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BIONOMICS AND NATURAL CONTROL OF THE CONE AND SEED INSECTS OF PONDEROSA PINE IN IDAHO AND ADJACENT WASHINGTON AND MONTANA

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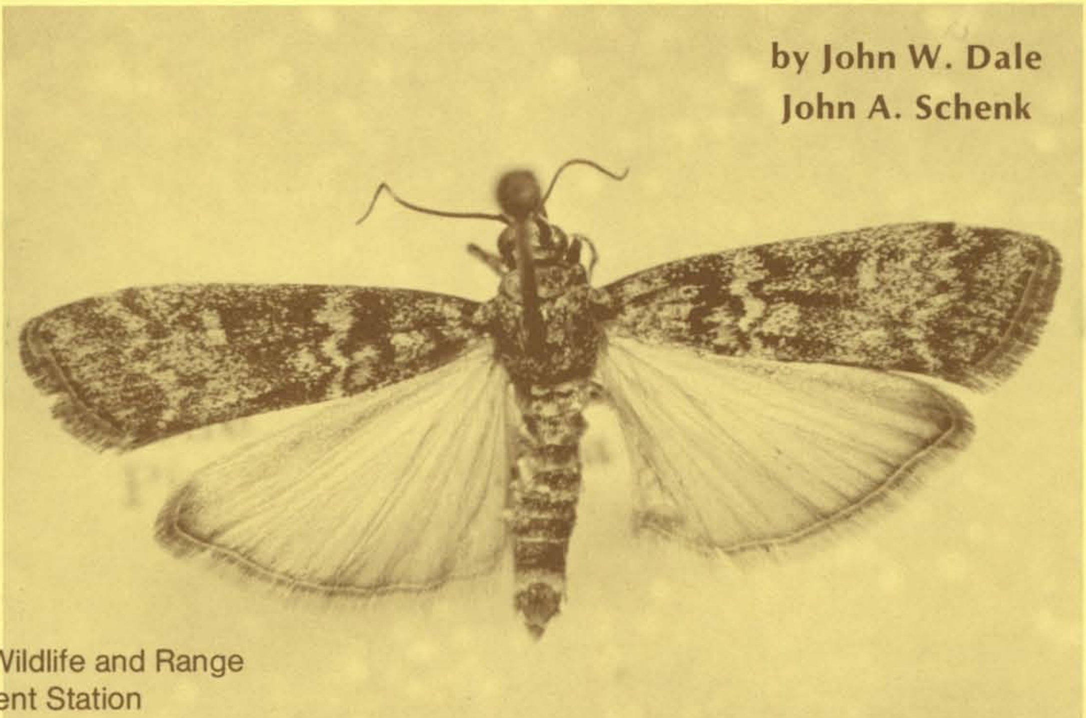

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ABSTRACT

The life history and habits of the cone and seed insects of ponderosa pine, *Pinus ponderosa* Lawson, are discussed. Recommendations for mitigating seed losses in seed production areas and seed orchards are proposed. The major mortality factors operating on these insect pests were: entomophagous insects, severe winter temperatures, cone-crop failure, interspecific competition, cone (scale) response to spring moisture, drowning, and vertebrate predators. Major pest species were: *Laspeyresia miscitata* Heinrich, *L. piperana* (Kearfott), and *Conophthorus ponderosae* Hopkins. *Dioryctria auranticella* (Grote), *D. abietella* (Denis and Schiffermueller), *Eucosma ponderosa* Powell, *Leptoglossus occidentalis* Heidemann, and *Asynapta keeni* (Foote) showed potential for causing serious seed losses.

Key words: Cone and seed insects, insect behavior, ponderosa pine, seed orchards, seed production areas.

Bionomics and Natural Control of the Cone and Seed Insects of Ponderosa Pine in Idaho and Adjacent Washington and Montana

John W. Dale and John A. Schenk

INTRODUCTION

Ponderosa pine, *Pinus ponderosa* var. *ponderosa* Lawson, is the most extensively planted and the second most important commercial tree species in Idaho (Wilson 1962). Natural reproduction intermittently occurs when a heavy cone crop and favorable weather conditions are combined with a minimum of losses to insects and other destructive agents. Thus, artifical regeneration following logging or wildfire is important in the silviculture of ponderosa pine, and an adequate source of quality seed is prerequisite.

Tree improvement programs and the need for easily accessible seed sources provided the impetus for the establishment of progeny test plantations and the organization of a forest tree improvement program in Idaho. Federal, state and private cooperators agreed to concentrate on ponderosa pine (Wang 1967), and four 5.2-ha (13-acre) plantations were established in southern Idaho in 1966. A similar program was initiated in 1971 in northern Idaho.

Seed orchards and seed production areas will not replace natural stands in the near future as a source of seed required for the extensive reforestation programs underway or planned. Knowledge of the relationships between fluctuations on cone crops, environmental factors and insect-caused seed losses would permit seed collections of maximum quantity at minimum cost. Application of this knowledge to stands nearing economic maturity also would permit timing of regenerative cuttings to obtain desired levels of reproduction commensurate with climatic conditions.

Cone and seed insects of ponderosa pine in the western United States were investigated first by Miller (1914, 1915). He described the habits and damage of the scolytid *Conophthorus ponderosae* Hopkins, and the seed moths, *Laspeyresia* spp. Some of his specimens were described as new species by Hopkins (1915) and Heinrich (1926), and were used by MacKay (1959) to provide larval descriptions of *Laspeyresia piperana* (Kearfott) and *Hedula injectiva* Heinrich (Koerber 1967).

Interest waned until tree improvement programs were initiated on a large scale in the 1950s, and the publication by Keen (1958) of a comprehensive summary of the information provided by earlier workers. Insects affecting seed production of pine in California were studied by Ruckes (1963), who developed a taxonomic key of the genus *Conophthorus,* including observations on the life history of *C. ponderosae.* Koerber (1967) conducted a comprehensive study of the insect complex affecting ponderosa pine seed production in California. Hedlin (1967) evaluated the damage caused by *L. piperana* in British Columbia and described its life stages. Hedlin (1974) also reviewed the insects affecting the cones and seeds of conifers in British Columbia. Kinzer et al. (1970, 1972) reported on the habits, life cycle and damage of *C. ponderosae* in New Mexico. Seed losses in ponderosa pine in Idaho and adjacent Washington and Montana were reported by Dale and Schenk (1978).

METHODS

Site (Stand) Description

Ten intensive study sites (stands) were selected throughout the range of ponderosa pine in the study area to represent a variety of geographic and physiographic conditions (Fig. 1, A-J). They also were selected for their potential as seed production areas, and for frequency and

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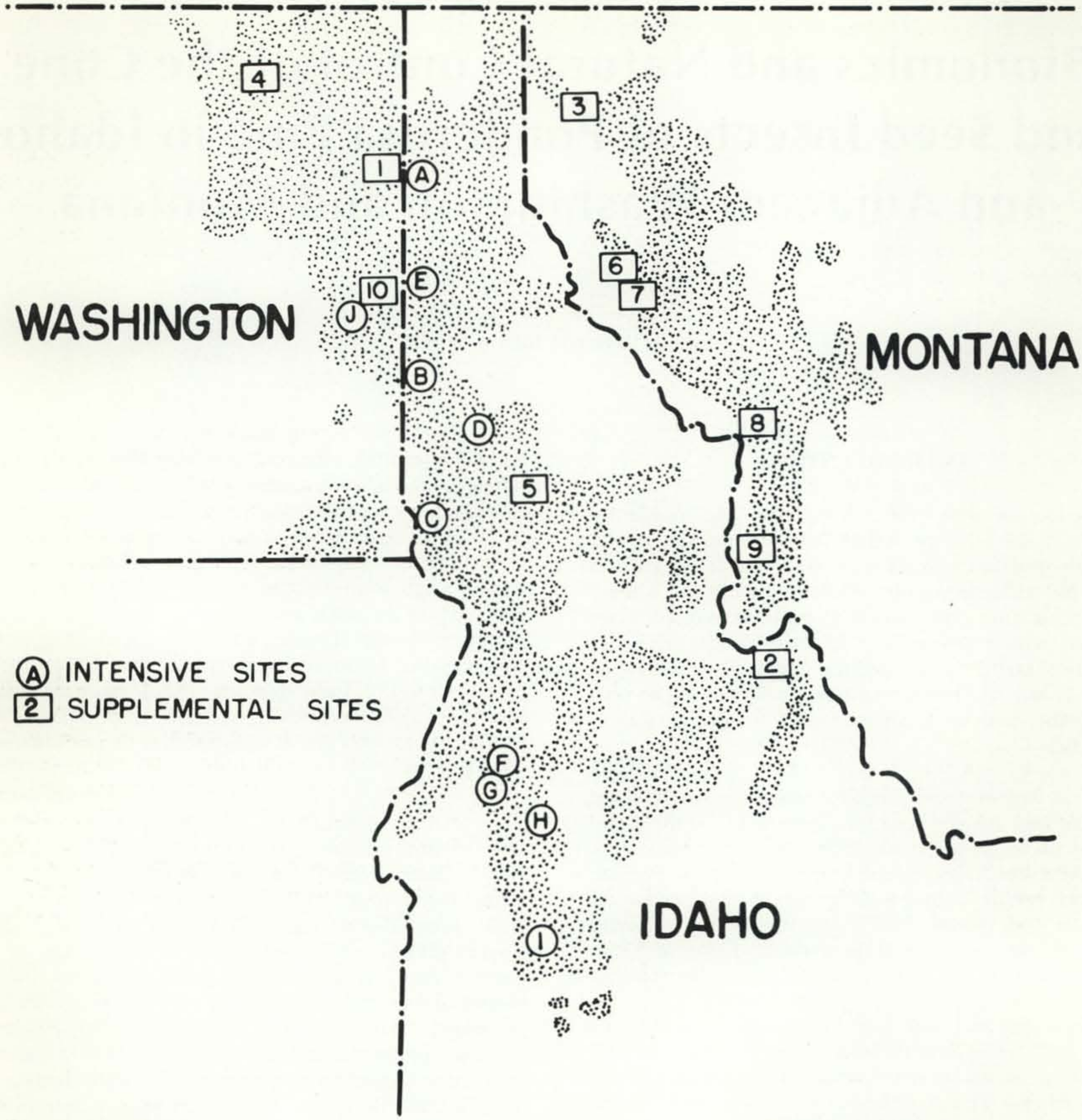

Intensive Sites	
Blanchard, ID	A
Potlatch, ID	B
Waha, ID	C
Helmer, ID	D
Mica, ID	E
New Meadows, ID	F
Council, ID	G
Cascade, ID	H
Idaho City, ID	I
Cheney, WA	J

Supplemental Sites	
Elk, WA	1
Salmon, ID	2
Libby, MT	3
Kettle Falls, WA	4
Kooskia, ID	5
Thompson Falls, MT	6
St. Regis, MT	7
Lolo, MT	8
Darby, MT	9
Rockford, WA	10

Fig. 1. Distribution of ponderosa pine and the location of intensive and supplemental study sites in Idaho and adjacent Washington and Montana.

size of cone crops (determined by the number and age of old cones on the ground and number of scars and remnants of rosettes on the branches).

Most of the intensive study sites were sampled three times (once each month from June through August). The more distant sites were sampled only twice, while those nearby were sampled additionally in May and September. Ten supplemental sites (Fig. 1, 1-10) were sampled once or twice during the entire study period to determine more definitively geographic distribution of the major insect species.

Ten circular 0.04-ha (1/10-acre) plots were established on each intensive study site at varying grid intervals to accommodate variation in stand area. One dominant ponderosa pine on each of the 10 plots per site was measured for height, diameter at breast height (dbh) and age. Recent growth of each of these trees was determined from ring counts per outer inch (2.54 cm) of increment cores taken at breast height. Density, species composition, and cone production were measured at each plot to obtain estimates for the site. Aspect, percent slope, elevation, stand history, and topography also were recorded for each site. Site indices were determined from curves provided by Lynch (1958) and each site identified to habitat type (Daubenmire and Daubenmire 1968; Steele et al. 1975, 1976). A circular plot (124 m^2) was established on each site to provide data on presence, constancy and abundance of understory vegetation. All observations were evaluated in relation to presence, abundance and biologies of the cone and seed insect species. Relationships between site (stand) characters, cone production and insect-caused seed losses have been reported elsewhere (Dale and Schenk 1978).

Relative Abundance of Insect Species

Numbers of seed moths and cone midges were estimated from the product of the estimated number of cones per acre (0.4 ha) and the mean number of insects per cone. Numbers of cone beetles (*C. ponderosae*) and coneworms (*Dioryctria* spp.) per acre (0.4 ha) were estimated from the mean number per infested cone and the number of infested cones on the 10 plots (obtained by actual counts in climbed trees). These numerical estimates, combined with the type and amount of damage, provided subjective evaluations of the relative importance of each insect species.

Life History and Habits

One cone-bearing ponderosa pine was selected per plot for intensive cone collection. A ponderosa pine nearest the plot boundary was selected for those plots having no cone-bearing trees. Cone samples were collected from these trees from May through August to ascertain damage type and amount, and various data on life history and habits for each insect species present.

Samples consisted of eight cones (4 each from the north and south aspects) from the upper third of the crown (long, large branches and low numbers of cones precluded efficient sampling from the lower crown). Two cones from each aspect of the tree were placed in rearing chambers to obtain adult insect specimens. The remaining cones were examined by the axial-slice method, followed by a complete scale-by-scale examination. The number of individuals and the number of seeds destroyed were recorded by species and life stage in each cone, along with the numbers of aborted and sound seeds.

Table 1. Location and characteristics of intensive study sites.[a]

Location	Symbol [b]	Elevation (ft)	Aspect	Slope %	Basal area (ft^2/ac)	Stems/acre	% crown closure
Blanchard, WA	A	2,300	S	1	154	312	50
Cheney, WA	J	2,250	S	1	140	152	40
Mica, WA	E	3,200	S	7-12	11.4	28	20
Potlatch 1, ID	B	2,560	N	0-25	133.5	110	75
Potlatch 2, ID	B	2,600	NW	4-30	169	219	50
Potlatch 3, ID	B	2,560	S	4-30	125	141	65
Helmer, ID	D	3,100	S	2-10	21[c]	17[c]	25
Waha, ID	C	3,800	S	15	41	97	50
New Meadows, ID	F	4,500	NW	5	61.2	184	40
Council, ID	G	4,400	SW	5-40	95.5	71	50
Cascade, ID	H	4,900	SW	0-30	56.8	104	75
Idaho City, ID	I	4,900	S	2-25	100	190	45

[a] 1 ft = 0.305 m; 1 ft^2 = 0.093 m^2; 1 acre = 0.405 ha; 1 ft^2/ac = .023 m^2/ha.

[b] Refers to locations on Fig. 1 (facing page).

[c] Site composed of groups of ponderosa pine bordering abandoned homestead.

Table 2. Characteristics of ponderosa pine component of study sites.[a]

Site	Stocking % BA (ft^2/ac)	Stocking % Stems/ acre	Mean height (ft)	Mean DBH (inch)	Mean age	Mean growth rate[b]	Site index (base 100)
Blanchard, WA	91.6	83.0	72	15.0	84	14	77
Cheney, WA	100.0	100.0	61	13.5	80	19	68
Mica, WA	96.5	96.4	39	10.5	30	5	93
Potlatch 1, ID	95.9	98.2	97	15.9	80	15	106
Potlatch 2, ID	100.0	100.0	98	15.2	84	15	105
Potlatch 3, ID	100.0	100.0	80	15.6	86	18	85
Helmer, ID	100.0	100.0	62	14.4	35	6	115
Waha, ID	100.0	100.0	57	12.9	52	11	84
New Meadows, ID	99.7	99.5	59	14.9	52	10	89
Council, ID	95.3	94.3	71	15.6	50	9	100
Cascade, ID	98.6	98.1	59	13.2	49	11	89
Idaho City, ID	88.0	94.2	77	14.8	58	14	100

[a] 1 inch = 2.54 cm; 1 ft^2 = 0.093 m^2; 1 acre = 0.405 ha.

[b] Mean number of rings per outer inch of sapwood per 10 trees.

[c] Site composed of groups of ponderosa pine bordering abandoned homestead.

Additional cone collections were made at both the intensive and supplemental sites to provide corroborative or new information on the life histories and habits of particular insect species. Laboratory rearings also were conducted to supplement field observations.

Adult parasites were obtained from the regular cone collections placed in rearing chambers, and also from spring collections of cones that had overwintered on the ground or on trees.

RESULTS AND DISCUSSION

Most phases of the study were severely affected by a late spring frost in 1966, which reduced the 1967 cone crop, and a general crop failure in 1969 and 1970. Many sites possessing unique or desired physical and vegetational characteristics could not be included due to the absence of cones. Similarly, naturally high variability in cone production by individual trees precluded continuous annual studies of population fluctuations and damage levels on specific trees.

Site Characteristics

The location and general characteristics of the intensive study sites are presented in Table 1. The characteristics of the ponderosa pine component of the sites are provided in Table 2, and habitat types are presented in Table 3. These data, along with the life histories and habits of the insect species, were examined to provide the recommendations for management of seed production areas presented later.

Table 3. Habitat types for the intensive study sites, 1967-1969.

Site	Habitat Type[a]
Blanchard, WA	Intergrade: *Pseudotsuga menziesii/Physocarpus malvaceus* – *Pseudotsuga menziesii/Calamagrostis rubescens* – *Arctostaphylos uva-ursi* phase
Cheney, WA	*Pinus ponderosa/Agropyron spicatum*
Mica, WA	*Pseudotsuga menziesii/Physocarpus malvaceus*
Potlatch 1, ID	*Pseudotsuga menziesii/Physocarpus malvaceus*
Potlatch 2, ID	*Pseudotsuga menziesii/Physocarpus malvaceus*
Potlatch 3, ID	*Pseudotsuga menziesii/Physocarpus malvaceus*
Helmer, ID	*Abies grandis/Pachistima myrsinites*
Waha, ID	*Pseudotsuga menziesii/Symphoricarpos albus*
New Meadows, ID	*Pseudotsuga menziesii/Physocarpus malvaceus*
Council, ID	*Abies grandis/Spirea betulifolia*
Cascade, ID	*Pseudotsuga menziesii/Symphoricarpos albus*
Idaho City, ID	*Pseudotsuga menziesii/Carex geyeri*

[a] From Daubenmire and Daubenmire (1968), Steele et al. (1975) and Steele et al. (1976).

Species Complex

A total of 48 insect species, representing 24 families and 8 orders, were collected from ponderosa pine. These and other species collected in Idaho were reported by Kulhavy et al. (1975). Only 16 of these species are classed as damaging, while 26 are entomophagous, and the remaining 6 are inquilines or secondary invaders.

The pine seed chalcid, *Megastigmus albifrons* Walker (Hymenoptera: Torymidae), was suspected as a damaging species (Keen 1958), but was not found in any of the thousands of ponderosa pine seeds examined. Koerber (1967) also did not find this species infesting seeds in California, but Kinger et al. (1972) collected it in New Mexico.

Dichelonyx crotchi Horn (Coleoptera: Scarabaeidae) has been reported to damage conelets of ponderosa pine (Koerber 1967). This species has not been recorded in the Pacific Northwest (Hatch 1971), and was not observed during the study period.

Laspeyresia miscitata Heinrich (Lepidoptera: Olethreutidae)

Description of Life Stages and Life Cycle

Two species of *Laspeyresia*, *L. miscitata* Heinrich and *L. piperana*, were collected in the study area. Both are similar in appearance. *Hedula injectiva* also closely resembles these *Laspeyresia* species and has been recorded infesting ponderosa pine cones in California, Nevada and Oregon (Heinrich 1926). It was not collected during the present study. Koerber (1967) concluded that *L. miscitata* is not a hybrid of the other two species as suggested by Heinrich (1926), and that the three species are morphologically and biologically distinguishable.

Adult. The adults of *L. miscitata* are noticeably smaller than those of *L. piperana.* The costal margin of the forewings is black, interrupted by white markings. The background coloration of *L. miscitata* is dark grey, while that of *L. piperana* is light grey.

Adult emergence from cones commenced 2 weeks after the cones were removed from the field in March and placed in rearing chambers under laboratory conditions (23°C ± 2°). Emergence was completed in about 2.5 weeks. Males emerged an average of 6 days earlier than females in the laboratory; however, there was no difference between emergence of the sexes from field cages. Emerged adults showed a 1.17:1 sex ratio in favor of the males ($\chi^2 = 4.18$, n = 673). When adults were furnished with a sugar-water solution in the laboratory, longevity of both sexes was about 5 days (Merkel and Fatzinger 1966); however, only one was observed in an actual feeding attempt.

Egg. Freshly deposited eggs are white, oval and 0.49 to 0.67 mm long, with finely reticulate chorion. They become reddish in color with embryo maturation. Eclosion occurred in 9 to 10 days at 28° C.

Larvae. First instar larvae have black head capsules, and a smoky-grey prothoracic shield. Lateral setae are quite prominent relative to the inconspicuous setae of later instars. Prolegs are more developed in this instar than in subsequent ones, and the claws of the thoracic legs are bifurcate and setaceous.

The first four instars could not be distinguished by analysis of head capsule measurements, probably due to a mixture of the two *Laspeyresia* species. Head capsule pigmentation of the second through fourth instars is very similar to *L. piperana* (MacKay 1959), making separation of these four instars of the two species impossible. However, mature (fifth instar) larvae of *L. miscitata* can be distinguished from those of *L. piperana* by the absence of the light-colored bands on the head capsule described by Koerber (1967) as present on *L. piperana.* Because of the inability to differentiate the earlier instars of the two species, it was necessary to assume similar life cycles and behavior during those stages.

Pupae. Pupation occurred in cones maintained in the laboratory at 12° C, but did not at 5° C. Newly formed pupae were creamy-white, but changed to a pale amber color within a few hours as they sclerotized, and were black just prior to adult emergence. Sex is identified by length of antennae and the position of the genital opening (Tripp 1954). Koerber (1967) noted that *L. miscitata* pupae can be distinguised from *L. piperana* pupae by the more rounded anterior end of *miscitata* when viewed ventrally.

Bionomics

Behavior. Adults emerged from early May into June at elevations of 600 to 900 m (2000 to 3000 ft). Cones suspended from trees in plastic-screen cages at about 15 m (50 ft) opened more frequently, permitting a protracted emergence period. Emergence from cones caged on the ground, in sun or shade, was less frequent but with greater numbers emerging per interval than from cones on the trees. Apparently emergence requires only short, daily (or infrequent) periods of cone dihiscence.

Moths were active during all daylight hours in the laboratory, but were observed in the field only from 2 to 6 p.m. Adults of both sexes are strong fliers, and when released flew either with or against a slight evening breeze. Flight elevation from the release point varied from close to, and parallel with, ground level to an almost vertical ascent.

Mating occurs in the late afternoon or early evening. An apparent courtship behavior was observed on one occasion in a field cage. The smaller male approached a female while vigorously fluttering his wings. He then thrust his head under the posterior of the folded wings of the female, who subsequently moved away. The rejected male zig-zagged within a small area while continuing the vigorous wing movement. During this time, he came within 2 cm of a second female, and repeated the same wing beating and movement as with the first female. Then, in an instant, the male reversed position and clasped the second female with his hindlegs and claspers, after which he was dragged for about 5 cm. The pair soon became quiescent and apparently remained in copulation for 15 hours.

Prior to oviposition, the female moves over the cone surface while probing with the tip of her ovipositor. Upon finding a suitable location, she arches her abdomen and occasionally also lifts her wings. Eggs may be deposited singly, but clusters are more common. In the laboratory, eggs were laid in crevices between scales, on tips of scales, and between the papery scales clothing the cone peduncle. An average of 5.5 (2 to 22) eggs were laid per cluster, with each female laying an average of 29 (4 to 48) eggs. Dissection of females showed an average of 246 (133 to 398) oocytes. A few eggs were deposited on the plastic film tops of the rearing cages. However, attempts to induce oviposition on surfaces other than those of cones or cone parts were unsuccessful. Eggs are difficult to detect, and very few were found in field collections.

Upon eclosion, first instar larvae crawl along the crevices between the scales and may traverse a small cone in about 30 minutes while searching for a suitable point of attack. Movement is aided by silk trails, which appear particularly useful when the larvae leave the crevices and crawl up and over scale apophyses.

Entrance into the cones usually is accomplished within 2 hours at the interface between two scales. Once penetration is achieved, the larva mines just beneath the surface of a scale for a short distance. It then either continues this reddish colored mine directly towards a seed, or it will tunnel through one or several scales before proceeding to a seed. A larva occasionally will mine a circular path laterally across the interior surface of several scales before turning toward a seed. A larva that initially mines to an aborted seed will continue its search for an acceptable seed. Finding such a seed, the larva mines in the developing seed coat to the micropyle, the point of entrance. The first instar larva and its mine are easy to detect in scale tissue, but very difficult to detect in the seed coat.

A larva remains within the first seed through the second or third instars. Movement into a second seed occurs in early July, and feeding damage is most intense during the remainder of that month. Damage after 7 August usually is insignificant.

Both seeds of a pair only rarely were infested simultaneously. If a seed adjacent to an infested seed is sound, it is attacked by the larva boring laterally into it only after the first seed is entirely or partially consumed. The mine is lined with tightly woven silk that, along with resin-impregnated frass, holds the seeds to a small ridge of scale tissue located at the interface of the two seeds. Thus, release of damaged seeds is prevented when the cones dehisce and their number can be determined even in old cones. Frass and borings from the second seed are removed and packed in the vacated first seed. A larva moves to damage additional (1 to 17) seeds on other scales after consuming the first pair. This movement usually is circumferential, but movement parallel to the axis is not uncommon.

In late July or early August, the larva mines through the tips of the seed into the cone axis. There is only one entrance hole into the axis for each larva, and this feature can be used to determine the number of mature larvae that once infested vacated cones. Thus, several years of population data can be gathered in 1 year if the age of the old cones is classified.

The larvae mine galleries in either direction within the axis. High populations per cone will completely consume the axis, leaving only thin partitions between galleries. The silk-lined galleries never intersect even when many larvae are present. Thus, in the presence of high populations, a few larvae may be forced to remain in the last seeds consumed. The larvae apparently do not feed on the vascular tissues, and axial mining may be directed primarily to provide suitable overwintering habitat.

Each larva returns to its last mined seed after constructing its axial gallery. At that time a circular exit hole is cut in the seed coat, leaving an operculum attached by silk threads. The majority of these exit holes are cut in the fall; however, some may be cut in late winter or early spring just prior to pupation.

This species usually overwinters in the axis as fifth instar larvae. However, a few larvae collected in January and February molted after being placed in artificial galleries

Table 4. Infestation per cone by *Laspeyresia* spp. in Idaho, Washington and Montana.

No. of insects per cone	No. of cones examined			Percent cones infested		
	1967	1968	Total	1967	1968	Total
1	88	52	140	26.3	9.1	15.4
2	63	65	128	18.8	11.3	14.1
3	52	73	125	15.5	12.7	13.8
4	38	63	101	11.3	11.0	11.1
5	36	64	100	10.8	11.2	11.0
6	20	58	78	6.0	10.1	8.6
7	11	36	47	3.3	6.3	5.2
8	8	31	39	2.4	5.4	4.3
9	5	38	43	1.5	6.6	4.7
10	3	17	20	0.9	3.0	2.2
11	2	14	16	0.6	2.4	1.8
12	2	14	16	0.6	2.4	1.8
13	2	11	13	0.6	1.9	1.4
$>$ 13	5	37	42	1.5	6.5	4.6

Table 5. Proportion of *Laspeyresia* spp. populations showing extended diapause at various locations in Idaho, Washington and Montana, 1968-1969.

Site	1968		1969	
	Cones per acre	% diapausing population	Cones per acre	% diapausing population
Council, ID[a]	2063	0.0	0	70.0
New Meadows, ID	337	10.3	3	33.9
Cascade, ID	612	10.8	0	46.7
Idaho City, ID	1081	11.9	0	9.8
Cheney, WA	4478	13.8	0	36.4
Waha, ID	2380		0	10.9
Blanchard, WA	1037		0	0.8
Salmon, ID			0	3.5
Kooskia, ID			0	5.2
Kettle Falls, WA			0	2.7
Libby, MT			0	4.8
Darby, MT			0	13.4
Lolo, MT			0	4.4
Thompson Falls, MT			0	17.0
St. Regis, MT			0	8.9

[a] Population primarily *L. piperana*; other sites, primarily *L. miscitata.*

in clay blocks. Thus, a small portion of a population may overwinter as fourth instar larvae, and exit holes are constructed in the spring.

The number of larvae per cone in 1968 increased along with a marked increase in the cone crop. The proportion of cones with six or more larvae was much greater in 1968 (Table 4). Greater population densities per cone may be attributable to low mortality during the mild winter of 1967-1968, and to the apparent tendency for this species to "saturate" a tree before moving to the next.

A varying proportion of the larval population enters diapause (Table 5). An increase in percentage entering diapause was expected with the decrease in cone crop in 1969, and this generally did occur. The populations at Council, ID, which were composed primarily of *L. piperana,* showed the greatest increase of diapausing larvae.

Pupae are present by mid-March at 660 to 750 m (2200 to 2500 ft) elevation. When pupal transformation is near completion, the pupa pushes its way through the axial gallery to the seed using its caudally directed spines. The pupa then pushes through the operculum until two-thirds of its body length protrudes from the opening. The adult emerges through a split along the mid-dorsal line of the pupal case. Except for a few overly active pupae that fall to the ground, the pupal cases remain in place after adult emergence.

Distribution within crowns. Distribution of *Laspeyresia* spp. within tree crowns was determined by examining cones from eight open-grown trees in northern Idaho. The crowns of these trees were divided into four cardinal quadrants, and horizontal strata of 3 m (10 ft) each (Fig. 2). Normally, 8 cones were collected from each quadrant, and 32 from each stratum, but all were removed from a quadrant if fewer than 8 were present.The cones were examined for the number of holes in the rachis, and the number of *Laspeyresia* larvae killed during the preceding winter. The results also were compared with the counts taken from the upper and lower portions of the north and south sides of the tree crowns sampled during the damage evaluation of 1967.

There were no significant differences between cardinal directions in the percentage of cones infested either in 1967 (Table 6) or in the eight-tree sample in 1968 (Table 7). However, the infestation rate in 1968 was significantly greater ($P < 0.05$) at 12-15 m (40-50 ft) than at the lower levels. Percentage insect mortality at the 9-12 m (30-40 ft) and 12-15 m (40-50 ft) levels was significantly ($P < 0.05$) less than at the lower levels. The average number of insects per cone also was greater at 12-15 m (40-50 ft) and in the western quadrants, but the differences were not significant.

The results disagree with those of Kraft (1968), who reported that the heaviest infestations of *L. toreuta* (Grote)

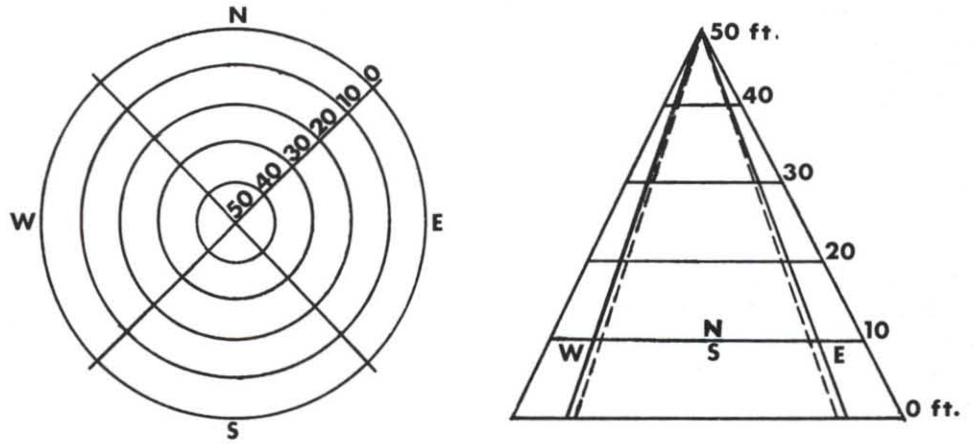

Fig. 2. Schematic representation of the stratification used to sample eight ponderosa pine in northern Idaho, 1968 cone crop.

Table 6. Percent cones infested by *Laspeyresia* spp. by crown location in northern Idaho, 1967.

Crown location	% Infested[a]	Number examined
Upper North	52.6	177
Upper South	57.3	187
Lower North	52.8	53
Lower South	55.0	89

[a] Any two values not vertically scored by the same line are significantly different ($P < 0.05$).

were at the 0-3 m (0-10 ft) levels in open-grown stands of jack pine, *Pinus banksiana* Lambert. He suggested that this was due to the low-flying behavior of ovipositing females. These females may disperse to higher levels once within the crowns. No such tendency was evident for the *Laspeyresia* spp. infesting cones of ponderosa pine. The difference in vertical distribution between the eastern and western species may be due to the differences in population densities. Kraft reported maximum infestations of 26 percent; the minimum in the eight sample ponderosa pines was 68 percent.

A multiple comparison among mean number of insects per cone at the various stratum-quadrant locations (Table 8) showed a tendency for greater concentration of insects in the upper, south, and west portions of the crown. However, there were no significant differences in the number per cone at the various height strata or quadrants when considered separately (Table 7).

Natural Control

Parasites. Six species of parasites of *Laspeyresia* were reared from infested cones collected throughout the study area (Table 9). The absence of a given parasitic species from a specific site may be due to inadequate sampling of low host populations. Similarly, rates of parasitism (Table 10) may be underestimated because cone collections from which the percentages were derived did not always contain all the parasitic species known to be present at the sites. Linear correlation analysis failed to reveal any relationship between diapause in the host population and parasitism by *Apanteles laspeyresiae* Viereck or total parasitism.

Individual parasitic species were of minor importance in most situations. However, *A. laspeyresiae* and *Phanerotoma laspeyresiae* Rohwer showed potential as natural control factors when the host population is limited by small localized cone crops. *Hyssopus* spp. also reached a relatively high level (> 10%) at one site.

The larva of *A. laspeyresiae* usually is found in the region of the fifth abdominal segment of its host larva and is quite small even as late as December. Thus, it can be assumed that most of the parasite's growth takes place sometime during the 3 months prior to host pupation. It also is probable that the onset of host pupation stimulates completion of larval development of the parasite as has been reported for *Phanerotoma toreutae* Caltagirone by pupation of *L. toreuta* (Harbo and Kraft 1969).

The larvae of the first four species in Table 9 usually emerge from the host larva in March or April just prior to pupation. Larvae of *A. laspeyresiae* occasionally delay

Table 7. Infestations of *Laspeyresia* spp. by crown locations of cones in eight open-grown ponderosa pine, northern Idaho, 1968.

Height and quadrant location of infested cones	Total number cones collected	Percent cones infested	No. insects per cone		Percent insects dead
			Mean	Max.	
0-10 ft (0-3 m)	158	68.4[a]	3.19[b]	34	30.3[b]
10-20 ft (3-6 m)	195	67.7	3.39	21	33.1
20-30 ft (6-9 m)	226	73.0	3.27	22	30.8
30-40 ft (9-12 m)	164	74.4	3.40	16	19.8
40-50 ft (12-15 m)	75	92.0	4.38	19	14.0
North	197	78.2	3.38	14	24.2
West	199	71.9	4.11	22	24.4
South	210	69.5	3.41	34	25.9
East	212	72.2	3.28	19	27.9

[a] Any two values not vertically scored by the same line are significantly different ($P < 0.01$).

[b] Any two values not vertically scored by the same line are significantly different ($P < 0.05$).

Table 8. Comparison of the mean number of *Laspeyresia* spp. per cone in the strata and quadrants of eight open-grown ponderosa pine in northern Idaho, 1968.

Quadrant	S	W	W	E	N	S	W	E	W	W	S	N	N	E	E	N	S	E	S	N
Strata (ft)	45	45	15	5	45	5	25	15	5	35	35	5	25	25	35	35	15	45	25	15
No. insects	5.55	4.82	4.53	4.42	4.19	4.11	3.85	3.81	3.80	3.73	3.56	3.55	3.38	3.30	3.19	3.10	2.94	2.94	2.76	2.67
[a]		—	—																	
			—	—	—	—														
				—	—	—	—	—	—											
					—	—	—	—	—	—	—	—								
							—	—	—	—	—	—	—	—						
								—	—	—	—	—	—	—	—					
										—	—	—	—	—	—	—				
											—	—	—	—	—	—	—	—		
													—	—	—	—	—	—	—	
														—	—	—	—	—	—	—

[a] Any two means not underscored by the same line are significantly different ($P < 0.05$).

emergence until after pupation of the host, and larvae of *Hyssopus* spp. occasionally emerge from the host in the fall and overwinter in the host's axial gallery.

Apanteles laspeyresiae and *P. laspeyresiae* pupate in thin, silvery cocoons within the axial galleries. Larvae of these species, when removed from the cones, pupated but did not spin cocoons. *Hyssopus* spp. and *Zachalochlora milleri* Crawford also pupated in the axial galleries, and were the only species that produced more than one progeny per host larva, averaging 11.4 (1 to 43) and 5.0 (1 to 15), respectively.

Adult emergence of all parasitic species from the cones was synchronized with the emergence of the host. Thus, it is probable that eggs or first instar larvae of the host are parasitized by all but *Exeristes comstockii* (Cresson), particularly when consideration also is given to the feeding depth of later larval instars in the cone.

Exeristes comstockii is a common parasite of many lepidopterous larvae infesting branches and cones of conifers. It differs from the other species in that it is an external parasite of mature larvae (Cushman 1927). Thus, adults of this species that emerge in the spring must either parasitize diapausing larvae of the seed moth, or seek alternate hosts. Emergence from the cones was impeded in many cases by the small diameter of axial galleries which resulted in 22 percent mortality of this parasite.

Approximately half the adults of *A. laspeyresiae* lived only 1-2 days in the laboratory; however, when provided moist raisins as food, the remaining adults survived as long as their host adults. Longevity of *P. laspeyresiae* usually was 11 days, twice as long as the host adults. *Exeristes comstockii* survived a maximum of 4.5 weeks in the laboratory.

Mating behavior of *Z. milleri* was observed in the laboratory, although union of the pairs apparently never was consummated. The male mounted the female with the fore tarsi placed between the compound eyes and the antennae; the mesothoracic legs grasped her thorax just above and behind the precoxae along the episternum, and the metathoracic legs grasped the costal vein of the fore pair of her folded wings. The male then stroked the mouthparts and antennae of the female by rapid vibrations of his antennae, after which he either dismounted or rode passively for an undetermined time.

The sex ratios of all species but *Z. milleri* showed a dominance of females (Table 9). Although females of *Z. milleri* predominated at all sites except Kettle Falls, WA, the number of males in collections from Kettle Falls was so great that the combined ratio favored the males.

Table 9. Presence of the most common parasites of *Laspeyresia* spp. in cones of ponderosa pine collected from locations in Idaho, Washington and Montana, 1967-1969.

Parasite	*Apanteles laspeyresiae* Vier.	*Phanerotoma laspeyresiae* Rohw.	*Zacalochlora milleri* Crwfd.	*Hyssopus* spp.	*Exeristes comstockii* (Cress.)	*Campoplex laspeyresiae* Rohw.
No. observed	391	51	149	147	32	18
Sex ratio M:F	1:1.37	1:1.55	1:0.77	1:7.20	1:1.91	1:1.57
χ^2	**	ns	ns	**	ns	ns
Darby, MT	X	X	X	X		
Lolo, MT	X			X		
St. Regis, MT				X		
Thompson Falls, MT						
Libby, MT						
Kettle Falls, WA	X	X	X	X		
Rockford, WA	X	X	X	X	X	X
Cheney, WA	X	X	X	X	X	
Kooskia, ID	X			X		
Salmon, ID	X	X				
Idaho City, ID	X		X	X	X	X
Cascade, ID	X	X	X			
Council, ID	X					
New Meadows, ID	X		X	X	X	
Waha, ID	X			X		
Helmer, ID	X			X		
Potlatch, ID	X	X			X	X
Mica, WA	X	X	X	X	X	X
Blanchard, WA	X	X				

** ($P < 0.01$)

ns Nonsignificant

Stratified cone collections within individual trees indicated that *A. laspeyresiae* was evenly distributed among the cardinal directions of the crown. Vertical distribution could not be determined due to the small numbers of larvae in the collected cones. In general, however, the within-tree distribution of this parasite closely paralleled that of its host.

The absence of parasites from cone collections at Libby and Thompson Falls could be due to the limited collections made from these and other areas in Montana. However, only one or two parasitic species were collected from several sites from which extensive collections were made and four were reared from cones collected at Darby, MT.

Predators. Predaceous species were extremely rare. A clerid, *Phyllabaenus* sp., which was collected from cones infested with cone beetles, also was collected from cones infested only by seed-moth larvae. One adult of another clerid, *Enoclerus schaefferi* Barr , was collected at each of the Darby, MT, and Kooskia, ID, sites, from open cones that had fallen to the ground. These cones contained only larvae of the seed moth.

Winter Temperature. Unusually severe temperatures during the winter of 1968-1969 were lethal to overwintering *Laspeyresia* larvae at lower elevations. For example, a temperature of -40° C (-40°F) at Potlatch (780 m) (2600 ft) resulted in 100 percent larval mortality in cones on the ground without snow cover. However, only 50 percent of the larvae were killed in cones covered by 46 cm (18 inches) of snow. Temperatures of -23° to -29° C (-9° to -20° F) for 60 hours killed almost 27 percent of the seed moth larvae at Viola Hill, 8 km (5 miles) north of Moscow, ID.

Mortality rates at temperatures of -29° to -43° C (-20° to -45° F) did not differ significantly between quadrants in the eight trees examined although a significant difference was found between the 6-9 m (20-30 ft) and 9-12 m (30-40 ft) strata (Table 7). This may be due to the occurrence of more severe temperatures below mid-crown level.

Levels of Cone Crop and Interspecific Competition. Koerber (1967) reported that supply of cones, and interspecific competition were the dominant factors regulating populations of cone and seed insects of ponderosa pine. These factors, in addition to the infrequent effect of extremely cold winter temperatures, were the primary causes of mortality in this study.

Good cone crops of ponderosa pine usually occur in Idaho every 5 years (personal communication, F.L. Sprague, USDA-FS retired). However, geographic variation is typical,

Table 10. Percent parasitism by species in populations of *Laspeyresia miscitata* in Idaho, Washington and Montana, 1967-1969.

Location	Year that hosts emerged	% of hosts in diapause	*Apanteles laspeyresiae*	*Zacalochlora milleri*	*Phanerotoma laspeyresiae*	*Exeristes comstockii*	*Hyssopus* spp.	*Compoplex laspeyresiae*	Total % parasitized
New Meadows, ID	1968	10.3	6.9	1.4	0.0	1.4	0.0	0.0	9.7
	1969	33.9	5.5	1.1	0.0	1.1	0.4	0.0	8.1
Council, ID[a]	1968	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	1969	70.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2
Cascade, ID	1968	10.8	7.5	0.8	0.0	0.0	0.0	0.0	8.3
	1969	46.7	4.0	0.0	0.7	0.0	0.0	0.0	4.7
Idaho City, ID	1969	9.8	2.0	3.8	0.0	+	13.6	0.0	19.4
	1970[b]		62.7	0.0	0.0	0.0	0.0	1.2	63.9
Mica, ID	1968	6.0	11.1	4.1	4.1	7.4	4.1	+	30.8
Blanchard, WA	1969	0.8	18.4	0.0	1.6	0.0	0.0	0.0	20.0
Waha, ID[a]	1969	10.9	16.1	0.0	0.0	0.0	3.2	0.0	19.3
Salmon, ID[a]	1969	3.5	12.0	0.0	36.0	0.0	0.0	0.0	48.0
Cheney, WA	1969	36.4	26.7	1.0	11.1	+	+	+	38.8
	1970[c]		8.3	0.0	25.0	0.0	0.0	0.0	33.3
Rockford, WA	1970		12.7	2.4	0.9	0.9	3.3	0.0	20.2
Kooskia, ID	1970[d]	5.2	7.7	0.0	0.0	0.0	7.7	0.0	15.4
Kettle Falls, WA	1970[d]	2.7	18.0	0.0	2.2	0.0	2.2	0.0	22.4
Libby, MT	1970[d]	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
St. Regis, MT	1970[d]	8.9	0.0	0.0	0.0	0.0	9.1	0.0	9.1
Lolo, MT	1970[d]	4.4	33.3	0.0	0.0	0.0	4.8	0.0	38.1
Darby, MT[a]	1970[d]	13.4	16.6	3.3	13.3	0.0	6.6	0.0	39.8
Thompson Falls, MT	1970[d]	17.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

[a] Moderate to abundant numbers of *L. piperana*.

[b] Thinning demonstration near the original location.

[c] One tree 400 yards from the original location.

[d] Estimates at these locations were obtained from hosts in diapause.

\+ Present at the location, but not collected in these samples.

with some areas reported as not producing a crop suitable for collection for as long as 14 years (personal communication, Mr. J. Isaacson, USDA Forest Service, Coeur d'Alene Forest Nursery, Coeur d'Alene, ID). Under such conditions, the competitive advantage of the various species becomes important in determining the subsequent composition of the cone and seed insect community. This competitive advantage is derived from the time and location of attack. Thus, species infesting early in the season have an advantage over those attacking later; species that are cone feeders are in better position than seed feeders.

Laspeyresia oviposits on cones infested by cone-tissue feeders as well as on non-infested cones. Cone dissections showed that their population potential is reduced by an amount equal to the portion of the cone crop attacked and destroyed by the cone beetle, *C. ponderosae*, and by *Dioryctria* spp. Intraspecific competion apparently is at most a minor factor, as evidenced by the rarity of larval cannibalism.

Laspeyresia miscitata emerges earlier in the spring than *L. piperana* and thus has a competitive advantage, which may partially account for the greater (7.5 to 1) abundance of *miscitata* at most sites (exceptions were Salmon and Waha, ID, where the two species were equally represented; and Council, ID, where *piperana* comprised more than 80 percent of the total population). Neither species was found in cones of lodgepole pine, *P. contorta* Douglas on the two sites (Blanchard and Cascade, ID) where this tree species was present. Thus, *L. piperana* apparently cannot avoid competing with *L. miscitata* and other species infesting ponderosa pine cones.

Other Mortality Factors. Closure of scales in response to high humidity on the ground apparently precludes emergence. Dead pupae were found in cones that fell in shaded areas and remained closed for much of the spring rainy season, but were rare in cones falling in dry areas, or in those that remained on the tree. Moisture that saturates the cone axis also may drown the larvae. Mortality by drowning (or freezing) was 76 percent in cones collected from a roadside ditch. Awareness of moisture-related mortality may have implications for possible management techniques in seed orchards and seed-production areas.

Direct and indirect predation by vertebrates also resulted in mortality of seed moths. For example, unidentified birds caught adult *Laspeyresia* in flight during late afternoon and early evening. Cone gathering and subsequent feeding on the seeds by squirrels resulted in death from desiccation of larvae in the exposed cone axes.

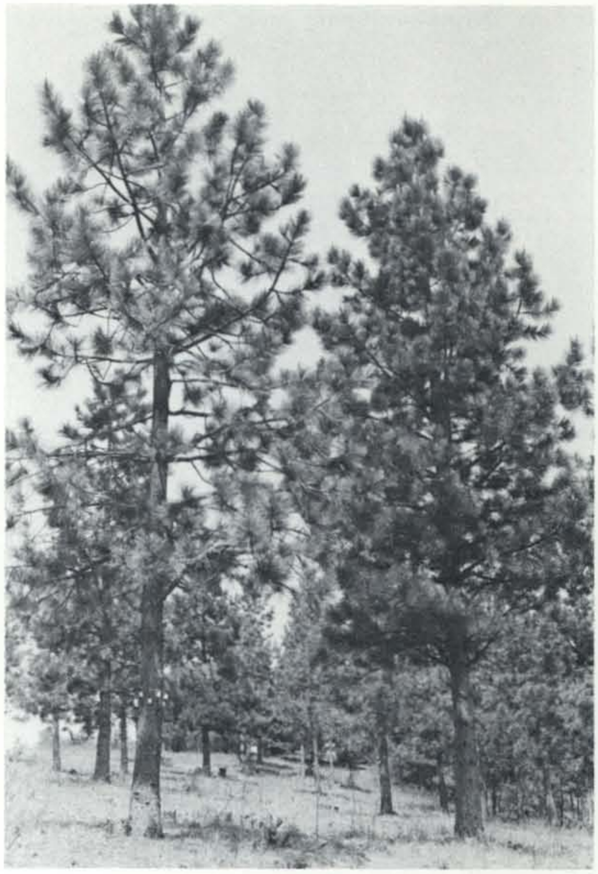

Fig. 3. Crown types used in examining the dispersal of *Laspeyresia* spp. and *Conophthorus ponderosae* between types. Left, sparse; right, luxuriant.

Influence of Stand and Site Characters

Foliage Density. There were no significant differences in *Laspeyresia* population levels among groups of trees classed as densely or sparsely foliaged (Fig. 3). Ovipositing females apparently are attracted to suitable host trees by other than image continuity. Thus, neither thinning of tree crowns, nor enhancing development of full crowns would be effective in preventing infestations.

Stand Density. Two density classes, based on the number of ponderosa pine stems per hectare (acre), were used to determine the influence of density on levels of cone and seed damage (Table 11). Those stands with more than 250 ponderosa pine stems per ha (100/acre) generally suffered greater damage than those with fewer than 250 stems per ha (equivalent to about 6 x 6 m (20 x 20 ft)) spacing. The possibility existed that the two density classes differed in the number of available cones. However, a *t*-test on the mean number of cones per acre for the two groups showed no significant difference at P less than .01 (a prior test indicated equivalency of variances). Subsequent *t*-tests showed that both measures of damage (% cone and % seed infestation) differed significantly ($P < .01$) between density classes. Thus, damage potential from *Laspeyresia* spp. apparently is greater in more dense stands of ponderosa pine. Furthermore, total cone crop is not necessarily affected adversely by the density of the subject tree, possibly as a result of compensatory increases in cone production on fewer, large-crowned trees. The higher damage levels in the more dense stands may be attributed in part to the behavior of adult moths. For example, Coyne (1968) and Tripp (1954) found that adults of related species normally crawl from old cones to second year cones on the same branch or tree. In dense stands, overlapping branches (or reduced flight distance) between adjacent trees would enhance dispersal and success of cone searches.

Crown Closure. No significant relationships between percent crown closure and either damage levels or cone crops in 1968 were shown by simple linear regression analyses, probably due to the effect of tree distribution. For example, crown closure in the New Meadows, ID, stand was estimated at 40 percent with 460 total stems per ha (184/acre), whereas the Cascade stand had 75 percent crown closure and a much lower density (260 stems per ha) (104/ acre). Thus, differences in tree distribution between stands, coupled perhaps with anomalies in location of sample plots and increased cone production per tree, precluded comparisons between crown closure classes.

Table 11. Relationship between ponderosa pine density and cone crop and damage levels by *Laspeyresia* spp. on 12 intensive study sites, 1968.

	>100 stems/acre			<100 stems/acre		
	No. cones per ac.	% cones infest.	% seed infest..	No. cones per ac.	% cones infest.	% seed infest.
	1037+	93	38	848+	73	22
	4478+	90	31	1595+	31	7
	6195+	93	56	2380+	76	33
	1689-	100	61	2063+	17	4
	1606-	93	24			
	377+	96	59			
	612+	91	40			
	1081+	97	66			
$\overline{x}$	2134	94	47	1722	49	16
s	2076	3.3	16	666	30	12
s^2	4,311,231	11	242	433,083	884	152

+ and - indicate increase and decrease in cone crop from previous year.

There was a significant difference between the means of each density class for % cones infested and % seeds infested. There was no significant difference for number of cones/ac. (All comparisons made using *t*-tests and $P < 0.01$.)

Habitat Type. Comparison of damage levels among the six habitat types represented suggested that greater losses occur in the drier types (Table 12), although the lower damage levels in the *Abies grandis/Pachistima myrsinites* and *Abies grandis/Spirea betulifolia* habitat types could be a function of stand density. For example, the Cheney, WA, stand was the only climax ponderosa pine type sampled, and it suffered a considerably higher level of damage than did the two less dense seral stands in the *Abies grandis/Pachistima myrsinites* and *Abies grandis/ Spirea betulifolia* types. However, as noted previously, high moisture conditions during the spring months inhibit opening of cones and adult emergence. Thus, mesic sites would be preferred locations for seed production areas to minimize losses to *Laspeyresia* spp., even though "off-site" for ponderosa pine. Furthermore, locating seed orchards and production areas in mixed stands of a climax type removed from ponderosa pine is indicated.

Growth Rate. A significant ($P < .05$), although low, positive linear relationship was shown between mean growth rate (number rings/outer inch) and percent of cones infested ($r^2 = .36$), seed loss per acre ($r^2 = .35$) and percent seed loss ($r^2 = .27$; $P < .01$). Stands showing mean growth rates of more than 14 rings per inch consistently suffered more than 90 percent cone infestations, while faster growing stands usually were less severely damaged (Table 12). It is doubtful that growth rate per se has a direct influence on the incidence or levels of damage; more likely, it is a reflection of stand density and site quality, although no significant relationship between site index (as calculated) and damage could be ascertained.

Laspeyresia piperana (Kearfott) (Lepidoptera: Olethreutidae)

Bionomics

The life history and habits of this species in British Columbia were described by Hedlin (1967), and are similar to those found in Idaho except that larval feeding on seeds after entry into the cone axis was not observed. Adult emergence begins in late May in Idaho at 900 m (3000 ft), about the time of pollen release of ponderosa pine, and ends in late June. Thus, emergence of *L. miscitata* is near

Table 12. Relationship of damage levels by *Laspeyresia* spp. to habitat type and stand characters of 12 intensive study sites, 1968.

Habitat[a]	Stand	Stems/ acre	Growth rate[b]	Cones/ acre	% cones infested	% seed infested
Pipo/Agsp	Cheney, WA	152	19	4478	90	31
Psme/Intergr.	Blanchard, WA	312	14	1037	93	38
Psme/Cage	Idaho City, ID	190	14	1081	97	66
Psme/Phma	Mica, WA	28	5	848	73	22
Psme/Phma	Potlatch No. 1, ID	110	15	6195	93	56
Psme/Phma	Potlatch No. 2, ID	219	15	1689	100	61
Psme/Phma	Potlatch No. 3, ID	141	18	1606	93	24
Psme/Syal	Waha, ID	97	11	2380	76	33
Psme/Phma	N. Meadows, ID	184	10	377	96	59
Psme/Syal	Cascade, ID	104	11	612	91	40
Abgr/Pamy	Helmer, ID	17	6	1595	31	7
Abgr/Spbe	Council, ID	71	9	2063	17	4

[a] Refer to Table 3 for full description.

[b] Mean number of annual rings per outer inch of sapwood per 10 trees.

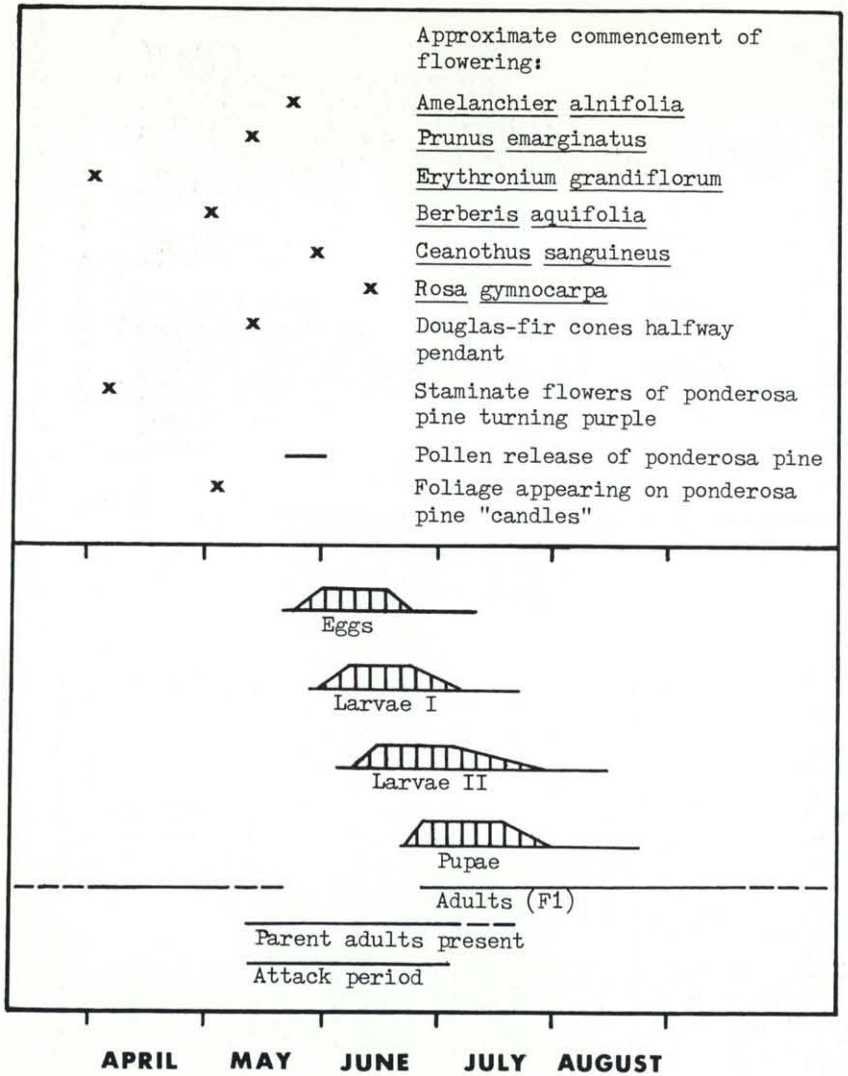

Fig. 4. Generalized life cycle and phenological relationships for *Conophthorus ponderosae* at Mica, ID.

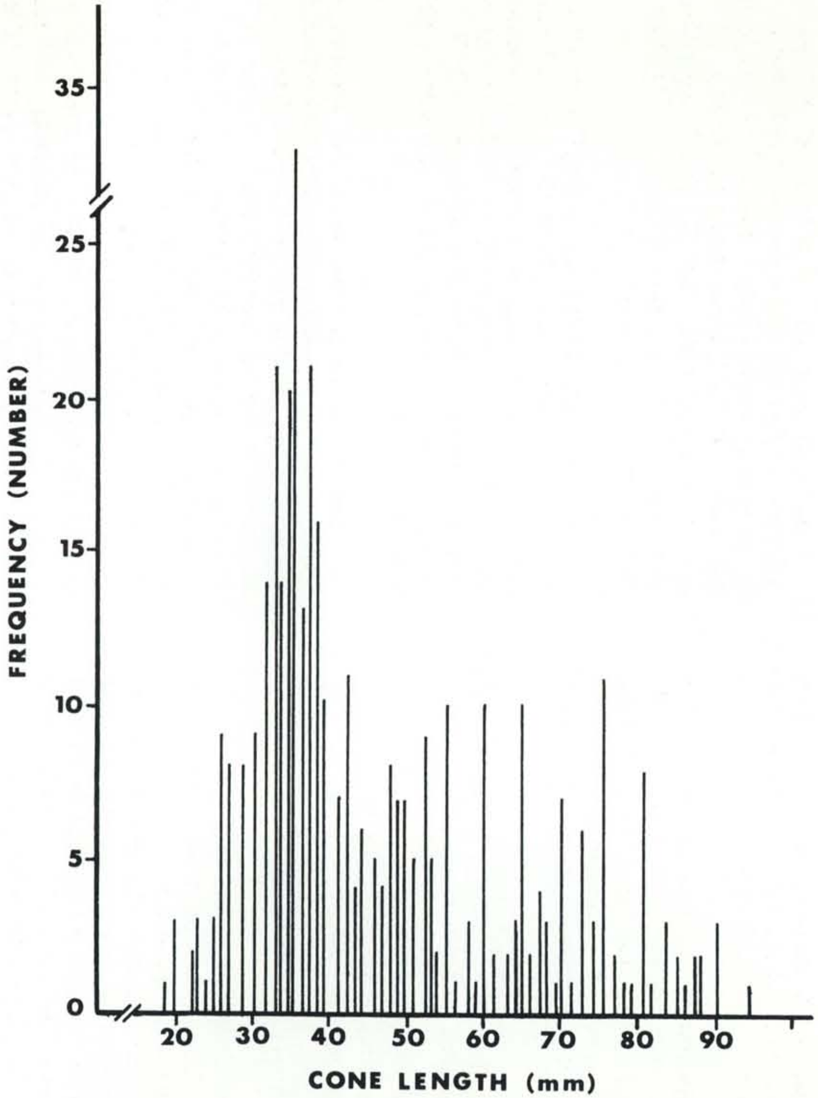

Fig. 5. Length of cones of *Pinus ponderosa* killed by *Conophthorus ponderosae* at Mica, ID, 1968-1969.

completion when that of *L. piperana* begins. The same pattern was observed in the laboratory. Duration of emergence was approximately equal for both species.

Laspeyresia piperana did not mate and oviposit when reared under the same conditions as *L. miscitata* in the laboratory. Average fecundity was 318 (126 to 430) eggs per female, and the oocytes of *piperana* turn orange in color during passage down the ovarioles, in contrast to those of *miscitata*, which remain white.

The nature and extent of damage by *L. piperana* could not be distinguished from that of *miscitata*.

Conophthorus ponderosae Hopkins (Coleoptera: Scolytidae)

Description of Life Stages and Life Cycle

Adult. Mature adults are shiny, cylindrical beetles with short, erect, reddish setae sparsely distributed on the elytra and pronotum. The pronotum is dark on both teneral and mature adults; however, the elytra of the latter vary in color from black through maroon to reddish brown, with black much more common. Approximately 4 percent of the adults examined had elytra with a striking reddish hue. Thus, mature coloration was not a function of age.

Initial attacks were observed during the second week of May (Fig. 4) when the majority of cones were 30 to 40 mm in length (Fig. 5) with the attack period lasting until early July.

Emerging females always were more numerous than males, with a male:female (M:F) ratio of 1:1.18 and 1:1.95 in 1968 and 1969, respectively (Table 13). However, in 1968, the M:F ratio of dead beetles in cones was 1:0.64, suggesting a higher mortality of males prior to emergence. A high mortality of males also was shown by M:F ratio of 1:2.4 for the attacking population in 1970. Godwin and O'Dell (1965) reported a ratio of 1:1 for emerging population of *C. coniperda* (Schwarz) and an attack ratio of 1:2.

Table 13. Sex ratios of adult *Conophthorus ponderosae* emerging from cones collected at Mica, Idaho.

Year	No. of beetles Male	Female	Sex ratio	X^2
1968	50[a]	59[a]	1:1.18	ns
1969	62	121	1:1.95	**
Total	112	180	1:1.61	**

[a] Count includes 14 male and 9 female beetles which died in the cones before emerging.
** P < 0.01

Sexes can be differentiated by the seventh and eighth abdominal tergites, which are fused in females but distinct in the males (Schaefer 1962). Females (3.47 ± .18 mm) are significantly (P > .01) larger than males (3.25 ± .24 mm); however, size is of minor value for visually separating the sexes. Size also is not significantly (P > .05) related to elytral color.

Egg. The eggs are ovoid, averaging 0.60 mm (0.56 to 0.62 mm) in width and 0.87 mm (0.78 to 0.91 mm) in length, milky-white, with an unsculptured, transparent chorion. Embryonic development is similar to that of *C. radiatae* Hopkins, as described by Schaefer (1962). Recently deposited eggs, collected from the distal end of the gallery, hatched in 4 days.

Larvae and Pupae. The larvae are apodous, soft-bodied, and white colored, except for the sclerotized head capsule. A frequency distribution of about 200 head capsule measurements revealed the presence of two instars, with the second instar possessing a head capsule greater than 0.45 mm in width (Fig. 6). The mean widths for the two instars (0.37 ± .03 mm, and 0.54 ± .02 mm, respectively) are less than those reported by Ruckes (1963) for this and other western species of *Conophthorus* but are a close approximation with Kinzer et al. (1970). The pupae are white, exarate, and otherwise typical of Scolytidae, and require 2 to 3 weeks for completion of development (Koerber 1967).

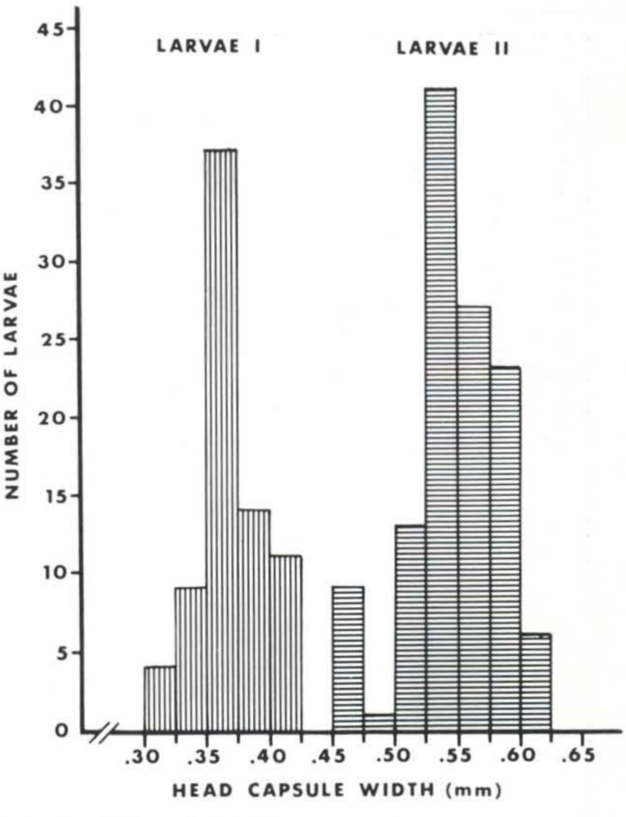

Fig. 6. Head width distributions of immature *Conophthorus ponderosae* at Mica, ID, 1968-1969.

The life cycle of *C. ponderosae* is presented in Fig. 4 in relation to various phenological events.

Bionomics

Behavior. The female usually attacks first and then is joined by a male. Occasionally, a second or third female also will enter the cone through the entrance gallery of the first or by boring another one adjacent to it, presumably resulting in polygamy. Kinzer et al. (1970) reported that attacks by *C. ponderosae* were not initiated in cones in cages containing only males or females, and suggested that mating occurs before, and is prerequisite to, cone attack. Isolated females in this study were unsuccessful in attempts to attack stems, buds and cones on branches placed in water. However, Lyons (1956) and Schaefer (1962) reported that other species of cone beetles mate before, during and after initial attack.

Kinzer et al. (1970, 1972) rarely encountered females unaccompanied by male *C. ponderosae*. However, single, ovipositing females in cones at Mica, ID, were common. Their presence, and the predominance of females over males in the attacking population, suggest that copulation occurs within the cones before emergence. Schaefer (1962, 1964) observed mating of *C. radiatae* in cones prior to emergence, and Williamson et al. (1966) found unaccompanied females of *C. monticolae* Hopkins laying viable eggs in cones of western white pine, *Pinus monticola* Douglas.

The male commonly is found behind the female in the egg gallery, loosely packing frass into the proximal portion of the gallery. A few males were found in front of the females, or in short side galleries. On occasion, cones contained a single male that apparently initiated the attack as no egg niches or other evidence of the presence of a female was observed.

Oviposition may begin soon after initiation of egg gallery construction. However, many broods were located only in the distal portion of the cones, suggesting that a short feeding period may be necessary for oviposition. Eggs are laid singly in niches cut into, or near developing seeds as the female extends the gallery. Frass is packed over the egg and contoured with the surface of the gallery wall. Eggs were not laid in the galleries as reported by Schaefer (1962) for *C. radiatae*. Assuming one female per cone, average fecundity of each female was 6.2 (1 to 26) eggs over the 4-year period at Mica, ID (Table 14). However, this is probably an underestimate, because each female may attack more than one cone. Kinzer et al. (1970) recorded mean fecundity at 6.7 eggs per female and a maximum of 16.

Table 14. Fecundity of *Conophthorus ponderosae* at Mica, Idaho, 1967-1970.

Year	No. cones sampled	Eggs per cone: Mean	Eggs per cone: Maximum	Eggs per acre	Cones per acre
1967	5	7.4	16	482	601
1968	69	4.0	14	1008	848
1969	11	7.1	a	1390	200
1970	39	9.8	26	1666	200
	Mean	6.2	18.6	1136	461

[a] Data missing.

The percentage of cones containing successful broods in 1968 (23%) was much lower than in 1969 (53% - two collections) and 1970 (64%) (Table 15) when the cone crops were only a fourth as large (Table 14). The average number of eggs laid per cone also was much lower in 1968 (Table 14). Thus, a female apparently is more likely to produce a successful brood in the first cone attacked during years of low cone production.

Small cones seemed more susceptible to successful attack than large cones, as the major part of spring emergence and first attack of the beetles occurs prior to complete development of the cones in late June or early July.

Table 15. Success of attack and brood production by *Conophthorus ponderosae* in cones of ponderosa pine at Mica, Idaho, 1968 through 1970.

Year	Cones killed by attack with							
	No egg gallery				Egg gallery present			
	Girdled only		Repulsed (resin)		Eggs and larvae present		No oviposition	
	No.	%	No.	%	No.	%	No.	%
1968	10	11.1	2	2.2	21	23.3	57	63.4
1969	10	8.0			45	36.3	69	55.7
1969[a]					105	63.2	61	36.8
1970	6	9.0		11.9	43	64.2	10	14.9

[a] Second collection made later in the summer.

This proved to be the case, as the majority of successfully attacked cones attained a length of 30 to 40 mm (Fig. 5) in early May (Fig. 7), roughly coinciding with the observed initiation of beetle emergence and attack (Fig. 4). Resinosis in the entrance (girdle) and egg galleries was the usual cause of unsuccessful attacks, but failures also resulted when resinosis was minimal. The majority of unsuccessful attacks resulted in cone death.

After completion of oviposition in a given cone, the parent adults normally vacate through the entrance hole, which is then repacked with frass. Occasionally, exit is made near the cone tip, and rarely on the side of the cone. Based on duration of attack period, Koerber (1967) concluded that each female is capable of destroying four to six cones, and Kinzer et al. (1970) reported that caged females attacked a maximum of four cones each. No more than two to four cones were attacked per female at Mica, ID.

Schaefer (1964) concluded that only those *C. radiatae* that attacked the smaller cones later emerged to make a second attack. A similar behavior was observed for *C. ponderosae*. Bedard (1968) reported that parent adults of *C. lambertianae* Hopkins emerged from sugar pine (*Pinus lambertiana* Douglas) cones which were still in a succulent condition just prior to hardening. The cones of ponderosa pine in this study area began to harden in late June, which also coincided with the last of the attacks by *C. ponderosae*. Morgan and Mailu (1976) reported that *C. coniperda* leave and re-enter infested cones in the fall. No evidence was found of this behavior for *C. ponderosae*.

Pupation occurs in the spaces formed between the scales when cones harden. Dissection of callow adults indicated that light feeding occurs prior to overwintering as mature adults near the cone axis. Because adults collected from cones in the spring possessed little visceral volume, and only small amounts of previously ingested food were found in the posterior of the hind gut, it was concluded that no feeding occurs during overwintering. Similarly, Henson (1961) estimated that 25 percent of the *C. coniperda* emerging in the spring had a 60 percent reduction in visceral volume. Godwin and O'Dell (1965) also reported that little if any food was ingested by the adult of *C. coniperda* until emergence from hibernation in the spring.

Infested ponderosa pine cones were stored at about 3° C (37° F) each winter during this study. Some of the adult beetles survived almost 2 years of this treatment. Koerber (1967) maintained adults in dry cones for over a year, and Ruckes (1963) recovered adults in 1958 from

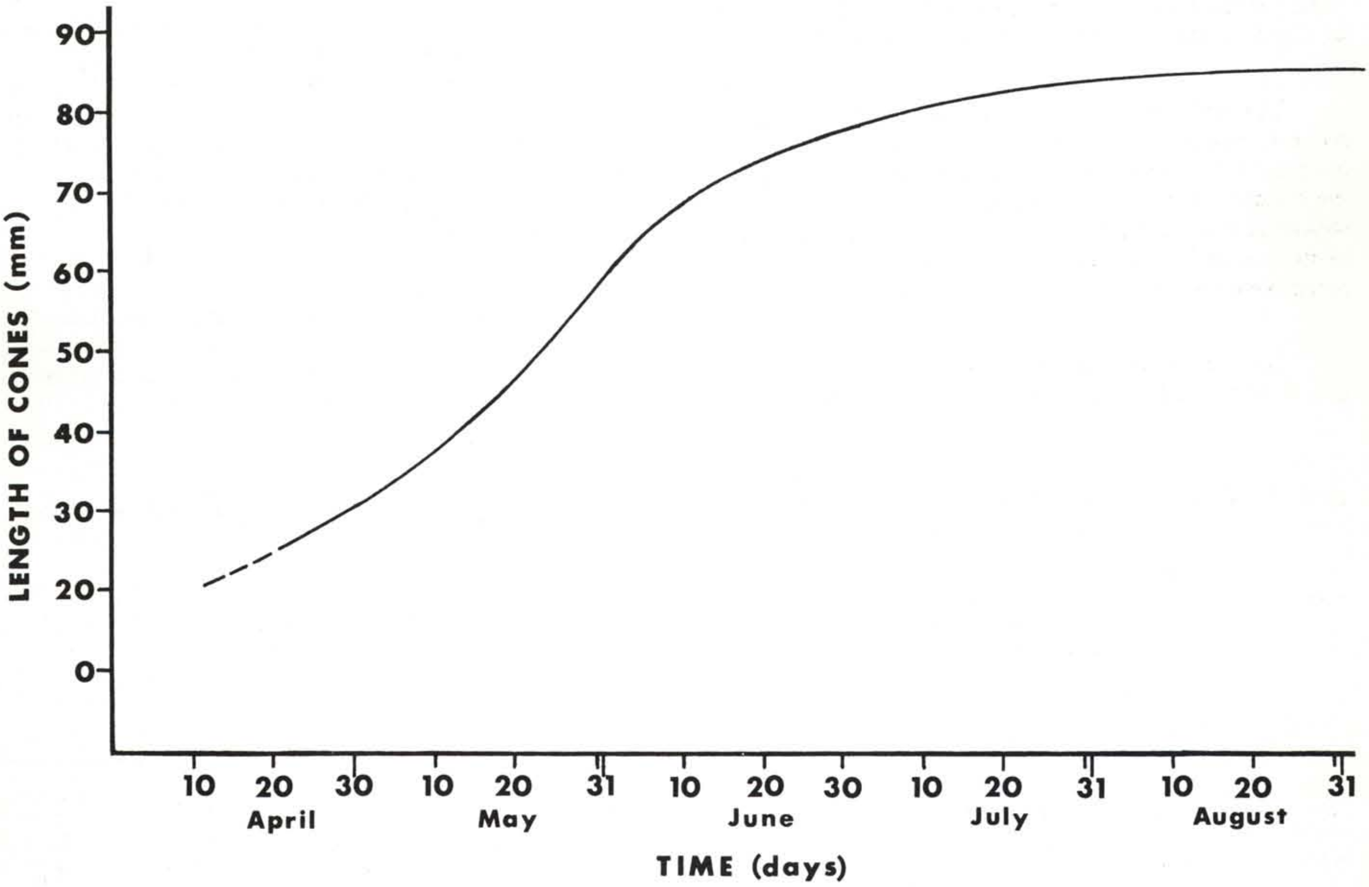

Fig. 7. Average growth of cones of ponderosa pine in Idaho, 1967-1968.

ponderosa pine cones attacked in 1956. This ability to enter facultative diapause provides a means of avoiding the consequences of a cone crop failure.

Natural Control

Parasites and Predators. Relatively few entomophagous species were reared from cones infested by *C. ponderosae.* The most common predator was the clerid, *Phyllabaenus* sp. Larvae of this species were found in cones from June through fall, although pupae were present in the third week of July. Adults were obtained from laboratory rearings. No more than 5 percent of the examined cones contained *Phyllabaenus*, and its effectiveness in significant reduction of host populations remains questionable.

Schaefer (1962) reported that some parent adults of *C. radiatae* continue feeding in the first attacked cones rather than making secondary attacks. These adults construct ventilation holes to their galleries which serve as entrance points for parasitic wasps. Ventilation holes were rarely constructed by *C. ponderosae,* and the small number of this type of parasite may be attributable to the lack of ready access.

A bethylid, *Cephalonomia utahensis* Brues has been reported as a predominant parasite of *C. radiatae* (Schaefer 1962) and *C. ponderosae* (Koerber 1967), but adults of this genus were collected from only one cone. One specimen was reared in the laboratory on cone beetle larvae. Feeding by this ectoparasite occurred on the side of the thorax, and dead host larvae with similar damage were found in the original infested cone. One host larva was observed with four parasitic larvae attached. Cocoons fitting the general description and host relationship were found in four other cones infested with *C. ponderosae.* Only 2 percent of the cones examined for parasites and predators exhibited evidence of this species.

Lyons (1956) reported the braconid, *Bracon rhyacioniae* Muesbeck as a parasite of *C. resinosae* Hopkins. Only three adults of this species were reared from *C. ponderosae* infested cones and all emerged from a single cone collected at Helmer, ID, in 1967.

A hemerobiid species (*Haemerobius* sp.) was reported as preying on cone beetle larvae in the spring (Schaefer 1962). Immature specimens of an unidentified species of this genus also were collected from cones during this study; however, these cones were infested by the pine coneworm as well as the cone beetle. Adult *Haemerobius* sp. were found in older cones on the ground.

Temperature. High temperature has been reported to cause mortality of cone beetles (Bedard 1966, Lyons 1956, Schaefer 1964). Bedard, for example, noted that larvae and pupae of *C. lambertianae* in cones of sugar pine were desiccated, shriveled, very hard and yellow-colored. Dead adults in the same cones were extremely brittle. No evidence of *C. ponderosae* mortality in any stage due to high temperature was found in infested cones collected in the fall of 1968; however, the effect of this factor was investigated further in a special collection of 123 cones from the Mica Peak, ID, seed production area. About half of these were collected from portions of tree crowns exposed to full insolation during most of the day. The remaining half were selected from portions receiving little or no direct sunlight during mid-day (10 a.m. to 2 p.m.). There was no significant difference ($P > .05$) in the number of adults produced per cone in the two groups. However, cones receiving full insolation were significantly larger ($P > .05$) than the shaded group when killed by the beetle.

Very severe cold weather occurred in late December, 1968. Temperature records were not kept at Mica but, based on those for other sites of similar elevation in northern Idaho, minimum temperatures were estimated at about -20° C (-4° F). Dissection of cones of the 1968 crop in early 1969 revealed only dead adults. However, samples of the 1969 crop showed an infestation level approximately equal to that of 1968, possibly as a result of immigrating adults from an infested stand 3 miles distant.

Interspecific Competition. The coneworm *Dioryctria auranticella* (Grote) often was found in the deteriorating cones where it not only competes with *C. ponderosae* for food and space, but physically destroys a portion of the beetle population. In 1970, about 61 percent of the cones from seven trees contained both species. The factor that determines the success of one species over the other was not ascertained. However, it was apparent that extensive galleries of the coneworm larvae caused a rapid desiccation of the cones. This was detrimental to continued feeding and development of first instar larvae of the cone beetle. In fact, the cone beetle usually was replaced if the cone also contained two or more larvae of the coneworm, which occurred in half the mutually infested cones examined in 1970. *Dioryctria abietella* (Denis and Schiffermueller) was not reared from any cones infested with cone beetles.

Influence of Stand and Site Conditions

Foliage Density. Henson (1962) found that *C. coniperda* oriented its flight toward dark silhouettes, and concluded that the greatest number of beetles should be aggregated on exposed branches of dominant trees. Observations during 1967 also suggested that trees with dense crowns of luxuriant foliage were more heavily infested by *C. ponderosae* than those with widely spaced limbs and sparse foliage.

Ten trees with dense branching and foliage, and ten with sparse crowns (Fig. 3) were sampled for differences in cone beetle infestation levels. All the cones on each of the 20 trees were examined. The mean infestation level in the densely crowned trees was almost 20 percent higher than in

Table 16. Infestation levels of *Conophthorus ponderosae* in trees of differing crown types at the Mica Peak Seed Production Area, 1968.

Tree Pair No.	Cones infested in each crown type			
	Luxuriant		Sparse	
	No.	%	No.	%
1	239	71.8	131	54.2
2	155	76.3	148	47.6
3	81	67.5	79	23.0
4	7	10.9	9	10.6
5	27	12.8	46	21.0
6	35	21.2	85	60.7
7	31	44.3	43	32.3
8	9	42.8	33	27.3
9	47	51.1	104	39.1
10	183	79.2	13	14.1
$\bar{x}$	81	53.9[a]	69	34.8[a]

[a] not significant at ($P < 0.05$)

the thin-crowned trees (Table 16); however, an *F*-test showed no significant difference ($P > .05$) between groups. The tendency for heavier infestations to occur in trees with dense crowns suggests that pruning and trimming should be studied as a possible cultural practice to keep cone beetle populations at a minimum, and to ascertain effects on cone yields per tree.

Stand Density. The cone beetle was found in substantial numbers only at Mica and Helmer, ID. Both of these stands were open-growing and relatively young, with good growth (Table 2). This small sample suggests that this pest is more likely to be a problem in open stands, such as seed-production areas and seed orchards. A tree spacing that allows maximum production of cones per tree apparently also will provide the most favorable habitat for the beetle. Thus, the manager is faced with a dilemma. Stand density can be reduced to increase cone production per tree and to facilitate collection, and thereby increase rates of infestation by the beetle; or density can be increased, which will reduce both cone production per tree and beetle-caused losses, but create a more favorable habitat for *Laspeyresia* spp.

Leptoglossus occidentalis Heidemann (Hemiptera: Coreidae)

Bionomics

Behavior. Mating begins as soon as hibernating adults emerge in the spring and continues throughout the summer. Courtship commences with a slow approach of a male to about 3 cm from either side or behind a female. He then sways from side to side, with further advances toward the female periodically interrupted by additional swaying motions. If responsive, the female draws in one hindleg and leans toward the male, or rises upon her forelegs. Copulation takes place either posterior to posterior, or with the male superior, and may last for 15 hours; however, individual females mated frequently in the laboratory, either with the same or several males. Although males frequently died after mating, the maximum longevity of 10 months under laboratory conditions was achieved by a male.

There may be a chemical stimulant emitted by the male that provokes a courtship response by the female. When a male approached one of two visually separated females in a cage, the behavior of the unapproached female was the same as that of the courted female.

The barrel-shaped eggs are laid in single rows on the needles of the host tree. Koerber (1967) reported that a female was capable of laying an average of 12 eggs per day every day for 3 months. Fecundity of reared individuals in this study averaged only 80 eggs per female, with a maximum of 148. However, fresh foliage was not provided every day as in Koerber's study. An average of 9.7 (1 to 20) eggs were deposited per row.

Nymphs reared in the laboratory were gregarious, particularly in the first instar. In the field, 2 or 3 nymphs were found together, but single individuals or groups of 4 or more never were observed. Nymphs retreated to the recesses at the base of cone rosettes when disturbed; adults took flight. Adults also showed a gregarious behavior in the laboratory not observed in the field.

All nymphal instars were common in the field during most of July and early August, but rare by 10 September. Duration of the five nymphal instars under laboratory conditions averaged 4.3, 5.3, 7.2, 12.5, and 15.7 days, respectively.

Distribution within Crowns. High mobility of this species precluded estimation of population levels, but in the Waha, ID, stand nymphs and adults were most abundant on the south and west sides of trees where insolation was greatest. A maximum of 25 adults and nymphs were collected from the lower branches of open-grown trees. Populations in the middle and upper crowns dispersed in response to the disturbance of branches during climbing. Although the adults could not be observed, their presence was manifested by the characteristic musty odor they emit when disturbed.

Natural Control

Parasites and Predators. None was observed either in the field or reared from collections of *L. occidentalis* Heidemann.

Autotoxicity. Koerber (1967) reported that adults emit a jet of clear fluid from either side of the thorax for a distance of 10 to 15 mm. This phenomenon was not observed during this study, but the effects were evident and may account for the common occurrence of only one adult per rosette during collections. If adults were disturbed in the presence of other *Leptoglossus,* most or all the individuals became sluggish in a few hours, then lost the use of the pro- and mesothoracic legs and subsequently the metathoracic pair, and ultimately lapsed into a state of flaccid paralysis. Death occurred in 2 to 3 days. Koerber (1967) reported that paralysis occurred in 10 to 30 minutes, but onset was never that rapid with the specimens of this study. One individual, paralyzed except for wing musculature, lived for 9 days and managed flight twice for 1 to 3 minutes.

Cone Crop Levels and Competition. The population in the Waha stand completely disappeared with the failure of the cone crop in 1969. Other tree species in or near the test stand also failed to produce cones, so cones of alternate hosts were not available. It is possible that they migrated quite some distance, and/or dispersed widely and reverted to alternate feeding habits.

Any species which reduces the number of available cones would be competitive with *L. occidentalis*; however, only the seed moths, *Laspeyresia* spp., are directly competitive for the seeds. Most of the damage by the seed moths in the study area occurred before 7 August, which could substantially reduce the food supply of the bug. However, the competitive position of *Leptoglossus* is enhanced by mobility that allows them to move to other host trees or species. Probably of far greater importance is intraspecific competition manifest by the release of an autotoxin when the bugs are subjected to population pressure or other stress. This may account for the common occurrence of only one adult per cone rosette.

Dioryctria auranticella (Grote) (Lepidoptera: Pyralidae)

Bionomics

It has been reported (Keen 1958) that eggs of this moth are laid on cone scales, but none was found on the cones collected during this study. Following the procedures of Merkel and Fatzinger (1966), adults were reared in the field and laboratory with only limited success. Two females in field cages laid 101 and 11 eggs, respectively, and these hatched in 10 to 13 days under August field conditions. The reddish-brown larva becomes clearly visible before hatching and imparts a reddish appearance to the egg through the transparent and reticulate chorion. The behavior of the first instar larvae and the location of their overwintering site remain unknown. Koerber (1967) believes that, because of similarities of life histories between this species and *D. disclusa* Heinrich, *D. auranticella* probably overwinters as first instar larvae in hibernaculae under the bark scales on needleless portions of twigs. Spring feeding of *D. disclusa* larvae occurs on staminate flowers prior to pollen release. The subsequent third and fourth instars migrate to, and attack, second year cones. Although this behavior was not substantiated for *D. auranticella,* it probably occurs because cone damage by this species always appears suddenly after pollen release in late May. Larvae, when first observed in the field, always were quite large, and the population consisted of 2 instars with mean head widths of 1.31 and 2.00 mm, respectively. Larvae continue to develop in cones during late May, June and July. Mature larvae cut exit holes and spin silken screens across and slightly inside the rim of the openings. The number of exit holes does not always equal the number of larvae in the cone when there are three or more larvae.

Pupae are present as early as mid-June. Duration of this stage averaged 15.5 days in the laboratory. Pupation reportedly occurs in sparsely lined cells in or on the cone surface tissue (Keen 1958). However, some infested cones were collected without larvae or pupae present, suggesting that they may drop to the ground to pupate, or had fallen prey to avian predators, although neither outcome was observed. No evidence of pupal diapause was found either in the field or laboratory. Adults first appeared in mid-July.

Natural Control

Predators and Parasites. The following entomophagous insect species were reared from cones infested by *D. auranticella: Ichnemon brunneri* Rohwer and *Campoplex concolor* (Rohwer) (Hymenoptera: Ichneumonidae); *Hyssopis novis* Girault (Hymenoptera: Eulophidae); and *Haemerobius* sp. (Neuroptera: Hemerobiidae). None was abundant.

A hemerobiid larva was collected in early June from a cone infested with two larvae of *D. auranticella,* and placed in a large gelatin capsule with one of the coneworms. The hemerobiid attacked the coneworm when the latter molted, and killed it within 24 hours. Further observation of predation was not possible because of a malformation of the predator's mandible which occurred during molting two days later.

Interspecific Competition. Cones infested by *D. auranticella* often support broods of *C. ponderosae* (e.g., ca. 86% and 99% in 1969 and 1970, respectively, in the Mica stand). *Dioryctria* larvae consume an undetermined proportion of the beetle population during their feeding. However, the attack by the cone beetle also causes increased deterioration of the cone. Field observations showed that this forced 3 percent of the coneworms to migrate to other cones. Intraspecific competition was negligible.

Other Factors. One instance of bird predation was found in which a coneworm was removed from a cone. Two male horntails, *Urocerus albicornis* (F.) were collected on a cone infested by coneworm. Although dislodged twice, the horntails returned to the same cone, indicating the persistence of an unknown attraction.

Dioryctria abietella (Denis and Schiffermueller) (Lepidoptera: Pyralidae)

Bionomics

Larvae of *D. abietella* were present in June through August. Those found early in June was associated with damage by *D. auranticella*, or physical damage such as sunscald, confirming Lyons' (1957) conclusion that "young larvae feed primarily between deteriorating scales of second year cones previously damaged by other insects . . . ." Although the larvae feed primarily on scale tissue, they occasionally destroy seed in the process. The frass is cleared from the gallery, and it accumulates in an irregular shaped reddish-brown webbed mass on the cone surface.

Measurements of third to fifth instar larvae were in agreement with those reported by Merkel (1962). The species originally described by Merkel has been reclassified as *Dioryctria* n.s. *abietella* group (Ebel et al. 1975). A maximum of 10 larvae per cone were found in 17 infested cones, with an average of 2.7 per cone.

Larvae pupated during July through September, and adult emergence occurred in August and September. The failure of some adults to emerge in the fall gives support to the report that some overwintering occurs in the pupal stage (Brown 1941). The larvae produced by adults emerging in the fall probably overwinter in hibernaculae in the first instar. Koerber (1967) reported that some larvae do not reach maturity in time to pupate before the onset of cold weather. These overwinter in hibernaculae in the cone, in ground litter, or under bark scales and bark crevices. None of the life stages was found in or on cones examined in the fall in the Mica, Waha or Helmer, ID, stands. Larvae pupating in the laboratory usually did so in thin cocoons at the juncture of the walls and floor of the rearing cages, although a few remained in the cones.

Natural Control

Parasites and Predators. None was determined attacking or emerging from cones infested exclusively by *D. abietella.*

Competition. Dioryctria abietella is a superior competitor to *Laspeyresia* spp., because its damage and consequent resin flow prevent dehiscence, which in turn prevents emergence of the seed moths in the spring.

Late instars of *D. auranticella* appear much earlier in the season than do those of *D. abietella.* Damage by the former does not appear detrimental to the development of *D. abietella* due to the latter's ability to thrive in drier, partially deteriorated tissue. Examination of 38 infested cones on a single tree showed about 47 percent infested with *D. abietella* and 53 percent by the pine coneworm.

Dioryctria abietella cannot successfully compete against *C. ponderosae.* Apparently the early attack by the cone beetle precludes establishment of *D. abietella* in the same cones. In 1968, for example, *D. abietella* was found in 5.2 percent of the cones at Mica, ID, and the cone beetle in 29.8 percent. One year later, the cone beetle infested 97.9 percent of the cones, and *D. abietella* was not found at all. Douglas-fir in the area did not produce a cone crop in 1969 and could not serve as alternate host. A few individuals could have survived that year in galls of the western pine gall rust, *Peridermium harknessii* Moore (Keen 1958), for *D. abietella* was present in low numbers in ponderosa pine cones in 1970.

Eucosma ponderosa Powell (Lepidoptera: Tortricidae)

Bionomics

Only one adult was observed in the field. This observation occurred on 30 June near Moscow, ID. Damage to cones was not apparent until late July, at which time an average of 3.9 larvae were found per infested cone.

Larvae from cones placed in rearing cages in mid-July pupated in late July and August in 1968; cones collected in late June, 1967, produced adults in July of the same year. Keen (1958) reported that pupation occurs during September and October. Removal of the cones to the laboratory may have resulted in an increased rate of development in this study.

Pupation in the laboratory usually occurred on the cone surface, or on the cage bottom in thin parchment-like cocoons. In the field, it is assumed that pupation takes place in the litter, because no larvae or pupae were found in or on cones examined in late August.

Pupae subjected to a temperature of 2.8° C from late October to February did not produce adults in 30 days, but emergence did occur after the pupae were subjected to an additional 2 months of cold treatment. Adult emergence was obtained in 18 days from another group after the pupae were subjected to a cold treatment of 2.8° C for 5 months.

Natural Control

Parasites and Predators. No entomophagous insect species were found associated exclusively with *E. ponderosa.*

Interspecific Competition. The competitive position of *E. ponderosa* is secondary to *C. ponderosae, D. auranticella,* and possibly *D. abietella.* It does not compete directly with *Laspeyresia* spp. or *L. occidentalis* because it feeds primarily on scale tissue rather than in seeds and axes as do *Laspeyresia* spp.

Asynapta keeni (Foote)
(Diptera: Cecidomyiidae)

Bionomics

Koerber (1967) reported that adults of this species are active from March into June in California. Adults were not observed in Idaho in the field, but larvae were found from June through October.

Larvae feed between the cone scales, usually near the seeds, but they also were numerous under the developing seed wings. Evidently, they feed on pitchy exudations from lacerated tissues.

Larvae drop to the ground to pupate, but the period during which this occurs could not be accurately determined, because some larvae remained in open cones as late as early October. Keen (1958) reported that a partial generation occurs with emergence of adults in the fall. In Idaho, a few adults emerged in the fall from cones of the August collection, but as Koerber (1967) also suggested, this early emergence may be due to the consistently low humidity in the laboratory.

Natural Control

Parasites and Predators. No species was found that could be associated exclusively with *A. keeni.*

Interspecific Competition. This species often is associated with damage by *Dioryctria* spp. because the damage from cone moths provides entrance into the cones. However, if cone moth damage is so severe that the cone dries up or is killed, the midge larvae cannot survive. In years of very small cone crops, heavy midge infestations might produce sufficient numbers of hollow or malformed seeds to be detrimental to those species feeding on seeds.

CONCLUSIONS AND RECOMMENDATIONS

The importance of cone-crop size in regulating populations of cone and seed insects was made evident from this and previous studies (Abrahamson and Kraft 1965, Koerber 1967, Lester 1963, Mattson 1971, Schenk and Goyer 1967). Thus, manipulation of size, frequency and distribution of cone crops could be an important management tool. Further research should be directed to determining the efficacy of chemically thinning or eliminating cone crops on given sites when seed collection is unnecessary because of adequate reserves, reduced demand, or when other seed sources are available. If proven feasible, insect populations would be greatly reduced in years when cone collections are necessary. However, screening and testing the various chemicals and concentrations under varying environmental conditions would be not only time consuming and costly, but chemical use may be ecologically unacceptable in many cases.

Isolation of seed orchards from other stands containing ponderosa pine would help prevent rapid population increases from immigration after suppression operations, and has been suggested for other tree species (Morgan and Mailu 1976). Establishment of ponderosa pine seed orchards among the wheat farms in the Palouse region of eastern Washington may be more appropriate than the present practice of locating them within stands dominated by ponderosa pine.

It also would be desirable to establish seed orchards where the spring months normally are characterized by low evaporation rates or high precipitation levels. Cones of ponderosa pine remain closed with high humidity, inhibiting emergence of *Laspeyresia* spp. If seed orchards were contour-trenched during site preparation, many falling cones would accumulate in these trenches where they could be more easily collected and destroyed. Irrigation by sprinkling or flooding would serve to increase growth and productivity of the trees and to reduce the *Laspeyresia* population. Cones in the trenches would remain closed, or larvae would drown. A substantial portion of the previous cone crop may remain on the trees into summer; insects in these cones would not be eliminated by this method. However, these cones might be brought to the ground by mechanical tree shakers prior to irrigation.

To reduce losses caused by *Laspeyresia* spp., seed orchards or seed production areas: 1) should not be located in or near stands stocked predominantly with ponderosa pine; 2) should not be located within or adjacent to stands with crown closures greater than 50 to 60 percent; 3) should be located in mixed stands whose climax type is as remote as possible from ponderosa pine; and 4) should have seed trees spaced sufficiently to preclude branches of adjacent trees interlacing.

The cone beetle, *C. ponderosae*, is more likely to be most serious in open-grown stands, such as seed orchards, where destruction of the entire cone crop is possible. Increasing stand density will tend to reduce losses to the beetle, but increase those to the seed moths. A compromise is necessary. Because of the potential magnitude of the loss to cone beetles, seed orchards should be stocked to maintain the greatest crown closure compatible with sufficient cone production to meet management needs. This practice may increase susceptibility to seed moths, which may then require control treatments prescribed previously, or the application of direct chemical control.

The following cultural practices also have been suggested (Koerber 1967): 1) hand picking and destruction of infested cones to eliminate overwintering populations of *C. ponderosae*, *Laspeyresia* spp., and *A. keeni;* 2) eliminating brush and slash piles to reduce overwintering sites for *L. occidentalis*; and 3) burning or cultivating ground litter for reduction of *E. ponderosa* and *Dioryctria* spp.

populations. Unfortunately, many seed orchards and seed production areas in Idaho are located on slopes and soils where periodic cultivation might result in erosion. Prescribed burning may be more appropriate under those conditions.

Sampling cone crops any time between late July and seed release in late August or early September should provide an acceptable estimate of losses to the major insect pest species in this area. Managers then can predict net seed yields.

Selective chemical treatment is possible with systemic insecticides. In a preliminary study (Dale and Schenk, unpub.), ponderosa pine trees were injected with oxydemetonmethyl. The small cone crop in 1970 precluded a definitive bioassay and residue analysis, but the limited data indicated promise of good control of the cone and seed insect species attacking in the spring.

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