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Report

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CONE AND SEED INSECTS AND THEIR IMPACT ON WHITEBARK PINE

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ABSTRACT

Whitebark pine, *Pinus albicaulis* Engelm. is an important but declining high-elevation tree species in western forests. Regeneration of this species has been difficult and the impact of cone and seed insects unknown. Seven sites selected from the geographical range of whitebark pine in Idaho, Montana, Washington, Oregon, and California were examined for cone and seed insects and their impact. Ten different insect species were found affecting various reproductive structures of whitebark pine. Insects having the greatest impact across most sites were fir coneworm (*Dioryctria abietivorella* (Grote)) and western conifer seed bug (*Leptoglossus occidentalis* Heidemann). Coneworms infested up to 68% of cones collected, destroying up to 13% of the seed extracted. Seed bugs damaged up to 27% of the seeds. Pheromone traps for the ponderosa pine cone beetle (*Conophthorus ponderosae* Hopkins) and coneworms were tested. Ponderosa pine cone beetles were trapped at three of seven sites. Coneworms were trapped at two sites where pheromone traps were deployed. Further studies incorporating different cone crop levels of whitebark pine and other associated tree species are needed to fully determine the effect of cone and seed insects on whitebark pine seed and reproduction.

INTRODUCTION

Whitebark pine, *Pinus albicaulis* Engelm., plays a key role in the survival and distribution of wildlife species such as the grizzly bear (*Ursus arctos horribilis* Ord), Clark's nutcracker (*Nucifraga columbiana* Wilson) and the red squirrel (*Tamiasciurus hudsonicus*) by providing a high protein food source with its seeds and cones (Tomback 1978, Kendall 1983). Kendall and Arno (1990) indicate that long-term declines in cone production may affect wildlife community dynamics and emphasize the importance of adequate and consistent cone crops. As one of few tree species that grow in the subalpine community, whitebark pine plays an important role in watershed stabilization (Mumma 1990) and recreation and esthetic values (Cole 1990). Research has recently documented the rapid decline of this important species throughout much of the West. The decline is due primarily to the introduced white pine blister rust fungus (*Cronartium ribicola* Fisch.), periodic outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins), fire suppression, and forest successional processes (Keane and Arno 1993).

Regeneration of this species can be difficult because of many competing biological and cultural factors such as poor germination rates,

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slow growth, sporadic cone crops, and the widespread decline mentioned above. Cone production in whitebark pine is characterized by frequent years of small cone crops and less frequent years of moderate to heavy crops. Clark's nutcracker plays an essential role in the dispersal of whitebark pine seeds. Whitebark pine seeds sustain these birds during much of the year, but a large portion of the seeds that have been cached germinate and become future whitebark pine regeneration (Arno and Hoff 1989). Hutchins (1990) found that Clark's nutcracker harvested 36% of seeds in forested tracts and up to 99% of seeds from open grown trees. Cone and seed insects may threaten successful regeneration of whitebark pine by reducing seed production during some years. Likewise, bears, nutcrackers, and other wildlife species which use whitebark pine seed as an important food resource may also be negatively affected by the activity of cone and seed insects.

Whitham and Mopper (1985) found that the coneworm, *Dioryctria albovittella* (Hulst), significantly reduced cone production in pinyon pine (*Pinus edulis* Engelm.). In addition to direct impacts of cone and seed insects, there is potential of indirect effects such as birds avoiding foraging on insect infested cones thereby affecting seed dispersal. Christensen and Whitham (1991) found that birds avoided pinyon pine trees with insect-infested cones and sometimes avoided entire infested stands.

Prior to this study, information on the incidence and impact of insects on first- and second-year whitebark pine cones was largely unknown. However, several insects were thought to be probable associates. The western conifer seed bug, *Leptoglossus occidentalis* Heidemann, and coneworms, *Dioryctria* spp., are likely pests of first year conelets. Second year cones might be infested by the ponderosae pine cone beetle, *Conophthorus ponderosae* Hopkins; cone moths, *Eucosma* spp.; seed worms, *Cydia* (=*Laspeyresia*) spp.; coneworms, *Dioryctria* spp.; western conifer seed bug, *Leptoglossus occidentalis*; and seed chalcids, *Megastigmus* spp. (McCaughey and Schmidt 1990). Cone beetles destroyed 50-80% of limber pine (*Pinus flexilis* James) cones in some years (Keen 1958), and coneworms infested up to 40% of the cones (Nebeker 1970). Cone beetles can destroy 90% or more of the western white pine (*Pinus monticola* Dougl.) cone crop (Shea et al. 1983, Williamson et al. 1966). Seed bugs and coneworms impacted between 50-80% of cones in western white pine seed orchards (Connelly and Schowalter 1991, Haverty et al 1986).

The objectives of this study were to identify insects affecting reproductive structures, to quantify the impact of insects, to note the stage of cone development and seasons in which infestations occur, and to evaluate the efficacy of pheromone traps for monitoring cone beetles and coneworms in whitebark pine habitats.

METHODS

Seven sites were selected from the geographical range of whitebark pine in Idaho, Montana, Washington, Oregon, and California. We selected sites based on accessibility and number of whitebark pine trees of cone-bearing age. Sites varied in elevation, aspect, slope position, and latitude (Table 1). Fifteen trees were randomly chosen at each site. There were 14 treatments on each tree, with each tree serving as a treatment replicate. Treatments consisted of exposing cones to insects for various time periods during the 2-year cone development period. Most treatments consisted of exposure periods of approximately 1 month occurring at different months throughout the 2-year growing season. Some treatments exposed cones during an entire year of the 2-year growing period (exposed first or second year) or exposed cones during both years. Some cones were protected during both years. During the second year of cone development, cones in all but two treatments were caged to prevent foraging by Clark's Nutcracker. In order to apply treatments to cones that were mainly located in the upper crown on trees at all sites except Ball Mtn., it was necessary to climb the trees.

During 1995, when cone buds became prominent or flowers appeared in June and July 1995, individual branch tips were flagged to designate 14 flower clusters (treatments) on each of the 15 trees. Ripe pollen catkins were collected in June, then dried, and pollen was extracted. Flowers in each cluster were artificially pollinated to ensure cone production. At Ball Mtn., the number of flowers selected for treatment were tallied and monitored for losses during the first year. Flower and conelet losses at other sites were not quantified. Branches with cone clusters were wrapped with cotton bands below the cone clusters. Fine mesh cloth bags were slipped over the branch tips and secured with plastic bar-locks over the cotton bands, enclosing the cones (Figure 1). All cones were harvested in September 1996.

Table 1. Whitebark pine site characteristics.

Site	State	Elevation (feet)	Latitude (degrees)	Aspect	Slope Position
Gisborne Mtn.	ID	5,430	48	SE-SW	Upper
Seven Devils	ID	8,000	45	W-NW	Upper
Snowbank Mtn.	ID	7,525	44	E-SE	Ridge Top
Daisy Pass	MT	9,500	45	S-SW	Bench
Stormy Mtn.	WA	6,100	47	S-SW	Ridge Top
Mt. Hood	OR	5,430	45	S-SE	Bench
Ball Mtn.	CA	7,682	41	W-NW	Upper

Figure 1. Mesh cloth bags covering cone clusters to prevent insect attack.

Harvested cones were placed in individual sacks along with the designated tree, treatment number, and study site. Cones from each treatment cluster were examined to determine the number of live cones, number of cones with external evidence of insect damage, and number of cones damaged by birds. Cones were measured and cone scales were counted to determine potential seeds. Cones were then dissected and seeds extracted and counted. Seeds were categorized as normal, undeveloped, aborted, damaged by seedworms, or damaged by coneworms. Seeds from each cone were saved, pooled by treatment on each tree within a site, and placed in an envelope. A random sample, up to 100 seeds from each treatment per tree, were radiographed. The x-rays of each treatment/tree combination were sent to the Institute of Forest Genetics, Placerville, California for interpretation. X-rayed seeds were classified as filled (normal), physiologically abnormal, damaged by seed bug, seed chalcid, seedworms or coneworms, damaged by birds, or mechanically damaged. Identification of seed bug damage by x-rays can be difficult and sometimes confused with other types of physiological abnormalities. The x-ray interpreters were conservative in their definition of seed bug damage and made a second category referred to as "potential seed bug damage." This described damaged seeds with symptoms similar to seed bug feeding. Seed bug and potential seed bug damage are reported and analyzed separately.

Observations of insects affecting flowers, pollen catkins, and branch tips were recorded throughout the 2-year period, but not quantified.

Trece® Japanese beetle (Popillia japonica) pheromone traps baited with bubble capsules containing 40 mg racemic trans-pityol to attract ponderosa pine cone beetles were placed at each site in June of 1995 and 1996. Insects were collected monthly through September of each year. All Scolytidae trapped were sent to Dr. Donald Bright, Canada Agriculture, for identification. Pherocon 1C ® winged sticky pheromone traps baited with several different pheromone blends to attract coneworms were placed at Gisborne Mtn. in Idaho and Ball Mtn. in California. Insects were removed from traps at two week intervals and the pheromones were replaced mid-season.

To supplement our sample, during the months of July-September 1996, 25 additional cones that had not been selected for treatment were collected at five sites and placed in containers to rear insects. Percent infestation was determined for all cones sampled.

In addition to field studies, we analyzed a sample of whitebark pine cones routinely collected by USDA Forest Service (Forest Service) personnel from 11 sites throughout northern Idaho and Montana. These were sent to the Forest Service Nursery in Coeur d'Alene for seed extraction. We examined a sample of these cones at the nursery for external evidence of insect and bird damage. Percent infestation was determined for all cones sampled.

The impact of insects and other agents on whitebark pine was reported as the percent of cones or seeds damaged by each agent. In such data (a variable that estimates a percentage or proportion) the variance is a function of the mean. To eliminate this dependence, the data was transformed using the arcsine of the square root of the proportion. Adjustments for small samples were also made as recommended in Snedecor and Cochran (1971). Due to technical difficulties in pollination (timing, adverse weather), abortion of flowers or conelets, breakage of treatment branches, or animal and bird damage, some treatments were not represented at all sites. Because of these missing observations, the resulting data sets for cone and seed damage were unbalanced.

The SAS procedure, GLM – Tests of Hypothesis of Mixed Model Analysis, based on type III means squares was used to test treatment and location effects. Besides the main effects of treatment, location and their interaction, the random effect of sample tree within location was included. Due to the unbalanced data, the adjusted means could not be calculated for the multiple means test to further qualify significant differences for a main effect or interaction. As a guide to which treatments or locations are at the root of the significance, multiple mean tests were computed using Bonferroni t tests on the unadjusted means. The data presented in the tables of this report are the means of the percents found for each condition. All significant differences presented in these tables are based on the analyses of the transformed data.

RESULTS AND DISCUSSION

A total of 2,013 treatment cones were examined from the seven study sites. The number of cones from each site varied from 115 to 418. At Ball Mountain, 17% of the original flowers selected for treatment aborted. An additional 3% of first-year conelets aborted due to unknown causes. On all sites, nearly all the cones from the two treatments that were not caged to protect them from Clark's nutcracker were either missing or so damaged by birds that few seeds were extracted. The number of seeds x-rayed varied from 0 to 180 for each treatment at each location.

Cone length and number of extractable and filled seed varied by location. Cones with extractable seed ranged from 1.8 cm to 8.2 cm in size. Mean cone length varied from 4.5 cm to 5.6 cm by location. The smallest cones were found at Daisy Pass, the highest elevation site in this study (9,500 feet), whereas the largest cones were found at Mt. Hood and Gisborne Mtn. which were the lowest elevation sites (both at 5,430 feet). The number of seeds extracted per cone varied from 0 to 139. The percent of extractable seed from the maximum potential seed (2X the number of cone scales) ranged from 32% to 62%. The percent seed extracted from maximum potential seed in our study is similar to a previous study which ranged from 37% to 81% at a site artificially pollinated and from 26% to 53% at a site naturally wind pollinated (Hoff & McCaughey 1995).

Ten different insect species were found affecting various reproductive structures of whitebark pine (Table 2). The insect species and number of insects found varied considerably across sites.

Table 2. Insects found affecting whitebark pine reproductive structures.

Reproductive Structure	Insect
Flowers	white lined June beetle, *Polyphylla crinita* western flower thrips, *Frankliniella occidentalis*
Pollen	sawflies, *Xyela* spp. scarab beetle, *Dichelonyx fulgida* western flower thrips, *Frankliniella occidentalis*
Branch tips	twig boring *Dioryctria* spp.
Cones	fir coneworm, *Dioryctria abietivorella* ponderosa pine cone beetle, *Conophthorus ponderosa* western conifer seed bug, *Leptoglossus occidentalis* seedworms, *Cydia* spp. adelgids, *Pineus* spp.

INCIDENCE OF CONES WITH EXTERNAL EVIDENCE OF INSECTS BY LOCATION

Ponderosa pine cone beetles were observed at some study sites in cones not included in this study (Figure 2), and were found in pheromone traps at locations where they were not found in study cones. Incidence of coneworms and adelgids was quantified for treatments exposed for all of 1996 and for all of 1995-96 (Tables 3 and 4). The impact of White-lined june beetles, sawflies, scarab beetles (Figure 3), and the twig boring *Dioryctria* was not quantified.

Cones infested by coneworm (Figure 4) ranged between 0-50% for cones exposed during the second year of their development. Damage to cones due to coneworms at Daisy Pass was zero, which was significantly less than damage at Gisborne, Mt. Hood and Ball Mtn. Adelgids were found only on cones at Seven Devils and Stormy Mtn. for this treatment. In some instances, the adelgid population was so heavy the entire cone appeared white (Figure 5). However, the effect of adelgids on whitebark pine seed production is still unknown. Adelgid feeding has minimal effects on seed of western white pine (Manya Stoetzel, pers. comm.)

Figure 2. Whitebark pine cones infested with ponderosa pine cone beetles, *Conophthorus ponderosa*. Note characteristic pitch tubes at the base of the cones.

Table 3. Mean percent cones infested by location for treatment exposed all of 1996.

Location	# of Cones Sampled	% Coneworm[1]	% Adelgid[1]
Gisborne	25	44 a	0 b
Seven Devils	26	15 ab	15 a
Snowbank	11	36 a	0 b
Daisy Pass	11	0 b	0 b
Stormy Mtn.	19	10 ab	26 a
Mt. Hood	14	50 a	0 b
Ball Mtn.	39	43 a	0 b

[1] Means within columns which share the same letter code are not significantly different at the 0.10 level when the transformed percents were tested.

For the treatment exposed all of 1995-96, cones infested with coneworms ranged from 0-68%. The incidence of coneworms at Mt. Hood was significantly greater than Snowbank, Daisy Pass, and Stormy Mtn. No adlegids were found in this treatment.

Table 4. Mean percent cones infested by location for treatment exposed 1995-1996.

Location	# of Cones Sampled	% Coneworm[1]	% Adelgid[1]
Gisborne	23	22 ab	0
Seven Devils	18	17ab	0
Snowbank	13	15 b	0
Daisy Pass	7	0 b	0
Stormy Mtn.	5	0 b	0
Mt. Hood	19	68 a	0
Ball Mtn.	60	43 ab	0

[1] Means within columns which share the same letter code are not significantly different at the 0.10 level when the transformed percents were tested. No alpha codes in a column mean there were no significant differences.

Figure 3. Scarab beetles, *Dichelonyx fulgida*, on whitebark pine pollen catkins.

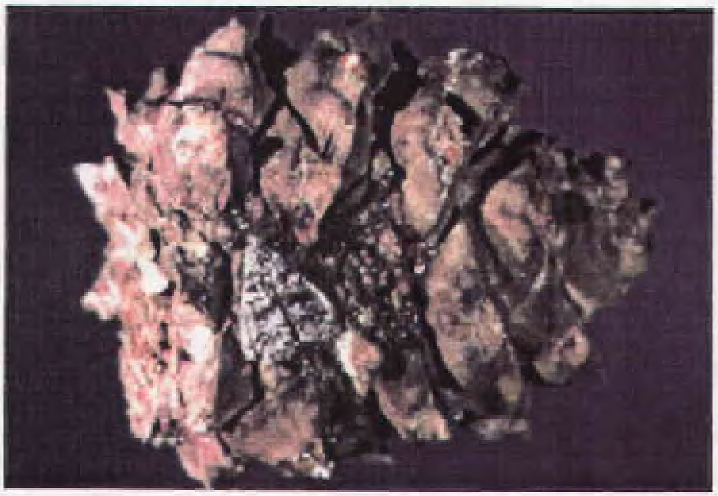


Figure 4. Fir coneworm adult, *Dioryctria abietivorella*, on damaged whitebark pine cone.

Figure 5. Adelgids, *Pineus* spp.on whitebark pine cone.

IMPACT ON SEED BY LOCATION

Data were quantified for coneworms, seedworms and seed bugs and their effect on seeds recorded by location for the treatments exposed for all of 1995-96 (Table 5) and exposed all of 1996 (Table 6). X-ray analysis showed a variety of physiological damage and damage due to feeding by seed bugs. Seed bug damage ranged between 0.1 and 26.9% in the two treatments (Tables 5 and 6). The potential seed bug damage category ranged between 1.8 and 39.3%. An adult seed bug was observed on a whitebark pine cone at Gisborne Mtn. in late summer (Figure 5).

Proportions of filled seed, seed with possible and actual seed bug damage, and seed damaged by coneworms were significantly different ($p < 0.10$) between locations (Tables 5 and 6). Results show that the proportion of seed bug damage and potential seed bug damage were significantly greater at Snowbank and Daisy Pass, two of our higher elevation sites. This may be because relatively few insects occur at high-elevation sites, resulting in less competition for seed bugs from other insect species. The possible relationship between seed bug damage levels and elevation needs further study.

Table 5. Mean percent seed damaged by location for cones exposed all of 1995-1996 (both years of cone development).

Location	# of Trees Sampled	% Filled seed (normal)[1]	% Coneworm[1]	% Seed bug[1]	% Potential Seed bug[1]	% Other physiological damage
Gisborne	9	86.2 a	1.0	1.9 bc	4.5 bc	7.2
Seven Devils	5	58.4 ab	1.0	1.3 c	10.6 bc	25.6
Snowbank	5	31.5 b	2.3	9.0 ab	27.4ab	32.7
Daisy Pass	3	30.4 b	0.2	24.0 a	39.3a	6.3
Stormy Mt	3	73.0 a	0.2	1.2 c	9.8 bc	16.0
Mt. Hood	7	78.8 a	1.3	2.7 bc	5.3 bc	13.9
Ball Mtn.	14	77.8 a	1.6	1.1 c	1.8 c	19.4

[1] Means within columns which share the same letter code are not significantly different at the 0.10 level when the transformed percents were tested. No alpha codes in a column mean there were no significant differences.

Table 6. Mean percent seed damaged by location for treatment exposed all of 1996 (2nd year of cone development).

Location	# of Trees Sampled	% Filled seed (normal)	% Coneworm[1]	% Seed bug[1]	% Potential Seed bug[1]	% Other physiological damage
Gisborne	11	74.8	1.5 b	3.6 b	5.6 b	16.1
Seven Devils	6	64.1	1.3 b	0.5 b	20.6 a	14.2
Snowbank	3	51.7	0.9 b	26.9 a	4.6 b	15.3
Daisy Pass	4	42.6	0 b	22.8 a	22.1 a	12.6
Stormy Mt	9	71.9	0.2 b	1.1 b	7.7 ab	19.9
Mt. Hood	7	71.3	13.2 a	0.1 b	3.2 b	25.4
Ball Mtn.	12	65.5	1.3 b	2.6 b	2.7 b	29.2

[1] Means within columns which share the same letter code are not significantly different at the 0.10 level when the transformed percents were tested. No alpha codes in a column mean there were no significant differences.

Percent seed damaged by coneworms ranged between 0 and 13.2% by location. The greatest amount of coneworm damage to seed occurred at Mt. Hood on cones exposed all of 1996 (during their second year of development). In addition to the direct effects of coneworm on seed production, the possible indirect effect of birds avoiding insect infested cones, and therefore caching less seed for regeneration, may be substantially higher. This phenomena has been documented for bird avoidance of feeding on insect-infested cones of pinyon pine (Christensen and Whitham 1991).

Figure 6. Adult seed bug, *Leptoglossus occidentalis*, found on whitebark pine cone.

EFFECTS OF EXPOSURE PERIOD ON SEED BY LOCATION

No significant treatment differences were found at Seven Devils, Snowbank Mtn., Daisy Pass, Stormy Mtn., and Ball Mtn. Significant differences between treatments ($p<0.10$) were observed at two of the seven locations. At Gisborne Mtn., treatment exposed August 1996 had significantly more seed bug damage than treatments exposed July 1995, all 1995, May 1996, July 1996 and closed 1995-1996. Treatments exposed August 1996 and all of 1996 had significantly more seed bug damage than the treatment exposed all of 1995 (Table 7). At Mt. Hood, treatment exposed all of 1996 had significantly more seed damaged by coneworms than all the other treatments. In summary, treatments exposed during August of the second year of cone development or during the entire second year of cone development had significantly more insect damage than other treatments

Table 7. Significant differences between exposure periods and insects for specific locations where significant differences were found.

Location	Exposure Period (Treatment)	Seed bug on Seed[1]	Coneworm on Seed[1]
Gisborne Mtn.	July 1995	0.61 bc	2.16
	August 1995	1.35abc	0.70
	September 1995	1.73abc	1.37
	All 1995	0.46 c	1.76
	May 1996	0.40 bc	3.42
	July 1996	1.67 bc	1.57
	August 1996	7.31a	0.56
	All 1996	3.64ab	1.46
	Closed 1995&1996	1.60 bc	1.51
	All 1995&1996	1.95abc	1.06
Mt. Hood	July 1995	0.38	0.95a
	August 1995	1.27	2.75a
	September 1995	0.31	0.85a
	All 1995	1.25	1.14a
	May 1996	0.67	1.07a
	August 1996	1.27	3.13a
	All 1996	0.14	13.19 b
	Closed 1995&1996	1.26	0.74a
	All 1995 & 1996	2.66	1.30a

[1] Means within columns which share the same letter code are not significantly different at the 0.10 level when the transformed percents were tested. No alpha codes in a column mean there were no significant differences.

Pheromone Trap Data

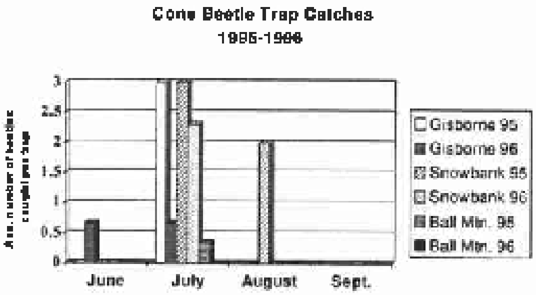
Six species of Scolytidae caught in the pityol-baited traps were identified (Table 8). *Pityophthorus* species were the most abundant with nearly 700 caught in 3 traps during July 1995 at Stormy Mountain.

Table 8. Scolytidae caught in pityol-baited traps.

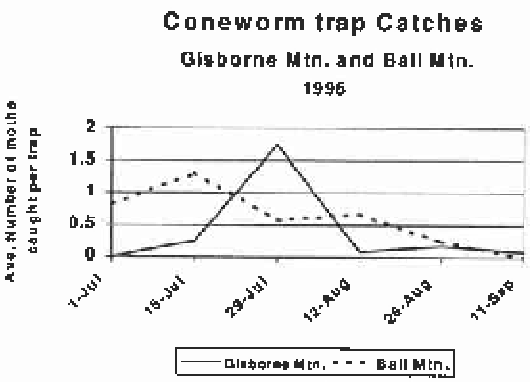
Conophthorus ponderosae
Pityophthorus absonus
Pityophthorus toralis
Pityogenes carinulatus
Ips latidens
Hylastes macer

Ponderosa pine cone beetles were collected at three of the seven locations - Gisborne Mtn., Snowbank Mtn, and Ball Mountain. No beetles were caught at Stormy Mtn., Daisy Pass, Seven Devils, or Mt. Hood in either year. Cone beetle trap catches were higher in 1995 than in 1996 at all three locations (Figure 7). Trap catches at Snow Bank were the highest of all locations during both years. Peak flight for cone beetles at all sites was in July. However, some were caught in June at Gisborne Mtn., a lower elevation site, and in August at Snowbank, a higher elevation site. Although ponderosa pine cone beetle caused a relatively small proportion of the damage to cones in this study, in some years and locations they may play a more significant role. Phermone trapping could be an effective monitoring tool for further investigations of cone beetle impacts in whitebark pine ecosystems and should be placed in early June to capture the beginning of the cone beetle flight period.

Figure 7. Average monthly ponderosa pine cone beetle trap catches at Gisborne, Snowbank, and Ball Mountains. in 1995 and 1996.



Peak flight for coneworms at Gisborne Mtn. and Ball Mtn occurred in July. However, peak flight for Ball Mtn. occurred 2 weeks earlier than at Gisborne (Figure 8). These results show that pheromone traps would need to be placed prior to July to be an effective monitoring tool for coneworms.



ADDITIONAL CONE COLLECTIONS

Extra cones were collected in mid-July and mid-August at Gisborne Mtn., Seven Devils, Snowbank Mtn., and Daisy Pass. Cones were also collected during August at two Montana sites outside our study areas, Baldy, Beaverhead NF (10,105 feet) and Yogo Peak, Lewis and Clark NF (8,800 feet). These were examined for external evidence of cone beetle or coneworm feeding and then placed in containers to rear adult insects. The coneworm infestation rate varied from 3% to 55% across sites and collection dates. In extra cones from Daisy Pass, we found 3% coneworm damage in the additional cones collected. Excluding Daisy Pass, overall coneworm infestation rate was 40% for cones collected in July and 40% for those collected in August. In our controlled treatment study, coneworm incidence averaged 33% in treatments exposed 1 or 2 years, excluding Daisy Pass which had no damage from coneworms on the study cones. Cone beetle damaged cones were only found at one site, Gisborne Mtn., impacting 0.2% of extra cones collected there.

We also examined a total of 1,214 cones collected from 11 different sites on five forests in Montana and Idaho that were sent to the Coeur d'Alene Forest Service nursery. The percent of cones infested with coneworms at the nursery averaged 25%. Cone beetles killed 0.5% of the cones we examined.

The year 1996 was considered a moderate cone crop year for whitebark pine (Lars Halstrom, pers. com.). During low cone crop years, the relative impacts of these insects may be much greater.

Figure 8. Average number of coneworms caught in pheromone traps at Gisborne Mtn. and Ball Mtn. in 1996.

SUMMARY

This study provides new information on the array of insects affecting whitebark pine reproductive structures, of the relative abundance of insects directly affecting cones and seeds, and of the variation that exists across the range of whitebark pine in Idaho, Montana, Oregon, Washington, and northern California. Results indicate that coneworms, seed bugs, and cone beetles have the potential to reduce whitebark pine regeneration. In this study, coneworms and seed bugs had the greatest impact on seed production. This effect likely would be even more pronounced during years of low cone crops. The indirect effects of bird avoidance of insect-infested cones (Christensen and Whitham 1991) could have an even greater impact on whitebark pine regeneration.

This study shows that insects impact whitebark pine cones and seeds even at very high elevations. Results suggest that various insect species may have different effects relative to elevation and geographical location. Due to the serious impact of white pine blister rust on whitebark pine, managers should consider protecting cones of resistant trees from cone and seed insects. Pheromone trap monitoring of coneworm and cone beetle populations could be a useful component of a whitebark pine restoration management system.

Future studies are needed to address the relationships among varying sizes of whitebark pine cone crops and impacts of cone and seed insects. Because most of these insects also feed on the seed from a variety of coniferous tree species, the influence of cone crop size of other conifers should also be investigated.

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