: \(F_{1,34} = 70.93, P < 0.0001\)) such that no consistent trend could be summarized. At Galena an interaction occurred between treatment and elevation (filled: \(F_{2,36} = 24.45, P < 0.0001\); non-insect: \(F_{2,36} = 26.32\),
that showed more filled seeds and fewer non-insect-damaged seeds at the upper elevation for the bagged and seed bug cones, but a reverse trend of greater magnitude for the caged cones.

Finally, the damage due to seed bugs and that due to all insects combined was similar in magnitude since at some sites seed bugs caused most of the insect damage. For both these categories, seed bug damage differed significantly among sites (seed bug: $F_{4,89} = 7.51, P < 0.0001$; all insects: $F_{4,89} = 9.24, P < 0.0001$), with Galena and Togwotee consistently showing less damage than Snowbank. Seed bug damage was greater at the upper subsite at Snowbank than the lower ($F_{1,89} = 4.13, P = 0.0451$). Bagged cones surprisingly showed more seed bug damage overall than caged cones ($t = 2.30, df = 34, P = 0.0277$) but no difference in total insect damage. At Galena, seed bug cones as expected showed more seed bug damage than either caged ($t = -9.35, df = 36, P < 0.0001$) or bagged ($t = -10.20, df = 36, P < 0.0001$) cones. Damage to seed bug cones did not differ between the upper and lower subsites at Galena.

Discussion

Seed Bug Feeding Experiments and Observations. The seed bug feeding tests proved that both immature and mature seed bugs can use whitebark pine cones and foliage as a food source both in the laboratory and in the field for 1- to 2-week periods. The seeds from the second field test with adults showed at least an 11% increase in seed bug damage over bagged or caged cones regardless of elevation, so it
is certain the cones were being used as a food source. It is important to note that the field experiments were necessarily conducted inside bags and cages, which are likely to have produced a warmer and moister microenvironment protected from wind and predators, and thus may have favored seed bug survival. In this experiment, elevation did not appear to limit survival of either adults or nymphs. It is likely that at least a portion of the injured and dead bugs were the victims of mechanical trauma rather than nutritional deficiency, since several dead bugs were found caught in the mesh of the cage. The missing bugs are more challenging to explain, since no obvious holes were found with the exception of a few bags and there were no gaps where the bags were wired to the branches. However, a few bugs may have escaped before they could be counted, or if they died they were difficult to locate in the dense foliage.

It is likely the needles provided some sustenance in the field tests as well, since laboratory observations showed that a portion of both adults and nymphs fed on needles, and 80% of the nymphs confined with foliage alone survived. The overall high survival rate of bugs confined in laboratory containers was aided by the protected conditions and the relatively brief period of confinement, but this as well as the number that were able to complete their final molt to adulthood provide further evidence for the ability of seed bugs to successfully feed on whitebark pine at least for short periods of time. In comparison, Koerber (1963) described experiments in which seed bug adults caged on Douglas-fir foliage were unable to survive more than 2 weeks, and nymphs lasted less than a week. However, first-instar nymphs were able to grow to maturity on the seeds of 13 different conifer species including six pines, so the inclusion
of whitebark pine as a seed bug food source accords well with the bug's generalist feeding habits.

The laboratory feeding observations were not sufficient in number or duration to enable definitive conclusions as to whether adult feeding behavior on whitebark pine differed markedly from that of nymphs or whether seed bugs favored ponderosa pine over whitebark pine as a food source. The proportion of adults that fed (one-half) and the percentage of time they spent feeding (59%) compare with laboratory observations of *L. corculus* on loblolly pine in which half of the 55 bugs observed fed for 33% of the time (Williams and Goyer 1980).

**Cone and Seed Analysis.** Several insects besides the seed bug that were found during cone dissection are noteworthy. The seed chalcid *Megastigmus* sp. has not been formally documented on whitebark pine. Although *Megastigmus* larvae damaged only 4.7% of the seed from one site, this genus is well known in a wide range of other conifers and is capable of damaging from 2 to 57% of a seed crop (Hedlin et al. 1980). Since most conifers other than firs are only infested by one species of seed chalcid, a positive identification of the species infesting whitebark pine would be of interest. Cecidomyiid larvae were also recorded for the first time on whitebark pine. They did not occur in large numbers and appeared to cause minimal damage in the form of resinous deposits around some seeds which may inhibit germination. The cone beetle *Conophthorus* sp. is notable for its virtual absence in whitebark pine. Although Kegley *et al.* (in prep.) trapped cone beetles at three of seven sites, it damaged less than 1% of cones. This genus is well represented in pines other than whitebark, including the
ecologically similar limber pine, where it destroyed 11.47% of cones and over 13,000 seeds in a 2-year study in northern Utah (Nebeker 1970). Cone beetle incidence and damage may increase during low cone crop years, but the current evidence suggests that whitebark pine suffers less from this cone insect than most other pines.

The results of this study differed from those of Kegley et al. (in prep.) in many respects, and the comparisons are illustrated in Table 9. One important distinction between the studies that could account for some of the variation in cone measurements and insect fauna was that Kegley et al. included sites in Washington, Oregon, and California and therefore covered more of the geographical and elevational range of whitebark pine. Although the cone crops were similar for both studies, the 3-year gap between them (1996 to 1999) would allow for some natural cycling of cone insect populations, which could further explain differences in insects found. Although precise measurements of past cone crop size do not exist for the sites used in this study, whitebark pine cone crop cycling in the Yellowstone ecosystem has been well documented since 1980 by the USGS Interagency Grizzly Bear Study Team (Haroldson 1999). This area had an overall moderate crop in 1996 followed by a poor crop in 1997, and another poor but highly variable crop in 1998. If the study sites of the current study also experienced poor cone crops in 1997 and 1998, then the populations of cone and seed insects may have dropped enough to result in the low incidence of insect damage in 1999. However, if geographical variation in cone crop size is the rule, the crop history of the current study's sites could easily differ from that reported for the Yellowstone ecosystem. Knowledge of each site's individual crop
TABLE 9. A comparison of cone and seed measures and insects found on whitebark pine cones in the current study vs. that of Kegley et al. (in prep.).

<table>
<thead>
<tr>
<th>Factor of comparison</th>
<th>Current Study</th>
<th>Kegley et al. (in prep.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cone length</td>
<td>5.5 to 6.6 cm, longest cones at two highest elevation sites</td>
<td>4.5 to 5.6 cm, shortest cones at highest elevation site</td>
</tr>
<tr>
<td>Number of seed</td>
<td>1 to 156 (fully developed)</td>
<td>0 to 208</td>
</tr>
<tr>
<td>extracted</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percentage of potential seeds</td>
<td>40.6 to 69.4%</td>
<td>32 to 62%</td>
</tr>
<tr>
<td>extracted</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percentage of filled</td>
<td>2.6 to 28.3%</td>
<td>36 to 77%</td>
</tr>
<tr>
<td>seeds</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cone crop size</td>
<td>Moderate to heavy</td>
<td>Moderate</td>
</tr>
<tr>
<td>Presence and prevalence of:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dioryctria sp.</td>
<td>Present in 0 to 5% of cones, damaged 0 to 4.3% of seeds</td>
<td>Present in 0 to 39% of cones, damaged 0 to 5% of seeds</td>
</tr>
<tr>
<td>Adelgids</td>
<td>Present on branches but not great numbers on cones</td>
<td>Present on 0 to 16% of cones</td>
</tr>
<tr>
<td>Seed bugs</td>
<td>Damaged from 0.3 to 2.1% of seeds, no difference in damage</td>
<td>Damaged from 0.9 to 16.9% of seeds, greatest</td>
</tr>
<tr>
<td>with elevation</td>
<td></td>
<td>damage at highest elevation site</td>
</tr>
<tr>
<td>Cecidomyiids</td>
<td>Present in cones at 4 of 5 sites</td>
<td>Not present</td>
</tr>
<tr>
<td>Megastigmus sp.</td>
<td>Damaged 4.7% of seeds at one site</td>
<td>Not present</td>
</tr>
<tr>
<td>Cydia sp.</td>
<td>Not present</td>
<td>Damaged 0.2% of seeds at one site</td>
</tr>
<tr>
<td>Conophthorus ponderosae</td>
<td>Possibly one beetle larva</td>
<td>Present in 0.2% of cones from one site</td>
</tr>
</tbody>
</table>

history would therefore be the most helpful in explaining the current cone insect population levels.

Another disparity was that Kegley et al. reported a "possible seed bug" category in their seed x-ray interpretation, reflecting the uncertainties surrounding this
analysis. An even more conservative approach was used in the current study such that any seed that was not definitely damaged by a seed bug or other insect was classified in the "non-insect damage" category. With the exception of the high seed bug damage of 16.9% reported by Kegley et al. from Daisy Pass, MT, the range of seed bug damage between the two studies was between 0.3 and 4.4%. The result from Daisy Pass led Kegley et al. to speculate on a relationship between higher elevations and increased seed bug incidence and seed damage. The current study found little evidence to support this idea, since there was an elevation difference in seed bug damage at only one site, and the two highest elevation sites overall showed the lowest incidence of seed bug damage. It is also worthy of note that no seed bugs were observed at any of the study sites at any time during this investigation, either on a cone or in the general area, and Kegley et al. reported seeing only one on a cone during the entirety of their field work. Although *L. occidentalis* is actively expanding its range eastward (Gall 1992) and is able to survive on many different conifer hosts, there is to date no evidence that it possesses an unusual aptitude for high elevations.

The uncertainties surrounding the appearance of seed bug damage to x-rayed seeds have been well documented. Pasek and Dix (1988) reported *L. occidentalis* damage to ponderosa pine seeds of between 8.6 and 27.9%, but stated that radiography is not suitable for detecting damage that occurs before seed coats harden, or for damage that results in an empty seed. The same problem appears in Douglas-fir and western white pine, in which late-season effects are detectable in x-rays but early-season effects including seed abortion are not (Connelly and Schowalter 1991). It
was hoped that the current study would shed some light on this uncertainty by demonstrating what seed bug damage looked like in seeds that were known to be fed upon either in the laboratory or in the field. However, the cones from the seed bug treatment in the field had seeds with varying degrees of imperfection (as did the cones from the other treatments) and it was not possible to distinguish except in obvious cases whether such damage was actually due to seed bugs. Krugman and Koerber (1969) were able to improve upon this situation for ponderosa pine with a detailed histological examination of seeds fed upon by *L. occidentalis* in the laboratory for varying periods of time at various stages of seed development. However, despite their substantial contribution, one of their concluding remarks was, "Even under semicontrolled conditions of forced insect attack, it is not always possible to detect the injury caused by this insect." DeBarr (1970) partially echoed this sentiment in an examination of *L. corculus* on slash pine (*P. elliottii* Engelm.), but gave an overall favorable rating of radiography as a technique for detecting seed bug damage.

Evidently the damage categories were more clear-cut, but since seeds from only two trees were used, the natural variation in seed appearance may have been somewhat limited. Also, it was possible to detect stylet puncture holes in the seed coats and this was used to confirm the x-ray analysis. Without this confirmation, it was necessary in the current study to adopt a conservative definition for seed bug damage.

As mentioned above, bagging and caging the cones may have affected the survival of seed bugs in the feeding tests, and it also appeared to affect the cones. The bagged cones at Galena and Togwotee overall were shorter, had fewer fully developed
seeds per cone, and had a lower percentage of potential seeds than the caged cones at these sites. The altered microclimate due to the bags may not have been favorable for cone maturation. The unexpected greater incidence of seed bug damage on bagged than on caged cones is not easily explained, since bags were held out away from cones by the cages underneath and should not have allowed feeding through the bag. This is not an impossibility, however, as Pasek and Dix (1988) reported a few seeds with seed bug damage from ponderosa pine cones bagged in a similar manner. They also described a five-fold increase in seed bug damage in unprotected cones versus bagged cones, indicating that seed bugs were much more of a factor in their study. A different pattern is described by Blatt and Borden (1996), who showed no difference between bagged and non-bagged Douglas-fir cones in the number of seedbug-damaged seeds and ascribed it to an overall low L. occidentalis population. In the current study the difference in seed bug damage to caged versus bagged cones was less than 0.5% and probably indicates a similar low-density seed bug population.

Another issue raised by caging cones is whether the cages affected natural insect feeding behavior by causing insects to avoid the caged cones in favor of non-obstructed cones. Without controlled tests this would be difficult to ascertain, but insects such as Megastigmus sp. and Dioryctria sp. that lay eggs in the cones early in the growing season would probably have been unaffected by cages placed on cones in July.

There were no striking within-site elevational trends in cone or seed characteristics with the exception of the percentage of filled seed per cone, which was
significantly lower at the upper subsites in four of the five sites. It is likely that the differences in elevation between subsites were not great enough to cause a marked change in altitude-related stresses. However, when comparing the five sites overall, the two highest sites, Galena and Togwotee, had the longest cones with the most seeds and the highest percentage of potential seeds per cone. These two sites also experienced the lowest incidence of seed bug and overall insect damage. These differences cannot be unequivocally attributed to higher elevation since these sites were also the furthest south and each site had a unique set of topographical and climatic factors that could have affected cones and seeds. For instance, Togwotee had an extremely high percentage of imperfect seeds per cone at both subsites, indicating the presence of some stressor, possibly a fungus, that was absent from the other sites. Some of the sampled trees from Seven Devils and Snowbank had blister rust cankers on their trunks and branches, but cone production and vigor did not appear to suffer.

The incidence of cone and seed insect damage in this study indicates that these insects are not a great threat to whitebark pine vigor and reproduction at these sites, although damage to seeds would likely increase in a low cone crop year. This damage could be even more serious if the Clark's nutcracker habitually chooses cones for seed removal which have the most viable seeds, as has been demonstrated in pinyon pine (Christensen and Whitham 1991). Such discrimination would result in less seed dispersal than if seeds were uniformly normal. Confirmation of this nutcracker behavior in whitebark pine would be valuable.
Although *L. occidentalis* was demonstrated to be capable of surviving on whitebark pine for short periods of time, it is unlikely that this insect normally prefers it as a primary food source. Since it can obtain food from so many other lower-elevation conifer species, perhaps it only occasionally ventures to the higher elevations of whitebark pine under pressure from intense competition or scarcity of cones at lower sites. Threats such as blister rust and the mountain pine beetle are undoubtedly greater challenges to the future of whitebark pine.
CHAPTER IV
THE CONE AND SEED INSECTS OF ALPINE LARCH
EMPHASIZING STROBILOMYIA SPP.

Introduction

Alpine larch, *Larix lyallii* Parl. is a deciduous conifer that grows in the subalpine and timberline zones in the mountains of the inland Pacific Northwest (Arno and Habeck 1972). It is limited to elevations between about 1520 and 3020 m. Its superior tolerance of high-altitude climatic extremes enables it to thrive on harsh sites that reduce other tree species to krummholz forms. It benefits the treeline community by providing watershed protection, wildlife habitat, and snow stabilization (Arno *et al.* 1992). Due to its poor lumber quality and inaccessibility, alpine larch has little potential for commercial exploitation, and the research it has received to date leaves many unanswered questions. For example, while it is known that large seed crops are infrequent, the factors besides frost which limit seed production have not been investigated.

One such factor could be cone and seed insects, although the evidence is largely anecdotal and the few published accounts lack details. Carlson and Ballinger (1992) reported placing mesh bags over cones to protect them from insect damage in a cross-pollination study with alpine larch, but the insects remain unspecified. The larch cone fly, *Strobilomyia* spp., which is known to occur on all other larch species worldwide (Michelsen 1988), may be of particular interest. Arno and Habeck (1972)
reported that a heavy crop of cones on alpine larch in the Washington Cascades in 1969 was almost entirely decimated by larvae of unidentified Diptera. A more concrete reference comes from Michelsen (1988) who reported that *S. macalpinei* Michelsen is known only from type material reared from cones of tamarack and alpine larch.

As an alternative to obtaining fly larvae from cones directly, which can be difficult in a tree species with infrequent cone crops, visual trapping has been used successfully on European larch to obtain adult cone fly specimens. (Roques 1986; Jenkins and Roques 1993; Roques *et al.* 1995). Colored traps that attract cone flies have the potential to capture specimens even when the cone crop is poor or non-existent since these insects are known to undergo prolonged diapause and it is possible that some may emerge every year whether an abundant cone crop exists or not (Roques 1989). The discovery of cone flies in alpine larch by trapping or by direct rearing from cones would provide valuable new information about the range and adaptive abilities of the genus *Strobilomyia*.

The objectives of this study were to (1) identify any cone and seed insects found on alpine larch cones; and (2) attempt to document the presence of larch cone flies in a stand of alpine larch using colored traps.

**Materials and Methods**

An attempt was made to locate current-year alpine larch cones in the summer of 1998 at various sites throughout the range of alpine larch, but no cones were found.
Colored traps were set up on 26 June 1999, on Carlton Ridge in the Bitterroot Range of Montana using methods similar to those used by Jenkins and Roques (1993). The stand, at an elevation of 2490 m, was predominantly alpine larch with some Engelmann spruce and whitebark pine. No current-year cones could be found on the larch. Twelve traps were constructed of plywood squares about 20 x 20 x 1 cm and covered on one side by either Letraset Pantone "Yellow A" paper (Letraset, Paramus, NJ), or posterboard sprayed with fluorescent yellow paint. Six of these traps each had two 1 x 20 cm purple strips of Letraset Pantone "Purple A" paper glued 6 cm from either edge. These traps were mounted vertically on stakes 2 m above the ground and secured with guy wires. The six plain yellow traps were mounted horizontally on stakes 40 cm above the ground and 2 m in front of the vertical traps. All traps were sprayed with Tangle-Trap® (The Tanglefoot Company, Grand Rapids, MI) and were changed every week or 2 weeks until they were taken down on 31 July. Five traps were sent to Jean Turgeon at the Great Lakes Forestry Centre in Ontario, Canada, to be examined for the presence of larch cone flies.

In addition, 100 cones were collected from two isolated alpine larch trees at 2290 m near Twin Lakes in the Bitterroot Range on 5 August 1999. Almost all cones examined hosted one or more Diptera maggots, and some puparia were found as well. Ten light mesh bags were placed over cones still on the tree to catch any larvae that dropped out of the cones. These cones as well as 200 additional cones were collected on 3 September. Most of these contained puparia. A portion of the puparia were removed from the cones while the remaining cones were left undisturbed and all were
placed in trays of vermiculite for rearing outdoors. In mid-November, 20 cones were removed from the trays and put in a refrigerator at 2°C. In mid-January, these cones were removed from the refrigerator and a portion were taken apart and the puparia removed. These were all placed in a tray of vermiculite and allowed to remain out at room temperature. One hundred cones were then selected at random from the total collection and dissected to record the presence of cone fly larvae or pupae.

**Results**

The colored traps were effective at trapping flies of many species, and densities reached over 200 flies per trap. However, no cone flies were found on the five traps examined.

On 31 January, two adult cone flies were discovered in the indoor vermiculite tray. These were identified as a male and female *Strobilomyia macalpinei* Michelsen by Jean Turgeon at the Great Lakes Forestry Centre in Ontario, Canada.

The mesh bags placed over cones on the tree caught many dead larvae and a puparium. Of the 100 cones dissected, 64 contained puparia or desiccated larvae. Seven cones contained two larvae and two contained three. Thirty of the remaining 36 cones had frass and damaged seeds.

**Discussion**

There has been no mention of *S. macalpinei* in the literature since its description in 1988 by Michelsen, who stated that this species was known only from
the type material reared from tamarack and alpine larch cones in Alberta in 1962 and 1965. The discovery of *S. macalpinei* in alpine larch in Montana is the first documentation of the species in the United States.

The variability possible in alpine larch cone crops is illustrated by the complete lack of cones at Carlton Ridge versus their great abundance only 60 km to the south on a few trees above Twin Lakes. The high frequency of cone fly maggots and puparia in the cones from Twin Lakes and the lack of adult cone flies on colored traps at Carlton Ridge may indicate that *S. macalpinei* has adapted to the irregularity of its food source by undergoing prolonged diapause, similarly to *Strobilomyia* spp. in Europe (Roques 1988). If *S. macalpinei* is unique to high altitudes as Michelsen (1988) suggested, an ability to synchronize its emergence from diapause with the size of the current year's cone crop would be especially advantageous for survival at elevations where cone crops are as infrequent as one year in ten and are patchy in distribution. The high frequency of cone flies in the available cones at Twin Lakes supports this supposition. However, the mechanisms that could underlie such synchronization are unknown. It has been hypothesized that prolonged diapause termination is related to climatic factors since the puparia are buried in the litter and are out of the range of direct influence from the tree (Roques 1989). One possibility is that temperatures during the time of seed cone bud differentiation in the season preceding emergence could affect the proportion of insects that actually emerge, as has been found by Miller and Ruth (1986) for the Douglas-fir cone moth [*Barbara colfaxiana* (Kearfott)] (Lepidoptera: Olethreutidae). Weather factors that affect cone production could therefore also be
involved in diapause termination (Roques 1989), although a positive correlation
between these two occurrences has been observed in some cases but not in others
(Turgeon et al. 1994).

If synchronization does not occur, it is possible that a portion of diapausing flies
emerges each year regardless of cone abundance, since the population as a whole
would then be more likely to survive events such as late frosts that could cause
synchronization to backfire by destroying cones but having no effect on insect
emergence (Roques 1989). The presence of cone flies on the colored traps where no
cones were present would have supported this hypothesis. However, more concrete
evidence is needed and will require further tracking of alpine larch cone crops and cone
fly populations over a wider area and for many successive years.

The lack of cone flies on the colored traps does not necessarily imply their
absence from the stand, since the remains of cone fly puparia were found in weathered
cones on the ground and in trees in the area, indicating their presence in cones at the
time of the last significant cone crop. Puparia were also found in 1998 in old cones
from sites in the Whitefish Range of Montana and in the North Cascades of
Washington. Populations of cone flies may therefore exist in alpine larch in many
diverse locations, and *S. macalpinei* is likely to be at least one if not the dominant
species.

The literature on *Strobilomyia* spp. states that third-instar larvae normally bore
an emergence hole in the cone in late summer or early fall and drop to the ground
where they form puparia and overwinter (Roques 1988; Michelsen 1988), but this
appears not to be the only possible scenario for *S. macalpinei*. Although 30% of the dissected cones were damaged and contained no larvae, and larvae that dropped from cones were found in the mesh bags, there were fully formed puparia in 38% of the cones. Roques (1988) stated that cone fly attack causes cones to become lignified and lose moisture more quickly than normal, and that this might hinder or block larval exit. This may have occurred in some of the dissected cones, but some of the larvae were able to form puparia and stay alive instead of succumbing to desiccation. However, adult emergence might then be impeded since puparia were usually found embedded in the cone axis. The two adult flies that were found in the rearing tray most likely came from puparia that had been removed from the cone.

Although the scope of this study was limited, it offers confirmation of *S. macalpinei* in alpine larch and suggests that its potential for seed damage may be high depending on cone crop frequencies. Further long-term observations could overcome the problem of alpine larch's rare cone crops and could address such questions as whether *S. macalpinei* is the only cone fly species that attacks alpine larch cones, how much impact it has on alpine larch reproduction, what kind of life history patterns and diapausin strategies it uses, and whether it possesses any unusual adaptations for its high-altitude environment.
CHAPTER V
CONCLUSIONS

The two studies of cone and seed insects on whitebark pine and alpine larch succeeded in meeting their objectives. It was demonstrated that *L. occidentalis* can use whitebark pine as a food source for short periods of time, with over 80% survival in field feeding trials and over 90% survival in laboratory tests. There was a lower percentage of filled seeds per cone at four out of five upper elevation subsites, but otherwise the effects of elevation on cone and seed characteristics and seed bug survival in field tests were not significant. No evidence was found to support the hypothesis of Kegley *et al.* (in prep.) that seed bugs may do more damage at higher elevation sites. Overall seed bug damage was 0.3 to 2.1%, and there was a difference of only 0.5% in damage between cones that were protected from seed bug feeding versus those that were exposed to open feeding, which indicates low seed bug densities at the study sites. Total insect damage ranged between 0.4 and 7.2%, and included damage by *Megastigmus* sp., an insect which has not been formally documented on whitebark pine. Uncertainties surrounding the accurate analysis of seed bug damage on x-rayed seeds were problematic and should be specifically addressed with further study.

The presence of the larch cone fly *Strobilomyia macalpinei* was confirmed in alpine larch cones, thus expanding the known range of this unstudied species. A sample of dissected cones revealed that 94% were damaged, and larvae or puparia were found inside 64% of cones examined. This cone fly has the potential to
substantially decrease alpine larch reproduction depending on cone crop size and frequency. Colored traps set out during late June and July in a stand of alpine larch with no cones failed to trap larch cone flies, but cone fly presence in the stand was ascertained from puparia in old cones. The flies may therefore undergo extended diapause, and further investigation is needed to ascertain what factors may trigger their emergence from diapause.

These two studies together provide evidence that cone and seed insects are alive and well at high elevations, although their impact on tree reproduction depends heavily on the availability of cones from year to year. Whitebark pine in a moderate to heavy cone crop year experienced minimal cone insect predation, while a spatially sparse cone crop in alpine larch received substantial infestation from cone flies. One season of observations is insufficient to draw any definitive conclusions, but these studies provide a baseline of data for further investigation.
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