

AN ABSTRACT OF THE THESIS OF

Sara C. Prueitt for the degree of Master of Science in Forest Science presented on July 18, 1997. Title: Effects of Environment and Genetics on Western Pine Shoot Borer, *Eucosma sonomana*, Infestation Levels in Ponderosa Pine Plantations of Central Oregon.

Abstract approved: _____

Darrell W. Ross

Infestations of the western pine shoot borer (*Eucosma sonomana* Kearfott) in young stands of ponderosa pine (*Pinus ponderosa* Lawson), were surveyed on the Deschutes National Forest. Elevation, slope, aspect, tree height, tree diameter, number of shoots in the terminal whorl, stand density, stand age and plant association for each stand were used in general multiple regression and logistic regression analyses to predict the percentage of infested terminal shoots. Using general multiple regression, taking the arcsin(square root(proportion of infested trees)), the models that were selected as the best predictors included (1) diameter, trees/hectare and elevation ($R^2=0.62$) and (2) number of shoots in the terminal whorl and stand age ($R^2=0.62$). Using logistic regression, the best model included number of shoots in the terminal whorl and stand age. Values for these stand characteristics can be used with the appropriate equation to estimate the percentage of terminal whorls damaged by shoot borer in a given stand. A companion study performed in six progeny test sites on the Ochoco National Forest

found significant differences in shoot borer infestations among 29 ponderosa pine families (P -value = 0.001, $R^2=0.62$).

Effects of Environment and Genetics on Western Pine Shoot Borer, *Eucosma
sonomana*, Infestation Levels in Ponderosa Pine Plantations of Central Oregon

by

Sara C. Prueitt

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented July 18, 1997
Commencement June 1998

Master of Science thesis of Sara C. Prueitt presented on July 18, 1997

APPROVED:

Major Professor, representing Forest Science

Head of the Department of Forest Science

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Sara Prueitt

Sara C. Prueitt, Author

ACKNOWLEDGMENTS

Many people have helped me complete this thesis, and I would like to acknowledge a few of these people here.

Darrell Ross influenced my thesis work more than any other person, just by encouraging me to make the research my own and by showing confidence in the work I did. I always felt that I could approach Darrell for advice, but more importantly I felt that I could make my own decisions without getting approval for each step.

For helping me develop the hazard rating model, I would like to acknowledge Brian Tandy of the Sisters Ranger District, and Matt Dettmeier and Jim Summers of the Bend/Fort Rock Ranger Districts for supplying information on the ponderosa pine stands. I would also like to thank Rusty Merritt of the Sisters Ranger District and Randy Gray of the Bend/Fort Rock Ranger Districts for the beautiful GIS maps.

For helping me with the genetics study, I would like to acknowledge Duane Ecker, of the Prineville Ranger District, Paul Berrang of the Winema National Forest, and William Randall of the Pacific Northwest Research Station for providing information on the progeny test sites in the Malheur and Ochoco National Forests.

I would also like to thank my parents, Carol and Gerald Prueitt, for the emotional (and occasionally the financial) support that was always given willingly. I have always been under the impression that they are continually amazed at how two artists raised a daughter with a yen for science. Perhaps the greatest gifts they have given me were a sense of creativity and an appreciation of the beauty in nature, which always come in handy when putting in many long days of field work.

I would also like to thank Jens Lovtang for giving me the hugs and encouraging words that kept me sane as I coped with classes, thesis work, and personal crises, sometimes all at once. I hope that I can also keep a sense of humor when he is in graduate school.

Finally, I would like to acknowledge the Pacific Northwest Research Station for providing partial funding for this study.

TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW	1
DEFINING THE PROBLEM	1
THE HOST/INSECT RELATIONSHIP	5
OBJECTIVES OF THESIS	13
Environmental influences	13
Genetic influences	14
 CHAPTER 2: EFFECTS OF ENVIRONMENT AND GENETICS ON WESTERN PINE SHOOT BORER, <i>EUCOSMA SONOMANA</i> , INFESTATION LEVELS IN PONDEROSA PINE PLANTATIONS OF CENTRAL OREGON	 15
ABSTRACT	16
INTRODUCTION	17
MATERIALS AND METHODS	19
Environmental influences	19
Genetic influences	25
RESULTS	26
Environmental influences	26
Genetic influences	30
DISCUSSION	36
CONCLUSIONS	38
LITERATURE CITED	40

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Plant association map of the Deschutes National Forest, showing stands that were surveyed	20
2. Least squares means and their 95% confidence intervals for shoot borer infestation	32
3. Least squares means and their 95% confidence intervals for average number of shoots	33
4. Least squares means and their 95% confidence intervals for average height ...	34
5. Least squares means and their 95% confidence intervals for average diameter .	35

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Average and range for each variable measured in stands of ponderosa pine in central Oregon	27
2. Results of logistic regression analyses for individual variables associated with 1996 shoot borer infestation in ponderosa pine plantations of central Oregon	28
3. Results of simple linear regression analyses for variables associated with 1996 shoot borer infestation in ponderosa pine plantations of central Oregon	28
4. Correlation coefficients of family least squares means in ponderosa pine progeny test sites, followed by the <i>P</i> -value of the correlation.	31

EFFECTS OF ENVIRONMENT AND GENETICS ON WESTERN PINE SHOOT BORER, *EUCOSMA SONOMANA*, INFESTATION LEVELS IN PONDEROSA PINE PLANTATIONS OF CENTRAL OREGON

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

DEFINING THE PROBLEM

The western pine shoot borer (*Eucosma sonomana*) has received little attention as a forest pest, but can cause significant damage to several pine species. Its larval stage feeds on the pith of the growing terminal shoots of most yellow pines, such as ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), and lodgepole pine (*Pinus contorta*) (DeBoo et al. 1971, Sartwell et al. 1980). The shoot borer seems to prefer the largest buds with the highest growth potential (Sower and Mitchell 1987), favoring the terminal shoot but also infesting the lateral shoots of the terminal whorl.

The shoot borer completes one generation in the course of a year, (i.e., they are univoltine). Shoot borer moths emerge in the spring, usually by early April in central Oregon (Mitchell and Sower 1988). Female moths fly to the tips of host trees and emit a pheromone that attracts male moths. After mating, the females oviposit on or near terminal buds. Larvae emerge in the same spring, enter the tip of a bud and mine the pith as the shoot elongates. By early July they finish feeding, leave the shoot on which they fed, and drop to the ground to overwinter as pupae.

The western pine shoot borer is an atypical pest in that its population levels are stable over long periods, and damage is chronic. Young ponderosa pine trees, from about 1.5 to 12 meters in height, are most heavily infested (Sower and Shorb 1984, Mitchell and Sower 1991, Williams et al. 1988). The growth of ponderosa pine terminal shoots is usually stunted by shoot borer feeding, but occasionally shoots are killed. This damage not only decreases height growth, but can also cause trees to become forked or crooked as the lateral shoots compete for dominance in the absence of a healthy terminal shoot.

Shoot borer damage is distinguished from damage caused by other shoot feeding insects by the shaving-brush or bottle-brush appearance of the infested shoot, caused by the stunted growth of the distal needles. In ponderosa pine stands of the Southwest U.S., the southwestern pine tip moth (*Rhyacionia neomexicana*) usually kills the shoots on which the larvae feed (Stevens and Jennings 1977). In lodgepole pine, shoot borer damage can be confused with damage caused by the lodgepole terminal weevil, *Pissodes terminalis* (Stark and Wood 1964). The shoot borer mines only the pith in ponderosa pine, leaving dark brown tightly packed frass in its path. The xylem and phloem are not damaged, so the shoot remains alive and erect (Stevens and Jennings 1977). In lodgepole pine, however, which has stems of smaller diameter, shoots are often killed when larvae etch, or bruise, the xylem (Mitchell and Sower 1991). Perhaps because of this difference in tree anatomy, infestations in lodgepole pine stands appear higher than in ponderosa pine stands because damage is more obvious.

Past management practices have changed the structure and composition of forests across the landscape, which may have created conditions that are more susceptible to high shoot borer infestation. Frequent, low intensity fires have historically occurred in ponderosa pine stands, which created open park-like forests with little understory. Agee (1990) describes natural ponderosa pine forests in central and eastern Oregon, that were historically shaped by a frequent, low-severity fire regime, as a mosaic of many different-aged patches. He explains that these patches were created when mature groups of trees succumbed to insects and disease. Fire would sweep through most of the light fuels on the forest floor, but burn the dead and decaying trees to create an opening for a new age class.

Fire suppression and silvicultural practices changed the fire history, and may be influencing shoot borer populations. Grant (1958) observed that the most significant shoot borer damage in British Columbia occurred in young open-grown trees, and Stoszek (1973) found that infestation levels were substantially lower in the uneven-aged stands in his study. The extensive clear cutting followed by planting in the 1970's and 1980's in central Oregon created larger patches that are very close to one another. As a result, large contiguous areas now provide ideal shoot borer habitat.

The impact that shoot borer damage has on ponderosa pine forests becomes increasingly important as the land base for timber production declines. Methods of controlling shoot borer populations have been developed, and, together with changes in fire suppression and silvicultural practices, these methods may help to increase the efficiency of wood production in pine stands.

In the late 1970's, the sex-attractant emitted by the female shoot borer was identified (Sower et al. 1979) and synthetically produced in order to disrupt mating behavior. To test the effectiveness of this synthetic sex-attractant, hollow fibers that contained a 4:1 mixture of a pheromone, Z-9- and E-9-dodecenyl acetate, were dispersed by airplane onto ponderosa pine plantations in southern Oregon. The nominal dosage of the pheromone was 15 grams/hectare. Tree damage was reduced by an average of 67% in the terminal shoots and 79% in the terminal and lateral shoots combined (Overhulser et al. 1980).

Similar experiments were performed using strips of polyvinyl chloride that were impregnated with the pheromone and hung at the base of ponderosa pine trees. In the first series of experiments, a nominal dosage of 3.5 grams/hectare was broadcast from strips spaced at 10m, which reduced damage by 83% (Sartwell et al. 1980), and, in the second series of experiments, a nominal dosage of 3.5 grams/hectare was broadcast from strips spaced as far as 50m apart reduced damage by 46% (Sartwell et al. 1983). In spite of the efficiency of this pheromone treatment, it has not been widely used because land managers do not have guidance on where to use it, or sufficient information to conduct a cost/benefit analysis.

THE HOST/INSECT RELATIONSHIP

Environmental conditions can have profound effects on insect development and reproduction, as well as the host-plant defenses and suitability as a food source. In this

study, I considered ponderosa pine stands that were within their natural ecological range, and the site and stand characteristics that would most likely influence either shoot borer populations or host tree susceptibility. An understanding of the host/insect relationship was used to decide which site and stand characteristics to investigate, and aided in the interpretation of results.

The effect that site conditions, represented by plant associations, have on shoot borer infestation rates were analyzed by Stoszek (1973) in the Klamath and Lake counties of southeastern Oregon. He surveyed shoot borer infestations in ponderosa pine plantations that were located in several zones, and found that the incidence of damaged leaders increased with more xeric site conditions. In the *Abies concolor* zone, the wettest of the zones, 3 of 16 sample areas were lightly infested and the rest were uninfested. In the mixed conifer zone three sample areas exhibited low infestation, six showed moderate levels, and one infestation was heavy. Infestation in the ponderosa pine climax zone was moderate for the *Ceanothus velutinus/ Arctostaphylos patula*, *Chrysothamnus/ Ceanothus velutinus*, and *Chrysothamnus/ Ceanothus prostratus* plant associations, but the incidence of infestation was uniformly high in dry habitats characterized by *Purshia tridentata*, *Wyethia* spp, *Artemisia tridentata*, *Ceanothus prostratus* and grasses. On fringe sites with sagebrush or grass cover, where ponderosa pine would not typically be found, infestations generally exceeded 70% of the leaders.

Two hazard rating models for central Idaho were developed in M.S. theses, but were never published in peer reviewed journals. In one hazard rating model, Luther (1980) found that the best model included a quadratic transformation of height/age and

a vegetative series ($R^2=0.64$). In the other hazard rating model, Robertson (1982) found that soils characterized as having low fertility, those with a sedimentary or granitic parent material, were correlated with high shoot borer infestation rates, while soils of higher fertility, those with an ash/loess or basaltic parent material, were correlated with low shoot borer infestation rates. The western pine shoot borer hazard rating model that was developed in his thesis for central Idaho included average annual height increment, elevation, geologic parent material and basal area of the plantation ($R^2=0.77$). Robertson noted, however, that the highest shoot borer infestation rates occurred on drier sites with low soil fertility.

Elevation seems to have a significant effect on shoot borer presence, with an upper boundary beyond which infestations do not occur. Mitchell and Sower (1991) observed that infestations of shoot borers were high in every lodgepole pine stand below about 1,800 m in elevation, and that stands above 2,000 m were uninfested. Robertson and Dewey (unpublished data) also found that shoot borer infestation decreased in ponderosa pine plantations as elevation increased; the mean shoot borer infestation rate for an elevation of 5,600 to 7,000 ft. (1,707 m to 2,134 m) was only 3%. Ross (1989) found no evidence of shoot borer infestation in the highest of three study sites, which was at an elevation of 1,950 m.

Perhaps elevation indirectly affects the activity or development of the shoot borer because of the colder temperatures found at higher elevations. It was observed that shoot borer moths flew only at night when the temperature was above 5 degrees Celsius (Mitchell and Sower 1988). Sites at higher elevations may be too cold at night

for moths to be active enough to fly to the tips of the pine trees for mating and egg laying. Additionally, the shoot borer requires at least 50 degree days above 5.5°C for the first pupae to begin to emerge, and 170 degree-days for 50% of the pupae to emerge (Mitchell and Sower 1988). At higher elevations, degree-day accumulations may be insufficient for shoot borer pupae to complete development before pine shoots become too mature, or delayed development may expose them to higher levels of predation and parasitism.

There are many other possible reasons for the effect of elevation on shoot borer populations. High elevations are characterized as having shorter growing seasons, less available-water, slower soil nutrient cycles and longer fire return intervals in addition to colder temperatures. Each of these could affect ponderosa pine phenology, vigor, and water relations, as well as shoot borer development and activity.

Related to elevation is the issue of tree phenology, i.e. the relationship between climate or seasonal changes and tree development. In a study on white pine weevil (*Pissodes strobi* (Peck)) and its damage to Sitka spruce (*Picea sitchensis* (Bongard) Carriere), Hulme (1995) found that Sitka spruce clones that were best synchronized to insect reproduction incurred more damage. The least damaged spruce trees burst bud earlier, which suggested to him that these trees were not selected by ovipositing females because they were not optimal egg laying sites. Hulme then manipulated weevil oviposition, finding that normally resistant trees became more susceptible to damage when oviposition was advanced, and susceptible trees became more resistant to damage when oviposition was retarded.

Thier and Marsden (1990) studied the relationship between tree height and shoot borer infestation in progeny test sites, in which ponderosa pine genetic families of the same age were compared. For trees that ranged from 62-76 cm, the shortest height class, they found that the percentage of trees with infested terminal shoots was 23%. For trees from 162-183 cm, the tallest height class, infestation was 76%. They concluded that there was a statistically significant increase in infestation rate with tree height. Ross (1989) found that site-preparation treatments in ponderosa pine plantations that produced the greatest reduction in competing vegetation resulted in the best height growth, but also the highest levels of western pine shoot borer infestation.

Attempting to correlate tree height with infestation levels can be misleading. If shoot borer larvae feed on terminal shoots, then trees on which they fed will suffer height growth reduction and this may bias the correlation. A potentially better way to study the correlation of tree growth to shoot borer damage is to observe diameter growth instead. Robertson (1982) found that the average diameter of ponderosa pine in a plantation was one of the best single predictors of infestation ($R^2 = 0.42$). Some of the other important variables in the same study were annual diameter growth, average annual height growth, and elevation.

Sower and Mitchell (1987) found that shoot borer infestation level was closely related to bud size, and was only weakly correlated to tree height. A statistically significant correlation was found between the sum of the terminal and lateral bud lengths in the terminal whorl and the subsequent infestations among these buds

($R^2=0.94$, $df=5$). Sower and Mitchell suggested that the ovipositing females select trees with the largest mass of buds at the tip of the tree, and then further select the largest bud in the mass, which would typically be the terminal bud. Another possible explanation for this correlation is that the resin ducts in small, narrow, shoots may be ruptured by the feeding larvae, allowing the pine to defend itself by encasing the larvae in resin. The apparent absence of shoot borer damage to smaller buds may simply be the product of a successful defense, before the shoot borer larvae create visible damage.

Steiner (1974) studied the eastern pine shoot borer, a moth so similar to the western pine shoot borer in appearance and behavior that they were considered the same species for many years. The only way to tell the two species apart, other than their geographic distribution, is to compare male genitalia (DeBoo et al. 1971). Steiner found that short varieties of Scotch pine in progeny test sites were most resistant to the eastern pine shoot borer, varieties of intermediate height were least resistant, and tall varieties were intermediate in resistance. Steiner also found a correlation between shoot borer resistance and latitude of origin, finding that the northern varieties were most resistant and the southern varieties least resistant. Northern varieties burst bud one to two weeks earlier than southern varieties, which is another example of how phenological asynchrony may interfere with shoot borer larval feeding.

In addition to time of bud burst, other genetically controlled traits may also influence shoot borer infestations. Maristany (1982) found that infestation in three progeny test sites was significantly different for the 96 families planted at each test site. For the year in which he surveyed shoot borer damage, infestation between sites was

significantly different (p -value=0.0001) and infestation between families was significantly different (p -value=0.0001). He concluded that resistance to shoot borer is genetically related, and that faster growing ponderosa pine families were not necessarily preferred by shoot borer.

In British Columbia, white spruce, *Picea glauca*, and Engelmann spruce, *Picea engelmannii*, progeny test sites were attacked by white pine weevil. Following the attack, Kiss et al. (1996) found that certain families were more resistant to the weevil infestation. They compared the foliar and bark terpene content of eight resistant families and eight families that were not resistant, and in preliminary results they found that these terpenes were good predictors of resistance. Terpene content is a highly heritable trait, often used to "fingerprint" clones, varieties, and seed sources, and is only minimally affected by environment (Hanover 1992). However, in another study that included the same insect, Bridgen et al. (1979) looked at the patterns of resistance in eastern white pine, *Pinus strobus*, and found no correlation between the monoterpenes that they studied and resistance to the weevil. The contradictory conclusions that these two studies reach may be due to the fact that they used different host tree species, or may be due to differences in experimental design, methods or environmental conditions.

Another provenance test in Europe examined the ability of European black pine, *Pinus nigra*, to resist the European pine shoot moth, *Rhyacionia buoliana* (Charles et al. 1982). In heavily infested stands, the differences between terpene content of attacked trees and trees that were not attacked was not statistically significant, however, in

moderately infested stands, differences between the attacked and non-attacked trees were significant. Charles et al. (1982) concluded that the terpene content in trees that were not attacked in the moderately infested stands protected these trees, but that there was some other unidentified factor, such as stand vigor, that influenced the overall resistance of European black pine to the European pine shoot moth.

Genetically influenced tree morphology, rather than terpenes, is probably what influences shoot borer infestation levels. Grant et al. (1989) studied morphological attributes in progeny of two ponderosa pine parents of the *ponderosa* variety ($p \times p$), and progeny of a cross between females of the *ponderosa* variety and pollen of the *scopulorum* variety ($p \times s$). The *Pinus ponderosa ponderosa* seed source came from what they called coastal habitats, in El Dorado County, California, and the *Pinus ponderosa scopulorum* seed source came from drier interior habitats, in Niobraro County, Wyoming. Progeny of the ($p \times s$) cross produced slower growing progeny with a greater degree of branching, shorter needles, and a lower density of stomata in comparison to progeny of the ($p \times p$) cross.

They concluded that these morphological differences were an evolutionary response to water stress. Shoot borer infestations have been found to be higher in trees with a greater degree of branching (ie, greater number of buds in the terminal whorl) (Sower and Mitchel 1987) and on sites that were dry (Stoszek 1973). Perhaps the infestation levels are higher on dryer sites because ponderosa pine trees with higher tolerance for drought, those with more branching, are able to survive on these sites.

Several other genetically influenced traits were identified in a companion study to the work done by Grant et al. (1989). Monson and Grant (1989) found that the families of the (p×s) cross also showed lower needle nitrogen contents and lower stomatal conductances than (p×p) families, which would lead to reduced transpiration rates in their drier interior habitats. The authors suggest that these findings support the theory that these traits are an evolutionary response, either to create a more favorable balance between the cost of producing photosynthetic machinery and the capacity to supply CO₂, or to the low nitrogen availability in drier climates. These papers suggest that ponderosa pine trees may vary significantly in their morphology and ability to grow under water stress, and that these variations are genetically controlled.

OBJECTIVES OF THESIS

Environmental influences

Before beginning this study, I formulated several hypotheses. The hypothesis with the greatest support seemed to be that environmental conditions which cause water stress in ponderosa pine would decrease the tree's ability to defend itself, leading to greater shoot borer damage. I tested this by comparing infestation rates among

plant associations that represented drier and wetter environments, and by comparing infestation rates among different slopes.

A second hypothesis was that trees with greater growth potential would incur more damage from shoot borer because these trees would provide a better source of food for the shoot borer larvae. This was tested by comparing infestation rates among stands with various average heights, diameters, and number of shoots found in the terminal whorl.

A third hypothesis was that stand structure would influence shoot borer population dynamics by influencing the quantity or quality of preferred food source. This was tested by analyzing correlations between infestation levels and host tree density.

Based on observations made by other researchers, I also hypothesized that trees at lower elevations, and above ten years of age, would incur more damage. This hypothesis was tested by comparing the infestation rates of stands at high, middle and low elevations (within the ponderosa pine range).

The primary objective in developing a hazard rating model was to provide a method of predicting whether a stand was at risk of serious shoot borer damage. A secondary objective was to make the hazard rating easy for land managers to use, and hence to use variables that were not difficult to measure.

Genetic influences

I tested the hypothesis that open pollinated half-sib families of ponderosa pine would differ in their ability to resist shoot borer damage across six sites. The primary objective was simply to determine whether some families resisted shoot borer damage better than others.

CHAPTER 2**EFFECTS OF ENVIRONMENT AND GENETICS ON WESTERN PINE
SHOOT BORER, *EUCOSMA SONOMANA*, INFESTATION LEVELS
IN PONDEROSA PINE PLANTATIONS OF CENTRAL OREGON**

Sara C. Prueitt, Darrell W. Ross

ABSTRACT

Infestations of the western pine shoot borer, *Eucosma sonomana* Kearfott, in young stands of ponderosa pine, *Pinus ponderosa* Lawson, were surveyed on the Deschutes National Forest. Elevation, slope, aspect, tree height, tree diameter, number of shoots in the terminal whorl, stand density, stand age and plant association for each stand were used in multiple regression and logistic regression analyses to predict the percentage of infested terminal shoots. Using general multiple regression, taking the arcsin(square root(proportion of infested trees)), the models that were selected as the best predictors included (1) diameter, trees/hectare and elevation ($R^2=0.62$) and (2) number of shoots in the terminal whorl and stand age ($R^2=0.62$). Using logistic regression, the best model included number of shoots in the terminal whorl and stand age. Values for these stand characteristics can be used with the appropriate equation to estimate the percentage of terminal whorls damaged by shoot borer in a given stand. A companion study performed in six progeny test sites on the Ochoco National Forest found significant differences in shoot borer infestations among 29 ponderosa pine families (P -value = 0.001, $R^2=0.62$).

INTRODUCTION

The western pine shoot borer, *Eucosma sonomana* Kearfott, is native to the western United States in the natural range of ponderosa pine, *Pinus ponderosa* Lawson, and lodgepole pine, *P. contorta* Douglas, which extends from British Columbia to Arizona (DeBoo et al. 1971, Sartwell et al. 1980). The shoot borer is univoltine, and occurs in low but chronic numbers. In central Oregon, moths begin to emerge from their pupal stage in early spring. Females fly to the tips of young pine trees, emit a pheromone that attracts males, mate, and oviposit on or near the terminal buds of the host tree. Later in the spring, larvae emerge, begin to mine the pith of the growing shoots, complete their feeding in July and drop to the forest floor to pupate (Mitchell and Sower 1988).

Ponderosa pine trees are first attacked between the ages of 5 to 10 years, or when they reach about 1.5 meters in height (Sower and Shorb 1984, Mitchell and Sower 1991, Williams et al. 1988). Sower et al. (1988) found that after trees are 15- to 20-years-old between 45 to 65% of the terminal shoots are attacked each year in ponderosa pine stands. The shoot borer behaves in a slightly different manner in lodgepole pine stands; attacks begin when young lodgepole pine are about 0.5 meters tall and a greater percentage of trees are infested.

The growth of ponderosa pine shoots is usually stunted by shoot borer feeding, although shoots can be killed. Shoot borer damage may cause trees to become forked or crooked as the lateral shoots compete for dominance in the absence of a healthy terminal shoot. Stoszek (1973) reported an average annual height growth reduction of

15% for a stand when 40% of the terminal shoots were infested, and a height growth reduction of 23% when 70% of the terminal shoots were infested. Sower and Shorb (1984) found that shoot borer damage to terminal shoots results in a potential height growth loss of about 27% for an individual tree, which was spread over 2 growing seasons. There was a 12% height growth loss in the year the terminal shoot was infested, and an additional 15% loss in the following year.

While the damage caused by shoot borer is not as noticeable as that caused by some pests, it can have a profound effect on height growth and tree form. This damage can be controlled with a pheromone-based mating disruption treatment. A synthetic sex-attractant, Z-9- and E-9-dodecenyl acetate, applied in a 4:1 mixture can reduce the damage done to terminals by up to 83 to 84% in ponderosa pine plantations (Sartwell et al. 1980).

The primary objective of this study was to create hazard rating models for shoot borer damage in ponderosa pine stands of central Oregon. A hazard rating model correlates particular stand conditions with the expected level of infestation; it does not identify which conditions directly cause the infestation. Land managers in, or in places similar to, the Deschutes National Forest can use the hazard rating models to identify stands at high risk of shoot borer infestation. As site and stand characteristics become increasingly dissimilar to those in the Deschutes National Forest, the relationship between them and the infestation levels will change, and the models developed in this study will be less likely to predict infestation accurately. The

models can be used by land managers to determine whether surveillance activities are needed, or to prescribe preventative measures.

A second objective was to determine whether trees that better resisted shoot borer damage were affected by genetically influenced traits in addition to environment. This companion study took place in 15-year-old progeny test sites in eastern Oregon.

MATERIALS AND METHODS

Environmental influences

Study area: Young stands of ponderosa pine were surveyed on the Sisters, Bend, and Fort Rock Ranger Districts of the Deschutes National Forest to determine shoot borer infestation levels and other site and stand characteristics. The survey began in July, 1996, after larvae had completed their feeding, and ended in September, 1996.

Thirty-five ponderosa pine stands were selected non-randomly to include a variety of stand ages, elevations and plant associations (Figure 1). A grid was placed over each stand map in order to select 12 plots that were systematically spaced throughout the stand. Each plot was located by pacing the predetermined distance.

Data collection: Ten trees per plot were sampled. The first five trees encountered while heading north were sampled, then, after turning left and moving over to the next tree, the first five trees encountered while heading south were

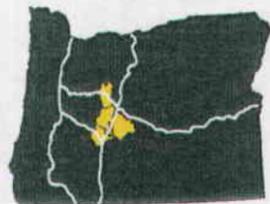
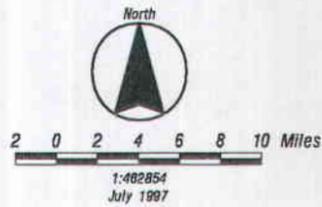
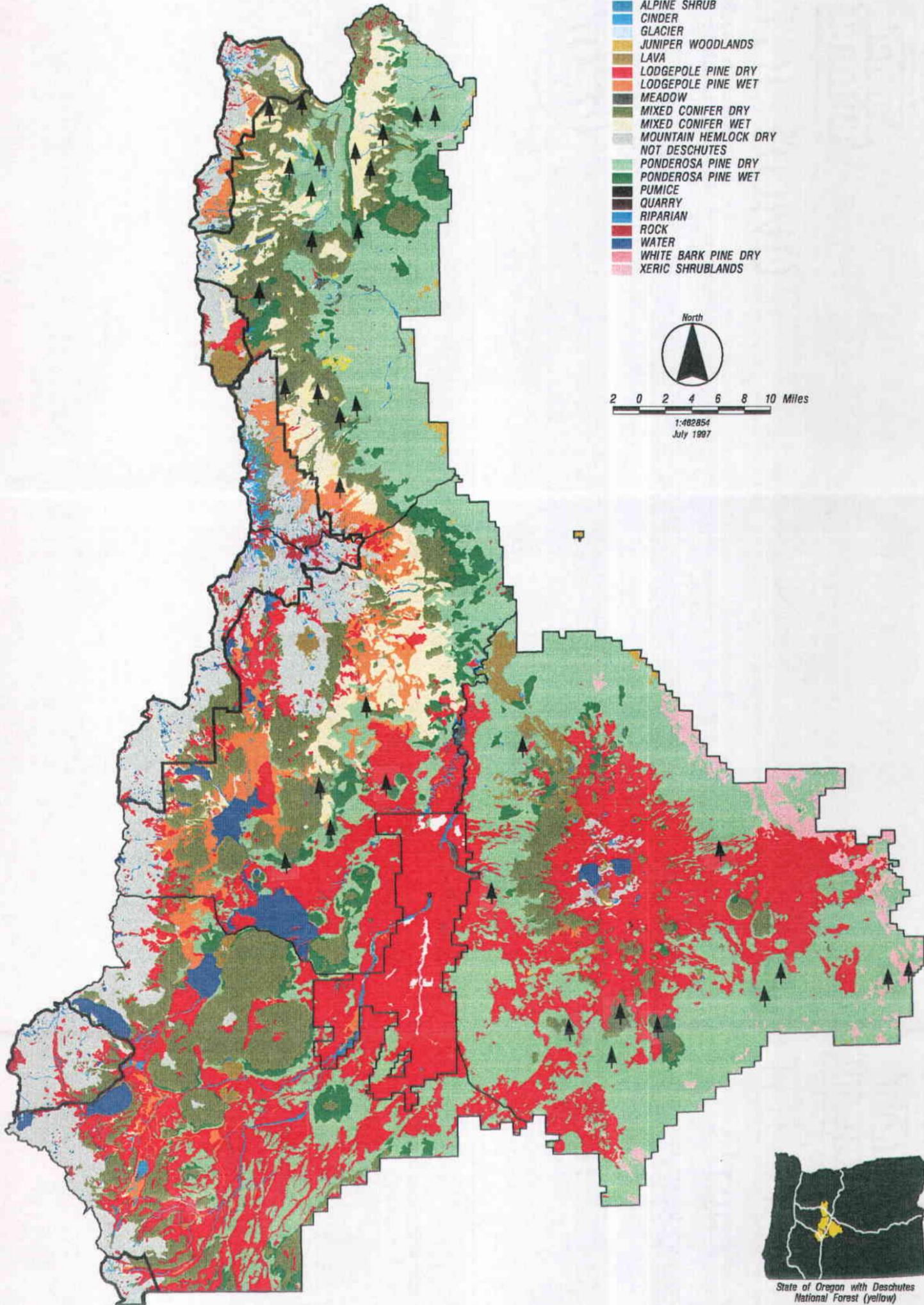
Figure 1. Plant association map of the Deschutes National Forest, showing stands that were surveyed.

Plant Association Groups with Surveyed Harvest Units for Deschutes National Forest



Legend

- Deschutes National Forest
- Wilderness
- Surveyed Stands- Sisters District
- Surveyed Stands- Bend District
- Surveyed Stands- Fort Rock District
- Plant Association Group
- ALPINE DRY
- ALPINE MEADOW
- ALPINE SHRUB
- CINDER
- GLACIER
- JUNIPER WOODLANDS
- LAVA
- LODGEPOLE PINE DRY
- LODGEPOLE PINE WET
- MEADOW
- MIXED CONIFER DRY
- MIXED CONIFER WET
- MOUNTAIN HEMLOCK DRY
- NOT DESCHUTES
- PONDEROSA PINE DRY
- PONDEROSA PINE WET
- PUMICE
- QUARRY
- RIPARIAN
- ROCK
- WATER
- WHITE BARK PINE DRY
- XERIC SHRUBLANDS



State of Oregon with Deschutes National Forest (yellow)

sampled. This sampling method was used because there were often dense patches of understory, or patches where no trees grew, which made rows or transects difficult to follow.

For each tree that was sampled, the terminal and all lateral shoots in the terminal whorl were scored for shoot borer damage. Height and diameter were measured on every other tree, so that in each of the stands 120 trees were scored for shoot borer infestation, and 60 were measured for height and diameter.

Stand age and plant association were determined from USDA Forest Service records (USDA, Forest Service 1994). Stand age was the number of years since seedlings were planted (not the actual age of the trees from seed). The plant associations included in the study, ranked in order of wettest to driest associations, were lodgepole pine wet (LPW), lodgepole pine dry (LPD), mixed conifer wet (MCW), mixed conifer dry (MCD), ponderosa pine wet (PPW), ponderosa pine dry (PPD), and xeric shrub land (XSHB).

Total tree height was measured to the nearest cm. Diameter was measured to the nearest mm. Calipers were used on small trees, and a diameter tape was used on trees too large for calipers. For trees under about 1.5 meters, diameter was measured 5-10 cm above the ground, and for taller trees it was measured 1.2 meters above the ground, because diameter at breast height for small to moderate sized trees was zero or misleading.

At five randomly selected points in each stand, possible host-tree density was estimated by counting the number of ponderosa and lodgepole pine on 1/20th hectare

circular plots. Ponderosa and lodgepole pines were the most common tree species encountered in the stands that were sampled. When non-host tree species were found in the plots, they were not counted.

A visual assessment of shoot borer damage was used because it is easy, least time-consuming, and estimates are conservative (Sower et al. 1984). Shoot borer infested shoots were identified by looking for shortened needles on the distal portions, or over the entire length, of the shoot. Other methods, such as looking for the larval exit hole, and swelling of the shoot at the exit hole, can be used along with stunted needle growth, but it is difficult and time consuming to examine taller trees for these traits. Sower et al. (1984) found that an experienced observer will score about 26% of the infested shoots as uninfested, when shoot borer infestation was surveyed by looking for shortened needles only, but these shoots are usually the result of larvae that entered late or died early and thus did little damage to the shoot. Sower and Shorb (1984) reported that shoots that were visibly damaged from the outside were almost always found to have shoot borer signs inside when the shoot was dissected (96% of the time), but that shoots appearing undamaged were also often found to have shoot borer signs inside them (37% of the time).

The average number of shoots in the terminal whorl, which can be thought of as the number of viable buds encountered by female moths during oviposition, was calculated from the infestation data. During data collection, each terminal shoot was recorded as infested or uninfested based on visual symptoms, as were all lateral shoots in the terminal whorl. By adding the number of infested and uninfested lateral shoots,

and the terminal shoot, the total number of shoots for the terminal whorl was determined.

Analysis: Multiple linear regression (SAS Institute Inc. 1989) and logistic regression (SAS Institute Inc. 1996) were used to develop models for predicting shoot borer damage. In the multiple linear regression, the response variable, proportion of terminal shoots infested, was transformed by taking the arcsin[square root (proportion)], in radians. In logistic regression, the proportion of infested trees, p , was calculated as a binomial distribution. The proportion, p , of infested trees can be back transformed by calculating the $\log[p/(1-p)]$.

While logistic regression is the more appropriate method to use for a response variable that is binomial, both methods were used because other hazard rating models developed for western pine shoot borer in ponderosa pine used multiple linear regression. These models also transformed the proportion of infestation by taking the arcsin[square root(proportion)]. By using the same statistical technique, comparisons between the hazard ratings are easier to make.

The proportion of terminal shoots that were infested was used as a measure of shoot borer infestation level, rather than proportion of terminal whorls (which would include trees with whorls whose laterals were infested but did not appear to have terminal shoot damage) because height growth loss, which is of concern to land managers, occurs only in trees with terminal shoot infestation.

Genetic influences

Study area: Six evaluation plantations managed by the USDA Forest Service on the Malheur and Ochoco National Forests were sampled. The seedlings planted in the evaluation plantations came from Silvies Seed Orchard. We randomly selected a block of 29 families, and analyzed these families over six evaluation plantations. The plantations that we visited were Jacks Creek, Delintiment Lake, Nicoll I, Coyote, Donnelly, and Copper.

The families planted in these sites were open pollinated half-sib families of ponderosa pine, from wild mother trees that were selected for their height and form. The plantations were 15 years old when the shoot borer survey was performed.

Data collection: The shoot borer damage was visually surveyed, as described in the hazard rating study. The plantations were sampled between August and September, 1995, after shoot borer larvae completed feeding. Height and diameter measurements were taken simultaneously to the shoot borer survey, and were supplied to us by the Forest Service. Diameter was measured at breast height.

Analysis: An analysis of variance was performed to determine if there were differences between the 29 families across the six sites (SAS Institute Inc. 1989). The response variable was not transformed because it was normally distributed. The 95% confidence intervals for infestation, diameter, height and number of shoots in the terminal whorl were calculated for each family, by taking the least squares means from an analysis of variance that included site and family. The same procedure was

performed on each family's mean height and diameter. Correlation coefficients were also calculated based on these least squares means by family and site.

RESULTS

Environmental influences

One stand in the Sisters Ranger District, in which 70% of the terminal shoots were infested (terminal whorl infestation rate of 76%), was a significant outlier. In all other stands terminal shoot infestation rates were between 0 and 43% (terminal whorl infestation rates of 0 and 54%). This stand was excluded from the analysis because its growth and shoot borer infestation was atypically large. It should be noted that a 70% infestation is possible, and has been reported by Stoszek (1973), who used visual survey methods similar to those in this study. However, Stoszek found infestation levels of 70% in dry fringe sites, on which ponderosa pine would not typically be found. The plantation in this study with a 70% infestation rate occurred in the ponderosa pine wet plant association.

The average and range for each variable are shown in Table 1. When analyzing variables individually, the results from the logistic regression analysis were reassuringly similar to those of the simple linear regressions. This is probably due to the fact that a fairly large number of trees were sampled in each stand to estimate infestation ($n = 120$). Results of the analysis for individual variables using both logistic regression and simple linear regression are shown in Tables 2 and 3.

Table 1. Average and range for each variable measured in stands of ponderosa pine in central Oregon

Variable	Average	Minimum	Maximum
<i>Infestation (%)</i>	20.14	0	43.33*
<i>Ave. diameter (millimeters)</i>	83.91	31.5	163.71
<i>Ave. height (meters)</i>	3.05	1.1	7.29
<i>Age of stand</i>	14	8	21
<i>Ave. number of shoots</i>	3.63	1.9	5
<i>Slope</i>	7.57	0	30
<i>Elevation</i>	4375	3000	5700
<i>Trees per hectare</i>	310	70	1180

* The stand with the greatest infestation, 70%, was not included in the analysis.

In the logistic regression analysis, stepwise procedures, which added variables to the regression model with *P*-values below 0.1 and removed variables with *P*-values greater than 0.1, were used to select the best model. The model selected using this procedure (model (1)) included average number of shoots and age of the stand.

$$(1) \quad \log(p/(1-p)) = -6.1850 + 0.7146(\text{ave no. shoots}) + 0.1407(\text{age})$$

$$(0.7709) \quad (0.1617) \quad (0.0293)$$

Standard errors are given below the parameter estimates.

Table 2. Results of logistic regression analyses for individual variables associated with 1996 shoot borer infestation in ponderosa pine plantations of central Oregon

Variable	<i>P</i> -value	n	y-intercept ± SE	Slope ± SE
<i>Diameter</i>	0.0001	34	-2.9397 ± 0.3287	0.0165 ± 0.0032
<i>Height</i>	0.0001	34	-2.6019 ± 0.2903	0.3488 ± 0.0763
<i>Age of stand</i>	0.0004	34	-3.5876 ± 0.5851	0.1449 ± 0.0378
<i>No. shoots</i>	0.0012	34	-4.1142 ± 0.8017	0.7099 ± 0.2072
<i>Slope</i>	0.1775	34	-1.2582 ± 0.2101	-0.0296 ± 0.0222
<i>Elevation</i>	0.4693	34	-0.8686 ± 0.8301	-0.0001 ± 0.0002
<i>Plant association</i>	0.5244	34	-1.3771 ± 0.2068	
<i>wetter</i>		17		-1.3771 ± 0.2068
<i>drier</i>		17		-1.5722 ± 0.2198
<i>Trees per hectare</i>	0.7162	34	-1.3996 ± 0.2467	-0.0002 ± 0.0006

Table 3. Results of simple linear regression analyses for variables associated with 1996 shoot borer infestation in ponderosa pine plantations of central Oregon

Variable	<i>P</i> -value	y-intercept ± SE	Slope ± SE	R ²
<i>Diameter</i>	0.0001	0.0898 ± 0.0583	0.0039 ± 0.0006	0.5332
<i>Height</i>	0.0001	0.1545 ± 0.0533	0.0867 ± 0.0159	0.4822
<i>Age of stand</i>	0.0002	-0.0310 ± 0.1079	0.0318 ± 0.0074	0.3623
<i>No. shoots</i>	0.0017	-0.0975 ± 0.1519	0.1415 ± 0.0412	0.2694
<i>Slope</i>	0.1647	0.4630 ± 0.0462	-0.0062 ± 0.0044	0.0594
<i>Elevation</i>	0.3748	0.5767 ± 0.1822	-3.664 · 10 ⁻⁵ ± 4.071 · 10 ⁻⁵	0.0247
<i>Trees per hectare</i>	0.8904	0.4212 ± 0.0532	-1.836 · 10 ⁻⁵ ± 1.322 · 10 ⁻⁴	0.0006

Stepwise procedures were also used in the multiple linear regression analysis to select the model that best predicts the proportion of terminal shoots that will be infested in a stand. The Mallows's C_p -statistics were high for all models, so this criterion was not used to select the best model. Models with Mallows's C_p -statistics that are close to the number of independent variables in the model are preferred. Large C_p -statistics indicates that there may be bias in the model. This may have occurred either because all variables were somewhat correlated with each other, or because the data were not normally distributed after taking the arcsin[square root(proportion)] transformation.

One of the best models selected in the multiple linear regression analyses included average diameter, elevation and trees per hectare.

$$(2) \quad \arcsin(\sqrt{y}) = 0.1989 + 0.0043(\text{ave diam}) - 4.89 \cdot 10^{-5}(\text{elevation}) + 0.0002(\text{trees/ha})$$

$$\quad \quad \quad (0.1315) \quad (0.0006) \quad \quad (2.820 \cdot 10^{-5}) \quad \quad (9.492 \cdot 10^{-5})$$

$R^2=0.62$. Standard errors are below the parameter estimates.

Another model, which may not be as useful to land managers who do not have the resources to do a survey of tree morphology, included age and the average number of shoots in the terminal whorl:

$$(3) \quad \arcsin(\sqrt{y}) = -0.5255 + 0.0312(\text{age}) + 0.1384(\text{ave no. shoots})$$

$$\quad \quad \quad (0.1371) \quad (0.0058) \quad \quad (0.0302)$$

$R^2=0.62$. Standard errors are below the parameter estimates.

Both logistic regression and multiple linear regression analyses indicate that the average number of shoots on ponderosa pine trees and the age of the stand are together good predictors of western pine shoot borer infestation, for 8- to 21-year-old stands in central Oregon.

Genetic influences

Some ponderosa pine families resisted shoot borer damage significantly better than other families ($F=2.26$; $df=5, 28$ ^{,140}; $P\text{-value}=0.001$), however there was no significant relationship between infestation and height, diameter or number of shoots in the terminal whorl. To illustrate this, a simple graphical analysis was used to show the relationships between infestation, tree height, diameter, and number of shoots in the terminal whorl (Figures 1- 4). The least squares means for each family, adjusting for site variation, and the 95% confidence intervals for these means were calculated and graphed for infestation, height, diameter and number of shoots. The families in all four figures are ranked from high to low resistance to shoot borer infestation.

The least squares means used for the simple graphical analysis were also tested for statistical correlation. The graphical analysis and the correlation coefficients show that shoot borer infestation was not associated with height, diameter, or the number of shoots in the terminal whorl (Table 4). When comparing ponderosa pine plantations that are the same age, it is apparent that families that are more resistant to shoot borer

damage do not necessarily have greater height, diameter, or number of shoots in the terminal whorl than families that are susceptible to shoot borer.

Table 4. Correlation coefficients of family least squares means in ponderosa pine progeny test sites, followed by the *P*-value of the correlation.

	No. of shoots	Tree height	Tree diameter
Infestation level	-0.07762 (0.6890)	0.21990 (0.2517)	0.13364 (0.4895)
No. of shoots in terminal whorl	-	0.15882 (0.4106)	0.10724 (0.5798)
Tree height	-	-	0.86384 (0.0001)

Infestation rates between the six progeny test sites were also significantly different ($F = 32.61$; $df = 5, 28$ ¹⁴⁰; P -value=0.0001), providing strong evidence that environmental conditions also influenced infestation.

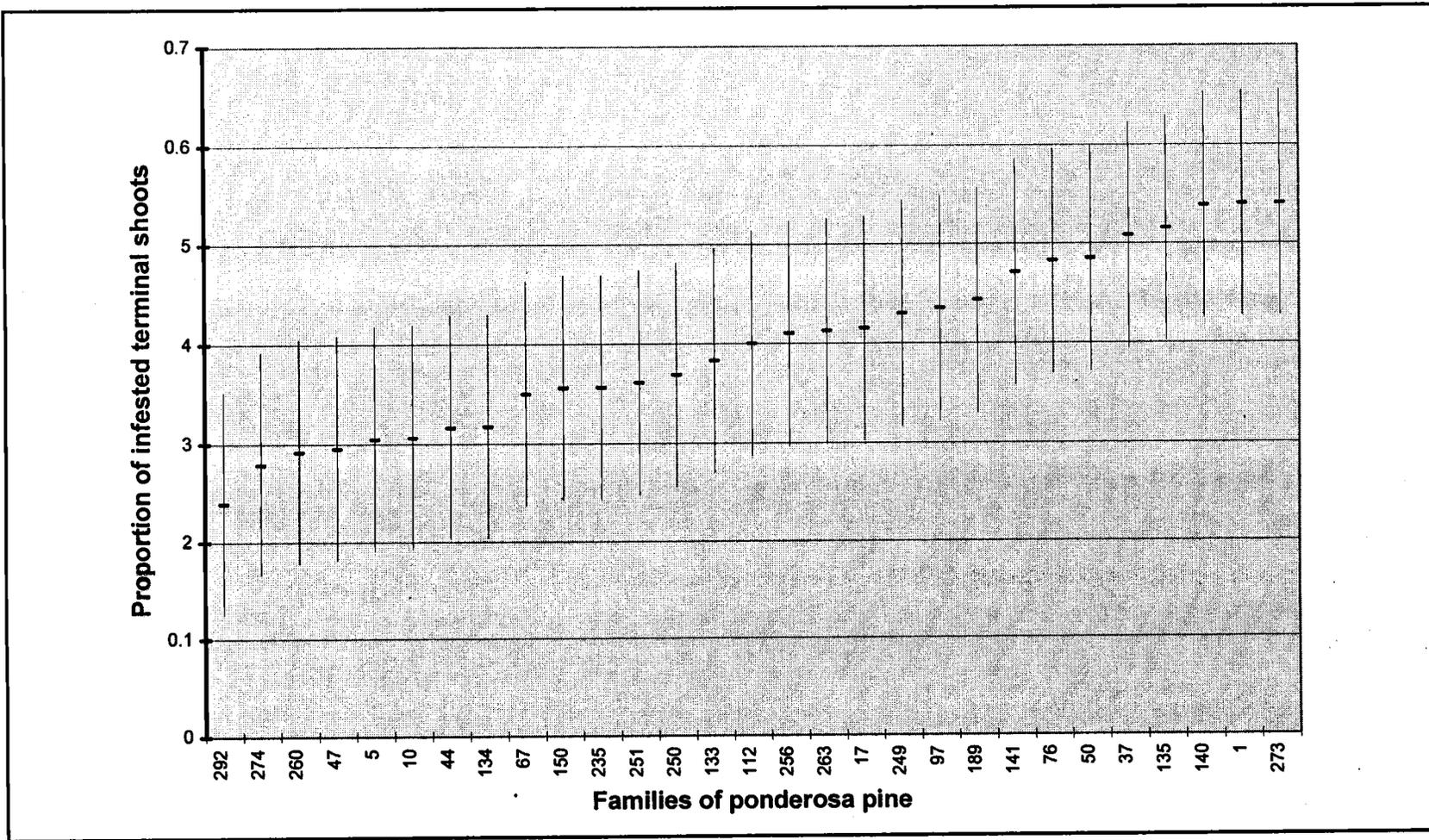


Figure 2. Least squares means and their 95% confidence intervals for shoot borer infestation.

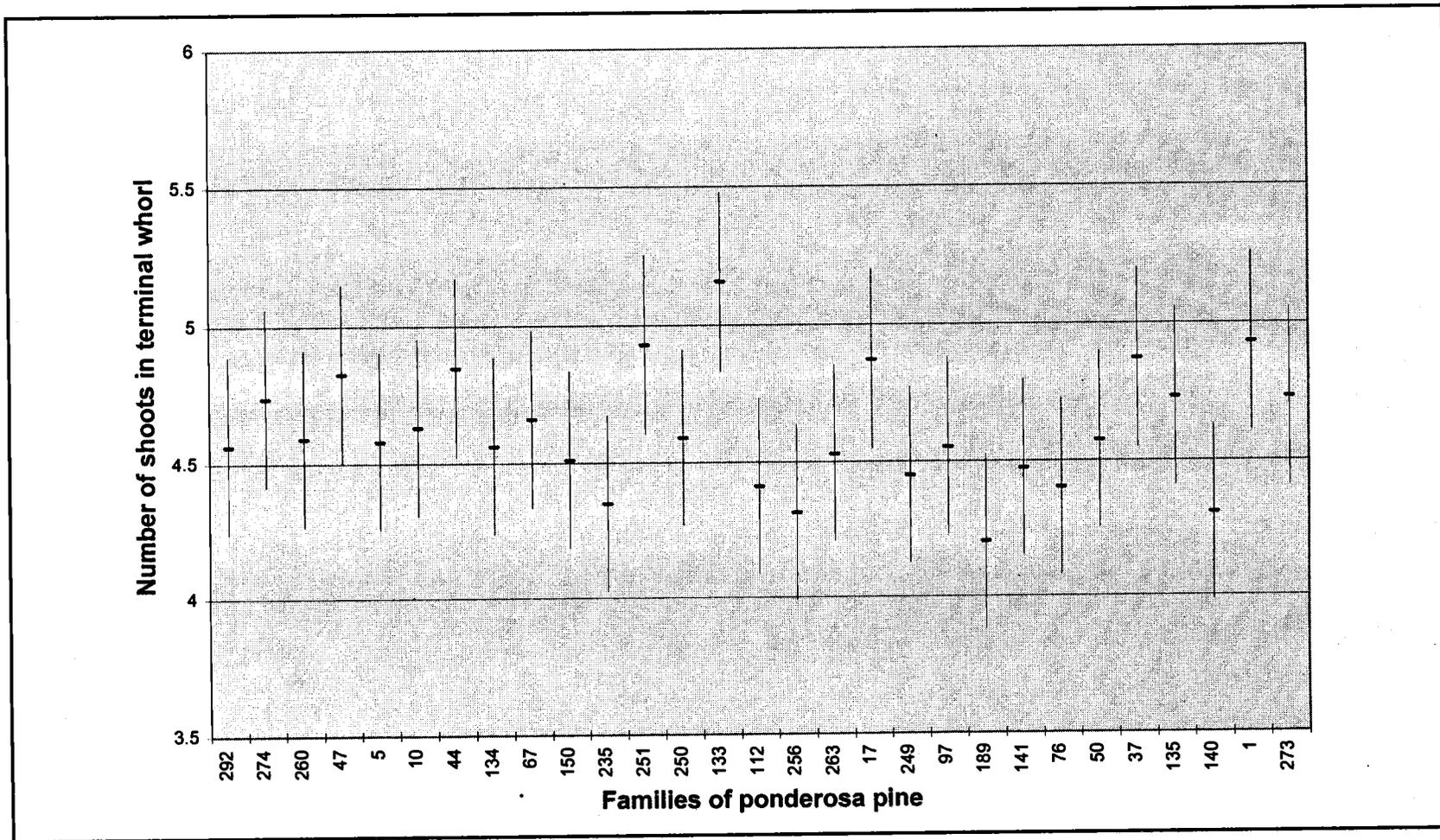


Figure 3. Least squares means and their 95% confidence intervals for average number of shoots.

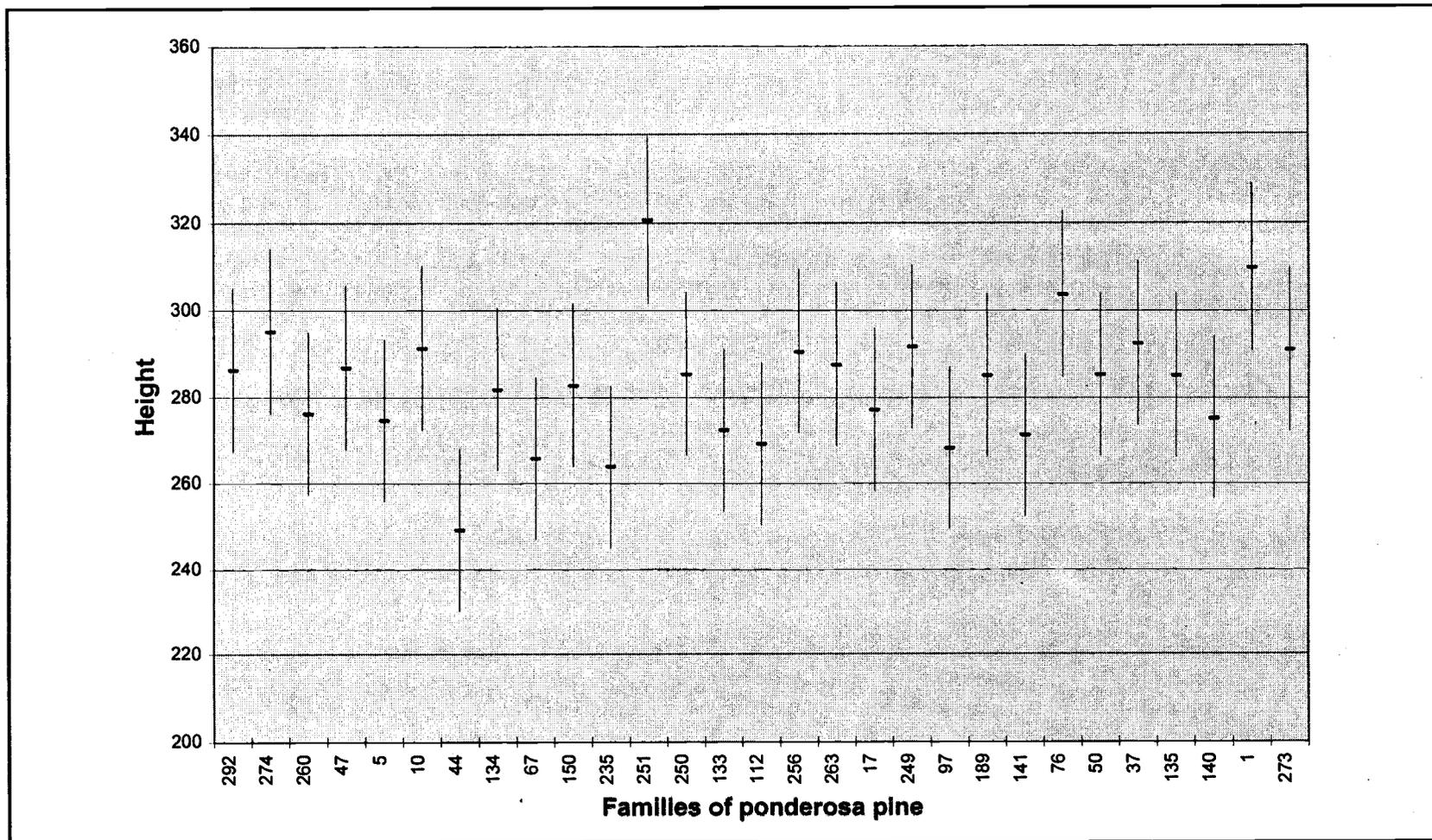


Figure 4. Least squares means and their 95% confidence intervals for average height.

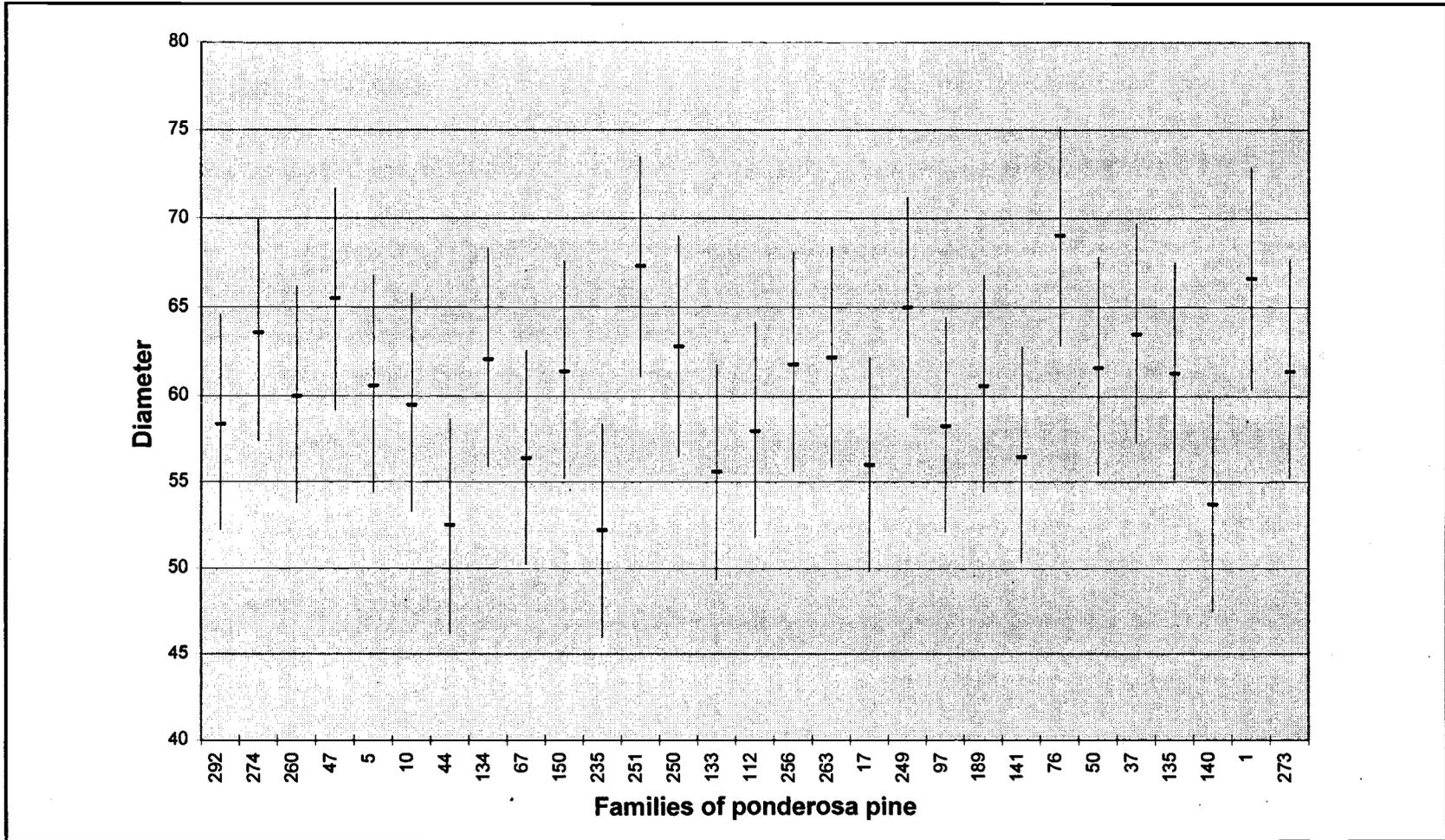


Figure 5. Least squares means and their 95% confidence intervals for average diameter.

DISCUSSION

Hazard rating models merely indicate which site and stand conditions are correlated with shoot borer damage. However, the hazard rating models discussed in the results section also seem to be supported by existing knowledge of the biology of the western pine shoot borer.

Model numbers (1) $\log(p/(1-p)) = -6.1850 + 0.7146(\text{ave no. shoots}) + 0.1407(\text{age})$ and (3) $\arcsin(\sqrt{y}) = -0.5255 + 0.0312(\text{age}) + 0.1384(\text{ave no. shoots})$ suggest that damage occurs to trees with a large number of buds in the terminal whorl that are older. Both the number of buds and the age of the tree would influence the quantity and quality of food for the larvae, because older trees generally have larger buds. The existing knowledge of the shoot borer suggests that they are more likely to attack shoots that come from the largest buds (Sower and Mitchell 1987). A significant correlation was found between the logarithm of the length of the terminal bud measured in the spring, and larval infestation later in the summer for the shoots that grew from these buds ($R^2=0.84$, $df=7$). Sower and Mitchell (1987) found an even better correlation when the terminal and lateral bud lengths of the terminal whorl were summed and compared to infestation among these buds ($R^2=0.94$, $df=5$). These findings suggest that females select trees with the largest mass of buds at the tip of the tree, and then favor the largest bud, which would typically be the terminal bud.

Model number (2) $\arcsin(\sqrt{y}) = 0.1989 + 0.0043(\text{ave diam}) - 4.89 \cdot 10^{-5}(\text{elevation}) + 0.0002(\text{trees/ha})$ suggests shoot borer infests stands that have trees with larger

diameters, are at low elevations, and have higher stand densities. Trees with larger diameters would have larger buds, which would be a better source of food. Trees at lower elevations would typically have a longer growing season, and shoot borer life cycles may be better suited to the lower, warmer, elevations. Those plantations with higher stand densities either had better survival rates or had more natural regeneration, because all of the plantations visited in this study were planted in a fairly standard density by the Forest Service. Both of these possibilities would suggest that stands with more trees/ha were on sites that had more favorable growing conditions. Competition in dense stands may have affected growth and site productivity, however the Forest Service usually thins stands before competition becomes a serious problem. Therefore, model (2) indicates that there are higher shoot borer infestations in stands that are more productive and which exist at an elevation that favors the shoot borer life history.

The results of the genetics study show that environment and genetics together seem to influence a tree's susceptibility to shoot borer damage. This may explain why the variability in the hazard rating remained fairly high, in other words, why the R^2 for each model was moderate, not high. Maristany (1982) also found that infestation was significantly different for the 96 families of ponderosa pine that he studied. For the year in which he surveyed damage, infestation between sites was significantly different (p -value=0.0001) and infestation between families was significantly different (p -value=0.0001). He also concluded that resistance to shoot borer is genetically

related, and that faster growing ponderosa pine families were not necessarily preferred by shoot borer.

In the hazard rating study, height and diameter were fairly good predictors of shoot borer damage in wild stands of ponderosa pine. However, in the genetics study, it became apparent that the families that are heavily infested are not necessarily the tallest families, nor the families with the largest diameters. The reason for this discrepancy may be that the trees in the genetics study were all 15-years-old, so height and diameter in the evaluation plantations did not vary as much as height and diameter in the stands used in the hazard rating model. While height and diameter are correlated with shoot borer infestation, there are probably other traits that influence (or are influenced by) height or diameter which more directly affect tree susceptibility. Traits such as the size of the buds, the quantity of resin ducts, or other characteristics that would make shoots a better and more accessible food source may actually cause trees to be more susceptible to shoot borer damage.

CONCLUSIONS

The hazard rating models show that older stands comprised of trees that have a greater number of buds in the terminal whorl are at higher risk of shoot borer infestation. Stands at lower elevations, with more trees/ha, comprised of trees with larger diameters are also at higher risk. Stands with more trees/ha probably had better growing conditions because rogue trees that grew from natural regeneration increased

the number of trees/ha. The single best predictors of shoot borer infestations were tree diameter and height.

The results of the companion study show that genetically controlled traits influence ponderosa pine's susceptibility to shoot borer damage. Site (i.e. environment) also significantly affects ponderosa pine's susceptibility. However, diameter, height and the number of shoots in the terminal whorl are probably not directly responsible for this susceptibility.

The damage caused by shoot borer can have a profound effect on ponderosa pine height growth and tree form. The studies discussed here begin to explain where shoot borer infestations will be higher and can aid land managers in deciding whether surveillance or pest management should be implemented.

As timber available for harvest continues to decrease, silviculturists will have to consider more economical ways of increasing yields from managed stands. Land managers can better estimate the risk of shoot borer damage, and take steps to control it, by using these hazard rating models and by considering the biology of the moth.

LITERATURE CITED

- Agee, J. 1990. The historical role of fire in Pacific Northwest forests, *In* Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State University Press, Corvallis, OR.
- Bridgen, M. R., J. W. Hanover and R. C. Wilkinson. 1979. Oleoresin characteristics of eastern white pine seed sources and relationship to weevil resistance. *For. Sci.* 25: 175-183.
- Charles, P. J., A. Delplanque, A. Marpeau, C. Bernard-Dagan, and M. Arbez. 1982. Susceptibility of European black pine, *pinus nigra*, to the European pine shoot moth, *Rhyacionia buoliana*: variations of susceptibility at the provenance and individual level of the pine and effect of terpene composition. *In* Proceedings, Resistance to diseases and pests in forest trees.
- DeBoo, R. F., W. L. Sippell and H. R. Wong. 1971. The eastern pine-shoot borer, *Eucosma gloriola* (Lepidoptera: tortricidae), in North America. *Can. Entomol.* 103: 1473-1486.
- Grant, J. 1958. Observations on a pine shoot moth, *Eucosma sonomana* Kft. (Lepidoptera: Olethreutidae). *Proc. Ent. Soc. Br. Columb.* 55: 26-27.
- Grant, M. C., Y. B. Linhart and R. K. Monson. 1989. Experimental studies of ponderosa pine. II. Quantitative genetics of morphological traits. *Amer. J. Bot.* 76: 1033-1040.
- Hanover, J. W. 1992. Applications of terpene analysis in forest genetics. *New For.* 6: 159-178.
- Hulme, M. A. 1995. Resistance by translocated Sitka spruce to damage by *pissodes strobi* (Coleoptera: curculionidae) related to tree phenology. *J. Econ. Entomol.* 88(6): 1525-1530.
- Kiss, G. K., A. D. Yanchuk, R. I. Alfaro, J. E. Carlson and J. F. Manville. 1996. Recent advances in research on white pine weevil attacking spruces in British Columbia. *In* Dynamics of Forest Herbivory: Quest for Pattern and Principle. USDA Forest Service General Technical Report NC-183.
- Luther, S. C. 1980. Western pine shoot borer infestation levels in ponderosa pine associated with site conditions. M.S. thesis. University of Idaho, Moscow.

- Maristany, A. G. 1982. Genetic differences in resistance of ponderosa pine to western pine shoot borer. M.S. thesis. University of Idaho, Moscow.
- Mitchell, R. G., and L. L. Sower. 1988. Phenology and heat accumulation as field guides for the seasonal history of the western pine shoot borer (Lepidoptera: Olethreutidae). *J. Econ. Entomol.* 81: 286-289
- Mitchell, R. G., and L. L. Sower. 1991. Life history of the western pine shoot borer (Lepidoptera: Olethreutidae) and effects on lodgepole pine in central Oregon. *J. Econ. Entomol.* 84: 206-211.
- Monson, R. K., and M. C. Grant. 1989. Experimental studies of ponderosa pine. III. Differences in photosynthesis, stomatal conductance, and water-use efficiency between two genetic lines. *Amer. J. Bot.* 76: 1041-1047.
- Overhulser, D. L., G. E. Daterman, L. L. Sower, C. Sartwell, and T. W. Koerber. 1980. Mating disruption with synthetic sex attractants controls damage by *Eucosma sonomana* (Lepidoptera: Tortricidae, Olethreutidae) in *pinus ponderosa* plantations. *Can. Entomol.* 112: 163-165.
- Robertson, A. S. 1982. Shoot borer hazard rating system for ponderosa pine in central Idaho. M.S. thesis. University of Idaho, Moscow.
- Ross, D. W. 1989. Western pine-shoot borer (Lepidoptera: Olethreutidae) response to site preparation in ponderosa pine plantations. *J. Econ. Entomol.* 82: 543-547.
- Sartwell, C., G. E. Daterman, T. W. Koerber, R. E. Stevens and L. L. Sower. 1980. Distribution and hosts of *Eucosma sonomana* in the western U.S. as determined by trapping with synthetic sex attractants. *Ann. Entomol. Soc. Am.* 73: 254-256.
- Sartwell, C., G.E. Daterman, D.L. Overhulser and L.L. Sower. 1983. Mating disruption of western pine shoot borer (Lepidoptera: Tortricidae) with widely spaced releasers of synthetic pheromone. *J. Econ. Entomol.* 76: 1148-1151.
- SAS Institute, Inc. 1989. SAS/STAT User's Guide, Version 6 Fourth Edition. Cary, NC, SAS Institute Inc.
- SAS Institute, Inc. 1996. SAS/STAT Software: Changes and Enhancements through Release 6.11. Cary, NC, SAS Institute Inc.

- Sower, L. L., G. E. Daterman, C. Sartwell and H. T. Cory. 1979. Attractants for the western pine shoot borer, *Eucosma sonomana*, and *Rhyacionia zozana* determined by field screening. *Environ. Entomol.* 8: 265-267.
- Sower, L. L., G. E. Daterman, and C. Sartwell. 1984. Surveying populations of western pine-shoot borers. *J. Econ. Entomol.* 77: 715-719.
- Sower, L. L., and R. G. Mitchell. 1987. Host-tree selection by western pine-shoot borer (Lepidoptera: Olethreutidae) in ponderosa pine plantations. *Environ. Entomol.* 16: 1145-1147.
- Sower, L. L., and M. D. Shorb. 1984. Effect of Western pine shoot-borer (Lepidoptera: Olethreutidae) on vertical growth of ponderosa pine. *J. Econ. Entomol.* 77: 932-935.
- Sower, L. L., G. E. Daterman, and C. Sartwell. 1988. Biology and impact of western pine shoot borer, *Eucosma sonomana* in the western U.S., pp. 102-109. *In* Insects Affecting Reforestation: Biology and Damage. IUFRO, Forestry Canada, Pacific and Yukon Region, Victoria, BC, Canada.
- Stark, R. W., and D. L. Wood. 1964. The biology of *Pissodes terminalis* Hopping (Coleoptera: Curculionidae) in California. *Can. Entomol.* 96: 1208-1218.
- Steiner, K. 1974. Genetic differences in resistance of scotch pine to eastern pine-shoot borer. *Great Lakes Entomol.* 7: 103-107.
- Stevens, R. E., and D. T. Jennings. 1977. Western pine-shoot borer: A threat to intensive management of ponderosa pine in the rocky mountain area and southwest. USDA For. Ser. General technical report RM-45.
- Stoszek, K. J. 1973. Damage to the ponderosa pine plantations by the western pine-shoot borer. *J. For.* 71: 701-705.
- Thier, R. W., and M. A. Marsden. 1990. Vertical growth response of ponderosa pine infested by western pine shoot borer, *Eucosma sonomana* Kearfott (Lepidoptera: Olethreutidae). *Can. Entomol.* 122: 343-347.
- USDA, Forest Service. 1994. Watershed Evaluation & Analysis for Viable Ecosystems (WEAVE), version 1.12. Deschutes National Forest, Bend, Oregon.

Williams, C. B., E. L. Smith, and T. W. Koerber. 1988. Damage appraisal and management of the western pine shoot borer, *Eucosma sonomana*, in pine plantations in California: a case study, pp. 110-123. *In* Insects Affecting Reforestation: Biology and Damage. IUFRO, Forestry Canada, Pacific and Yukon Region, Victoria, BC, Canada.