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WESTERN WHITE PINE: THE EFFECT OF CLONE AND CONE COLOR
ON ATTACKS BY THE MOUNTAIN PINE CONE BEETLE

by

Michael J. Jenkins

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology

(Entomology)

UTAH STATE UNIVERSITY
Logan, Utah

1982

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Michael J. Jenkins

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ABSTRACT

Western White Pine: The Effect of Clone and Cone Color
On Attacks by the Mountain Pine Cone Beetle

by

Michael J. Jenkins, Doctor of Philosophy

Utah State University, 1982

Major Professor: Dr. Donald W. Davis
Department: Biology

The relationship between clone and cone color in western white pine, Pinus monticola Douglas, to attack by the mountain pine cone beetle, Conophthorus monticolae Hopkins, was studied in the Sandpoint Seed Orchard, Idaho. A positive relationship was shown to exist during a 5 year field evaluation. Cone beetles were found to prefer dark colored cones and to attack certain clones at a higher rate than others.

Laboratory dissections did not indicate that cone color affected oviposition, brood development or brood mortality.

Olfactometer experiments demonstrated that olfactory stimuli are involved in the cone beetle attack sequence. Visual cues relating to cone color may be involved in the initial long range host orientation of attacking beetles.

(91 pages)

INTRODUCTION

Western white pine (Pinus monticola Douglas) was the most valuable timber tree in northern Idaho. It was a high market value and is among the higher volume-producing species in its forest cover type. In recent years production of western white pine has been severely limited by white pine blister rust. The disease is caused by Cronartium ribicola Fischer, a pathogen introduced to the United States from Europe in the early 1900's (Haig et al. 1941). It has decimated stands of western white pine throughout its natural range, especially in eastern Washington, northern Idaho, and western Montana, where host and climatic factors favor rapid and serious disease invasion (Hepting 1971).

In 1946 the U.S. Forest Service began a research program to develop blister rust resistant western white pine as a possible disease control measure. From 1950 to 1960 many resistant individuals were tested and in April, 1960 the Forest Service established the Sandpoint Seed Orchard using grafts from 13 trees showing resistance to white pine blister rust. F1 generation seed has been used to establish several F2 orchards in northern Idaho. The goal is 100 acres of F2 orchards producing sufficient seed for national forest planting (Bingham et al. 1963).

In 1977, 80 percent of the cones at the Sandpoint Seed Orchard were destroyed by the mountain pine cone beetle. Conophthorus monticolae Hopkins (Coleoptera: Scolytidae) (Hoff 1978). The beetle attacks and destroys young second-year cones before the cones are half grown (Keen 1958). The life history of C. monticolae has been thoroughly studied,

but additional information concerning beetle behavior would be valuable in development of control strategies.

Aspects of the beetle's behavior not previously studied are the effects of clonal variability and of pine cone color on beetle host selection. Steinhoff (1974) described the genetic basis for cone color inheritance in P. monticola and identified five cone colors ranging from purple to green. Hoff indicated, in a personal communication (1978), a possible connection between cone color and beetle attack.

This study tests the hypothesis that beetle attacks are related to cone color.

In testing the hypothesis the study had the following objectives:

1. To correlate clone and cone color in western white pine with percentage cones attacked by the mountain pine cone beetle.
2. To determine if beetle attraction to cone color results from visual, olfactory or other stimuli.
3. To determine if differences exist in the number or survival of cone beetles developing in infested cones of different colors.

REVIEW OF LITERATURE

Mountain Pine Cone Beetle *Conophthorus monticolae* Hopkins
(Coleoptera: Scolytidae)

Taxonomy

Miller (1914) first recognized the importance of cone beetles in reducing the amount of seed available for collection. Schwarz (1895) described the first species in this group as *Pityophthorus coniperda* Schwarz. Hopkins (1915) included this species in his original description of the genus *Conophthorus* which accommodated 14 other species of cone beetles, separated primarily on host tree occurrence (Chamberlain 1958). Based on Hopkins' taxonomy, Furniss and Carolin (1977) recognized 16 species of *Conophthorus*, 11 of them in the western United States. Hatch (1971) regarded many anatomical characters used by Hopkins as largely imaginary, but because of the importance of the genus failed to recommend synonymy. Wood (1977), however, saw no basis for recognizing more than one species and proposed synonymizing all western species under *C. ponderosae*. Wood's synonymy is based entirely on morphological characters, but he conceded that sibling species could occur in this group and that further biological studies are necessary to support this synonymy. In this dissertation *C. monticolae* is used as the scientific name for the mountain pine cone beetle because of its extensive occurrence in the literature. The following is Hopkins (1915) original description of the genus *Conophthorus*:

Pronotum with sides broadly rounded from near base to apex, slightly constricted beyond middle with base margined; abdominal

sternite 7 with posterior margin procurved; pygidium vertical when in contact with posterior margin of sternite; pronotal rugosities extending toward or to lateral margin; tarsi with joint 5 not as long as joints 1 to 4 united; antennal club compressed, not thickened at the base with 3 sutures on anterior and 2 on posterior face, sutures 1 and 2 without septum; eyes acutely emarginate. The genus Conophthorus is at once distinguished from Pityophthorus by the absence of sutural septa in the antennal club. (Hopkins, 1915, p. 429)

Hopkins (1915) described C. monticolae as follows:

Length 3 to 3.5 mm. Clothed with long, conspicuous, bright red hairs; pronotum coarsely asperate; the elytra coarsely and deeply punctured; the interstrial punctures less numerous on the disk, usually 7 to 10 between the declivital summit and the base of the elytra; declivity broadly, distinctly sulcate, suture without granules. (Hopkins, 1915, p. 432)

Keys useful in separating species of Conophthorus are presented by Chamberlain (1958) and Ruckes (1963).

The sexes are distinguished based on the appearance of the seventh and eighth abdominal tergites being fused in the female and separate in the male. This character has been described in several species of Conophthorus and likely occurs throughout the genus (Lyons 1956; Herdy 1959, Schaeffer 1962, Kinzer and Ridgill 1972). Females are also larger overall and have a larger head capsule than males. Thomas (1971) described anatomical and morphological characters of Conophthorus larvae and pupae.

Life history

Keen (1958) offered the most often cited description of cone beetle life history. Numerous other studies have been completed and can be used to formulate a rather complete description of the beetle's life history.

Strong thigmotropism keeps the beetles in overwintering sites, cones infested the previous year (Henson 1961b), until a specific

degree day accumulation has occurred in the spring (Shea et al. 1982). Once this requirement is met emergence will occur at mid-day when the temperature is between 27-35°C, relative humidity is low and there are 9 hours of light (Henson 1962). Emergence corresponds closely with initiation of strobilus elongation in spring (Williamson et al. 1966). Flight is most frequent on clear days, but will occur on overcast days if the temperature is high enough for beetles to move to exposed areas. Beetles will not fly when it is raining. Once initiated, flight is into the wind toward exposed parts of the tree where the temperature is the greatest. This is affected also by changes in the moisture gradient from the duff to the transpiring tree. The beetles orient to silhouettes of trees against the light sky. Repeated flights are common, but most beetles will fly only as far as necessary to find a suitable host. This results in intense searching of an immediate area and high local infestations. This attack behavior typically results in beetles landing in the upper crown of dominant trees on exposed branches (Henson 1962). Hall and Wilson (1974) also found the preferred site of attack to be the upper crown. The infestation then moves down with subsequent attacks. The height of scolytid flights corresponds to the height of the attack zone (Hosking and Knight 1975) and is affected by tree height, degree of exposure to sky, and cone-bearing branch length (Hall and Wilson 1974, Dale and Schenk 1978). The initial flight and attack period can last 30 days or more depending on the number of suitable days for flight during the period and the location of the overwintering cone (Shea et al. 1982).

Laboratory work done by Henson (1961a) with C. coniperda demonstrated the changes in adult beetle anatomy occurring during the attack

period. The gut of callow adults is empty and during the overwintering period there is a reduction in fat body. Emerging beetles ingest portions of the overwintering cone, resulting in increased amounts of fat body, initiation of gonadal development, and development of the vertical thoracic wing muscles. Morgan and Mailu (1976) suggested the first cone attacked is required for feeding and for the described anatomical changes and subsequent reproduction. Mating may occur prior to or during this period then oviposition occurs in the second cone located (Schaeffer 1964). Once the oviposition site is found the flight muscles rapidly degenerate, the space in the female thorax becoming filled with the ovaries. The autolysis and regeneration of the flight muscles may occur several times during the adult stage. Other researchers have observed this phenomena in aphids (Johnson 1953) and a variety of scolytids including Conophthorus (Henson 1961a, Bedard 1968), Dendroctonus (Reid 1958, Atkins and Farris 1962) and Trypodendron (Chapman 1956). Chapman (1956) suggested that this phenomenon occurs in all scolytids in which long periods are spent in plant tissue alternating with brief periods of flight.

Oviposition normally occurs during May and June, but can begin as late as July at high elevations. The female enters the cone by boring through scales near the base (Williamson et al. 1966). If mating has not already occurred, a male may enter the cone through the same hole and mate (Ruckes 1963; Kinzer et al. 1970; Dale and Schenk 1979). The female then bores an egg gallery up the cone axis, depositing eggs singly in niches to the sides of the gallery (Williamson et al. 1966). A single female may lay as many as 27 eggs utilizing up to five cones (Bedard 1968). A feeding period of 8-16 days follows each

oviposition period and occurs on the lateral portion of the cone just attacked. This eliminates searching by a beetle able only to crawl and is required for regeneration of wing muscles. Most adult females do not, however, attack five cones because of increasing mortality with time (Morgan and Mailu 1976). Factors contributing to mortality include reduced carbohydrate availability, increased resin flow and increased woodiness of cones with age (Mattson 1978).

Conophthorus eggs are milky white when laid and go through several developmental stages during the 25 day period to eclosion (Schaeffer 1962). Two larval instars have been reported for C. radiatae (Ruckes 1958, Schaeffer 1962), C. resinosae (Lyons 1956), C. ponderosae (Kinzer et al. 1970), C. coniperda (Odell and Godwin 1964) and C. monticolae (Williamson et al. 1966). The larval instars can be separated based on head capsule width. The first stadium is the main feeding period lasting 15-20 days. The second instar forms a niche for pupation. The pupal stage lasts 15-20 days and goes through four developmental stages recognized by changes in eye, mandible, and elytra color (Schaeffer 1962).

Callow adults of C. monticolae overwinter in brood cones commonly fallen to the ground (Williamson et al. 1966). Odell and Godwin (1964) and Henson (1964b) reported that some teneral adults of C. coniperda emerge in fall and may bore into first year cones and overwinter. This behavior is, however, unfavorable because of increased winter mortality. New adults of C. resinosae (Lyons 1956, Herdy and Thomas 1961) and C. lambertianae (Struble 1947, Ruckes 1957) have been observed to leave brood cones in late summer and enter current year's shoots. Dale and Schenk (1978) described single females of C. ponderosae mining in

conelets and new lateral shoots. Based on this type of behavior, McPherson et al. (1970) proposed a new species, C. banksianae McPherson, which infests twigs only (McPherson et al. 1970). Thomas (1971), however, found no morphological or anatomical distinction between C. banksianae and C. resinosae, and feels the designation of the new species is based solely on ecological evidence. Morgan and Mailu (1976) reported that new C. coniperda adults emerged and dispersed in fall prior to overwintering. There is only one generation per year in Conophthorus because by fall cones have hardened and are unsuitable for oviposition (Miller 1915; Bedard 1968).

Conophthorus does not appear to be subject to obligate diapause. Overwintering adults dissected from cones become active when warmed regardless of time of year (Henson 1961b). Morgan and Mailu (1976) indicated that cone beetles enter a temperature induced quiescence extending through winter. This observation is supported by previous work done by Schaeffer (1964).

A small percentage of overwintering beetles do not emerge until 2 years after attack, thus ensuring population survival in years when few or no cones are produced (Bedard 1968, Kinzer and Ridgill 1972).

Parasites and predators

There are only a few conspicuous parasites and predators of Conophthorus, none appearing to exert a high level of natural control.

Keen (1958) repeatedly encountered Eubadizon sp. (Hymenoptera: Braconidae) from rearings of infested cones. He also reared Spathius sp. (Hymenoptera: Braconidae) and larvae of Cleridae (Coleoptera), but was uncertain whether any of these were definitely associated with

Conophthorus. Spathius was also observed by Odell and Godwin (1964) emerging from cones infested with C. coniperda.

Schaeffer (1962) worked with C. radiatae and found Cephalonomia utahensis Brues (Hymenoptera: Bethyridae) to be the only natural enemy commonly encountered.

Ruckes (1956) found this parasite to be associated with C. lambertianae and C. ponderosae. The parasites overwinter as adults in infested cones and emerge later than cone beetles in spring. Adults enter cones via Conophthorus entrance holes, ventilation holes or cracks and oviposit one to six eggs on the integument of second instar cone beetle larvae or pupae. They feed on beetles then spin cocoons, pupate, emerge and disperse to other cones (Schaeffer 1962).

Cephalonomia hyalinipennis Ashmead has also been reared from larvae of C. coniperda (Odell and Godwin 1964) as has Eurytoma pini Bugbee (Hymenoptera: Eurytomidae) and Habrocytus sp. (Hymenoptera: Pteromalidae) (Herdy and Thomas 1961). Hall and Wilson (1975) described Cecidostiba dendroctoni Ashmead (Hymenoptera: Pteromalidae) as a parasite of C. banksianae and possibly other scolytids. In their study 15-40 percent of second instar larvae and pupae were attacked by this parasite. Ruckes (1963) recovered a chalcid parasite Tomicobia tibialis Ashmead from overwintering adults of C. lambertianae.

Lyons (1956) and Dale and Schenk (1979) reared Bracon rhyacioniae Muesbeck (Hymenoptera: Braconidae) from C. resinosae and C. ponderosae respectively. The most common predator found by Dale and Schenk (1979) in their study was the clerid Phyllabaenus sp.

Other natural enemies found by Schaeffer (1962) include the predators Temnochila sp. (Coleoptera: Troglitidae) preying on adult

cone beetles in overwintering cones and Hemerobius (Neuroptera: Hemerobiidae) preying on beetle larvae in spring. Cone beetle associates not preying on beetles directly, but competing for food or space include Ernobius punctulatus Fall (Coleoptera: Anobiidae) and Oscinella conicola Greene (Diptera: Chloropidae). Various other beetle and fly scavengers may also compete with cone beetles for food. Intraspecific attack among siblings has also been reported (Hall and Wilson 1975). In addition cone worms in genus the Dioryctria (Lepidoptera: Pyralidae) and cone moths in genus the Eucosma (Lepidoptera: Olethreutidae) can attack cones already inhabited by cone beetles and may then feed on immatures (Odell and Godwin 1964). Both Dioryctria and Eucosma are commonly encountered in cones of western white pine.

Nematodes of the genera Parasitaphelenchus and Neoparasitylenchus (Tylenchida: Nematodae) have been found in the haemocoel of adult C. monophyllae. These parasites can cause reduction in fat body and ovary size, decreased coordination and increased mortality of cone beetles (Poinar and Caylor 1974). A white fungus developing in duff has been reported by Keen (1958) and Odell and Godwin (1964). The mycelia of the fungus can engulf beetles in overwintering cones preventing them from feeding.

Other mortality factors

In preparing a life table for C. coniperda Morgan and Mailu (1976) determined that parasites and pathogens are the most important mortality factors acting on the larval and pupal stages. Resination, desiccation, drowning and freezing were found to be important mortality factors acting on the adult stage.

Santamour (1965) found the presence of cone beetles stimulates crystallization of fluid resin. This resin can build up on the legs and elytra, immobilizing and eventually killing the insect. Crystallized resin appears to be more harmful than fluid resin. Resination may be more important in older, less vigorous adults than young vigorous ones (Morgan and Mailu 1976). The effect of resin has also been studied by McPherson et al. (1970).

Henson (1964a) found that cone beetles can move about in their overwintering cones to avoid flooding, but in spring as snow melts and rainfall increases a percentage of adults can be expected to drown prior to emergence. Henson also found that beetles do not move to avoid overheating. Desiccation can cause additional mortality to adults (Bedard 1966, Morgan and Mailu 1976) and immatures (Schaeffer 1963).

Extreme cold during winter, as is common in northern Idaho, can cause additional mortality to adults overwintering in cones not insulated by snow cover (Dale and Schenk 1979).

Effect of cone crop size

Perhaps the most important factor regulating cone beetle population size is fluctuation in cone crop size (Mattson 1971, Dale and Schenk 1978, Forcella 1980). The availability of fresh cones for feeding by emerging beetles in spring may affect beetle survival and reproduction. Beetles can survive by initial feeding in old cones, but food quality does appear to be a factor (Morgan and Mailu 1976).

More important than food quality is food quantity, i.e. the number of cones available in a given area. Cone production in P. monticola

and other conifers is typically periodic with varying numbers of years between heavy crops (Rehfeldt et al. 1971; Franklin et al. 1974; Eis 1976). Beetle populations will tend to increase when successive moderate or heavy cone crops occur. The population will ultimately be limited in years when cone production is low. The intermittent seeding habit of conifers may be an adaptive mechanism decreasing losses by seed and cone insects (Henson 1964b). Mattson (1978) suggested seed and cone insects, by attacking cones during heavy crop years, remove the depressing effect of a large crop on subsequent crops thereby enhancing future abundance of host material by reducing it at present.

Control

Cone beetles can have heavy impact on pine cone crops. Heavy cone losses have been reported in sugar pine, ponderosa pine (Miller 1915), western white pine (Hoff 1978) and eastern white pine (Graber 1964). In Graber's (1964) study nine consecutive crops were destroyed by the white pine cone beetle. There is an increasing need to protect seed production areas and seed orchards from Conophthorus (Furniss and Carolin 1977).

A variety of practices has been attempted in efforts to control cone beetles. The best method is to eliminate them while in overwintering cones on the ground, either by hand gathering infested cones or applying insecticides, if available, to the ground prior to emergence (Miller 1915, Morgan and Mailu 1976). Prescribed burns are effective in accomplishing this as demonstrated by Miller (1978, 1979) versus C. resinosae. Henson (1964b) suggested using gametocides to suppress cone production for a year thereby reducing beetle populations for the

following year. By using 2,4-D some success was gained in the lab, but field benefit has not been demonstrated. Cultural practices including regulation of crown and stand density must also be considered in cone beetle management plans (Schenk and Goyer 1967, Dale and Schenk 1979).

Shea et al. (1982) have demonstrated the effectiveness of the insecticide permethrin in controlling C. monticolae when applied as a ground spray. Permethrin was selected based on residual toxicity tests of 11 insecticides against the mountain pine cone beetle (Haverty and Wood 1980). The use of permethrin and other strategies will be beneficial in existing and planned western white pine seed orchards and may have some application to seed production areas in natural stands.

Use of olfactometers

The use of olfactometers for assaying responses of insects to attractants and repellents has been employed with many agriculturally important insects (Chamberlain 1956, 1959) including the pink bollworm (Guerra 1968) mosquitoes (Gouck and Schrenk 1965) and the European pine shoot moth (Daterman 1972). Much has also been done in assessing olfactory responses of scolytids specifically, including Trypodendron lineatum Oliver (Francia and Graham 1967, Moeck 1970), Ips confusus Leconte (Wood and Bushing 1963), Ips pini Say (Seybert and Gara 1970), Scolytus multistriatus Marsham (Meyer and Norris 1967), Dendroctonus sp. (Rudinski 1962, 1976; Chapman 1963; Jantz and Rudinski 1965; Rudinski and Michael 1973; Rudinski and Ryker 1977), C. coniperda (Henson 1961b) and C. ponderosae (Kinzer et al. 1972).

Insect responses to odor in olfactometer studies depend on central nervous system integration of multiple inputs and outputs. Kennedy

(1978) drew attention to limitations of olfactometer studies due to the complex behavior involved in the observed responses. Kennedy (1977) pointed out the many ambiguities associated with olfactometers and stated that most may not distinguish different types of responses.

Western White Pine; *Pinus monticola* Douglas

(Coniferales: Pinaceae)

White pine is among the finest of the world's softwoods. By 1900 the supply of old growth eastern white pine (*P. strobus* L.) in New England and the Lake States had been exhausted (Strong and Webb 1970). In 1898 a rush of timber claims began in the Inland Empire (eastern Washington, northern Idaho and western Montana) marking the beginning of a 60 year period of logging and milling in the area. During the period 1920-1930 frequently over 300 million board feet, mostly of western white pine, was harvested annually (Andrews 1956). The amount of western white pine harvested exceeded, in volume and value, all other species logged (Haig et al. 1941).

Taxonomy, distribution and silvics

Western white pine is in subgenus *Strobus* Lemm., section *Strobus*, subsection *Strobi* Loud. (Little and Critchfield 1969) a group of pines of worldwide distribution. Five of these pines are native to North America (Steinhoff 1972).

Western white pine has blue-green needles in fascicles of five with stalked, curved cones 5-15 inches (12.70-38.10 cm) long. Cone scales are unarmed and seeds have a 1 inch (2.54 cm) long terminal wing. Western white pine is unusually windfirm and can reach heights of

150-180 feet (45.70-54.84 m) and 2-1/4 - 3-1/2 feet (0.76-1.07 m) dbh on good sites. The stem is long and straight with little taper, often branchless to 100 feet (30.44 m) (Harlow et al. 1979).

Western white pine is also known as Idaho white pine, white pine, silver pine and mountain Weymouth pine and is the state tree of Idaho (Fowells 1965, U.S.D.A. 1980). It grows from British Columbia to northern Idaho and northwestern Montana south through the Cascades of Washington and Oregon to the southern end of the Sierra Nevada Mountains of California (Critchfield and Little 1966). The geographic boundaries of western white pine are defined by climatic factors, being limited at low elevation by deficient water and at high elevation by unfavorable temperatures. Western white pine reaches its best development in northern Idaho and western Montana on moist, deep and well-drained soils (Haig et al. 1941, Fowells 1965) in areas with short, dry summers and cold winters with abundant snowfall (Wellner 1962). In the inland empire 3 million acres are occupied by white pine forests (Haig et al. 1941, Wellner 1973).

Western white pine occurs in mountainous country broken up by rugged topography (Defebaugh 1906) growing from sea level in the north to 7500 feet (2285 m) in the south. The best stands of western white pine follow moist river bottoms and lower elevations of the Priest, Coeur d' Alene, St. Joe and Clearwater River basins where they occur in 17 forest cover types, normally in mixed stands with a variety of other conifers (Wellner 1962).

Fire is an important destructive agent of western white pine stands and maintains the stands in an even-aged condition. Without fire, stands of the western white pine type progress from rich mixtures of

many species to climax forests of few species in which grand fir, western red-cedar and western hemlock or subalpine fir form the climax, depending on site moisture conditions. The even-aged condition of western white pine stands lends itself to regeneration using any of the even-aged systems including seed tree, shelter-wood or clear cut (Wellner 1973).

Reproductive phenology

The reproductive phenology of western white pine is similar to that of other soft pines. The literature concerned with phenology of forest trees is very extensive, with Pinus having been studied more often and completely than any other conifer genus (Owens and Molder 1977b). Bingham and Squillace (1957) aptly reviewed this literature with special reference to P. monticola.

Based on work by Owens and Molder (1977a, 1977b) the following summary of western white pine phenology can be presented. Pollen cones differentiate in August, 10 months before pollination. In April of the following year long shoot terminal buds (LSTB) end dormancy and begin elongation. Seed cones are differentiated and pollen cones end dormancy in mid-April. Meiosis in pollen cones occurs during mid-May with pollination following during mid-June. Male and female gametophyte development occurs during the summer ceasing in August and LSTBs become dormant in October. Male and female gametophyte development resumes in April with fertilization occurring in early June. Mature embryos develop by September and seed is shed. The entire elapsed time for production of mature seed is about 15 months.

The summary provided here presents average dates for trees studied near Vancouver, B.C. The time of initiation and duration of a given event varies throughout the range of western white pine. Temperature is the most important factor regulating onset and duration of growth and flowering. Elevation and latitude as they affect mean temperature are also important factors (Bingham and Squillace 1957). Growth can be increased by thinning and fertilization (Ryker and Pfister 1967).

Cone production in conifers is notoriously unpredictable, showing considerable fluctuation from year to year and location to location. Factors of importance in this periodicity include species, climate, insect, squirrel and bird damage and tree metabolism and vigor. These factors are important both individually and as they interact with one another (Puritch 1972). Other factors affecting cone production include frost, lack of pollination, apical stem breakage and genetic differences (Bordelon 1978). The relationship between cone production and diameter increment was studied by Eis et al. (1965).

In a 12 year study of cone production by Franklin et al. (1974), western white pine was found to be the most consistent producer of the several species studied. Rehfeldt et al. (1971) determined that female strobilus production in western white pine follows major cycles of 4 years and minor cycles of 3 years.

Cone production in western white pine is influenced by weather variables. Rehfeldt et al. (1971) studied western white pine in northern Idaho and found high strobili counts to be associated with water deficits in summer 2 years before pollination. Water deficits during late summer of the year preceding pollination reduced strobilus

development. Water deficits during early summer of the year in which cones mature caused increased strobilus abortion.

Eis (1976) worked with western white pine on Vancouver Island and attempted to correlate cone production with a number of climatic variables, including temperature and precipitation, during various periods before, during, and after initiation of bud primordia.

Methods for quantifying cone production in a variety of conifers have been developed by Dobbs et al. (1980) and Mattson (1979).

Genetic variability

Several studies have been made to determine the extent of phenotypic and genetic variability in western white pine (Bingham, Squillace and Wright 1972). Changes in elevation were shown to affect height, diameter, and mean annual increment growth, as well as branch angle, number and length of needles, cone scale width and length, and seed and cone production (Squillace and Bingham 1958, Hanover and Barnes 1962, Barnes 1967). In these studies the effect of microsite was determined to be of greater importance to phenotypic expression than climatic factors associated with changes in elevation. These studies indicated that where topography is variable and moisture critical selection pressures on seedling establishment and growth rate discriminate against gene infiltration from adjacent sites.

Townsend (1970) and Townsend et al. (1972) studied western white pine in northern Idaho and concluded that variability between populations has only a slight association with environmental gradients. Only minor differences were found in height growth, photosynthetic efficiency and oleoresin composition between pine populations

from different elevations. They concluded that effective cross pollination prevents large genetic differences in the northern Idaho portion of western white pine's range. The major differences found were in concentrations of two of five monoterpenes analyzed. These differences occurred only between widely separated seed sources and represent genetic differences unrelated to elevation or latitude. Similar differences in oleoresin concentration have been reported between the closely related eastern and western white pines (Hanover 1975). Hanover (1966a) discussed the genetics of monoterpene levels in western white pine and described differences existing between clones.

Cone color

The inheritance of cone color in conifers can be a complex matter. Copes (1972) determined that the inheritance of megastrobilus color in Douglas-fir is multigenic and may involve epistasis. He found that cones contain 11 flavonoids and that each may be controlled by a single gene. Single gene inheritance of floral color has been described for anthocyanin pigments in red clover (Taylor et al. 1971). Teich (1970) concluded that female conelet color in white spruce is controlled by one gene having two alleles, one promoting red, the other green, with pink heterozygotes. Carlisle and Teich (1970) found that male inflorescence color in Scotch pine is also controlled by two alleles of a single gene.

Pre-ripe cones of western white pine range in color from yellow-green to purple (Kingman and Jenkinson 1974). Steinhoff (1974) concluded that presence or absence of purple coloration is controlled by a single gene having two alleles one producing an effect dominant

to that of the other. Some variation in color does occur and may result from incomplete dominance, variable penetrance or the influence of environmental factors.

White pine blister rust,
Cronartium ribicola

In 1909 the white pine blister rust disease-causing fungus was introduced from Europe to the eastern United States where it attacked eastern white pine. The pathogen was introduced separately to the western United States on pine seedlings shipped from France to Vancouver, B.C. in 1921 (Haig et al. 1941, Boyce 1961). It is by far the most serious disease of western white pine (Hepting 1971).

Blister rust attacks numerous white pine species, but western white pine is among the most susceptible (Childs and Bedwell 1948). The high susceptibility of western white pine, the abundance of the alternate host (*Ribes* sp.), and the climate of eastern Washington, western Montana and northern Idaho (Hepting 1971), produced the most spectacular blister rust damage seen anywhere in the world (Bingham 1962).

The disease attacked all age classes of western white pine and spread rapidly throughout the Inland Empire. Early attempts at control through *Ribes* eradication, silvicultural practices (Moss and Wellner 1953), canker removal (Martin and Gravatt 1954) and the use of antibiotics (Moss 1961) proved largely unsuccessful. The extent and severity of the disease, and the inability to control it, resulted in changes in western white pine management. *Ribes* eradication and planting of western white pine were discontinued. Other tree species were favored and salvage of western white pine was accelerated. There

was increased emphasis aimed at development of rust-resistant strains of western white pine (Ketcham et al. 1978).

Most important in development of long range, less expensive, indirect control was the use of inherently rust-resistant planting stock. Work with breeding blister rust-resistant western white pine began in 1946 when it was observed that, even in stands with high rust mortality, certain individuals did not become infected (Bingham et al. 1963). Hanover (1962) described the developments in breeding blister rust resistant western white pine and possible rust-resistance mechanisms. Ten years of experimentation in selecting and breeding resistant individuals produced encouraging results (Bingham et al. 1958; Bingham et al. 1960; Bingham 1966, 1968, Bingham et al. 1969).

There were two important results of this work:

1. One-fourth of the canker-free pines from otherwise decimated stands, when crossed, produced F1 progeny possessing 30 percent resistance.
2. F2 progenies may produce seedlings possessing 50 percent resistance indicating heritability and genetic gain (Bingham et al. 1963).

Sandpoint Seed Orchard

These developments led, in 1960, to the establishment of the Sandpoint Seed Orchard. The orchard was established using 100 grafts from each of 13 progeny-tested blister rust-resistant parent trees. The orchard was established to accomplish three objectives:

1. To provide an area where management requirements of a grafted white pine seed orchard could be appraised.
2. To provide an interim source of partially resistant F1 seed for reforestation.
3. To provide a study area for future research on seed orchard problems.

F1 progeny seedlings surviving rust exposure were used to establish the Moscow Arboretum in Moscow, Idaho and subsequent orchards have been established in northern Idaho. The ultimate goal is the establishment of 100 acres of F2 orchards predicted to produce 20 million seed annually (Bingham et al. 1963). Several of these orchards are now established and the current management plan calls for phasing out the Sandpoint Seed Orchard by 1986.

Other seed and cone insects

A variety of other seed and cone insects attacks cones of western white pine. In a 3 year study in western Montana and northern Idaho Dewey and Jenkins (1982) found species of Eucosma (Lepidoptera: Olethreutidae) and Dioryctria (Lepidoptera: Pyralidae) to be second in importance to Conophthorus in damaging cones of western white pine. Barnes et al. (1964) also described Conophthorus monticolae, Eucosma rescissoriana Heinrich and Dioryctria abietella D. and S. as the most important insects attacking seeds and cones of western white pine. Kulhavy et al. (1975) listed in addition a midge Asynapta keeni Foote (Diptera: Cecidomyiidae) and a variety of other seed and cone insects of lesser importance. Asynapta was previously described by Felt (1935) as being reared from pine cones.

The taxonomy and biology of E. rescissoriana (Ollieu and Schenk 1966, Goyer and Schenk 1970) and D. abietella (Munroe 1959, Barnes et al. 1964, Hedlin et al. 1980) are known in detail. Both are major seed and cone pests of pines in North America and are repeatedly encountered in samples of pine cones, but are rarely of greater importance than Conophthorus on cones of western white pine.

METHODS

The purpose of this study was to determine if a relationship exists between clone and cone color in western white pine and attacks by the mountain pine cone beetle. Methods involved field analysis of attack rate and laboratory procedures to assess stimuli involved and to determine if differences exist in the number or survival of beetles in attacked cones of different colors.

Study Area

The Sandpoint Seed Orchard is located at 48°16'N, 116°34'W at an elevation of 2100 feet (639.80 m) on a National Forest Administration Site within the west city limits of Sandpoint, Idaho. The orchard's boundaries encompass 19.2 acres (7.77 ha) with 17.2 acres (6.96 ha) planted in trees.

Mean July temperature is 65.3°F (18.50°C) and mean January temperature is 25°F (-3.89°C) with a maximum of 104°F (40.0°C) and a minimum of -35°F (-37.22°C). The total growing season averages 121 days. Total yearly precipitation is 28.79 inches (73.13 cm) with low summer and high fall-winter distribution. Prior to establishment as an orchard the area served as a pasture.

Seed Orchard Design

Thirteen progeny-tested blister rust resistant western white pine parent trees were used in the original establishment of the orchard. Approximately 300 cuttings were taken from each of these 13 clones and

grafted to rootstocks from nursery-grown western white pine seedlings. This work was done by personnel of the Northern Idaho Forest Genetics Center, Moscow, Idaho during the period from 1958 to 1960. In 1960 the grafts were ready for outplanting into the orchard.

The irregular area of the orchard was divided into 14 blocks. Eight of these blocks were complete, containing 130 trees, 10 from each clone, and having dimensions of 190 by 240 feet (57.89 by 73.12 m). Six blocks were irregular containing various clonal assortments. Block eight contained trees from one clone only (Figure 1).

Each block was further divided into subblocks designated A, B, C, D and E. Subblocks were subdivided into sub-subblocks designated 1 and 2 each containing one representative from each of the 13 clones. The sub-subblock was the unit of randomization (Figure 2).

After planting most individuals of four high elevation clones and one clone showing low blister rust resistance were removed and replaced with five additional clones. The total number of clones represented in the orchard was, therefore, 18. A cedar stake was placed by each tree and contains a metal identification tag. An individual tree was identified by a block number, subblock number, a clone number and a sub-subblock number, e.g. 4A 17-2.

Before and after planting, cultural treatments including cultivation and weed control were performed in the orchard. Planting was completed on April 24, 1960.

A major problem in the orchard has been graft incompatibility between rootstock and scionwood. Overgrowth in the graft area has caused, and continues to cause death of numerous trees resulting in unequal numbers of trees and clones in all blocks.

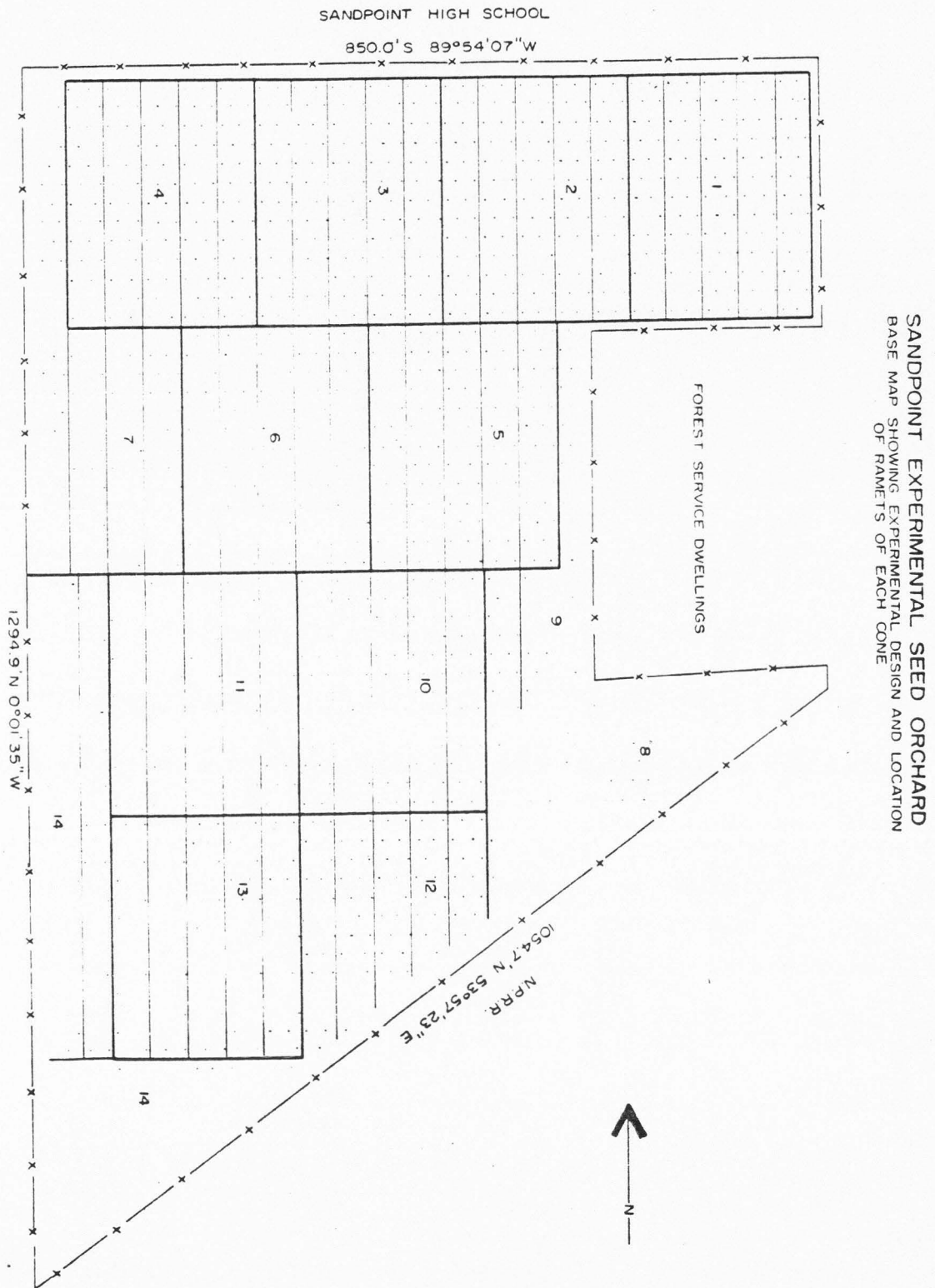


Figure 1. Reproduction of the original map used in establishment of the Sandpoint Seed Orchard. Map shows numbering scheme for blocks and tree locations.

SANDPOINT HIGH SCHOOL

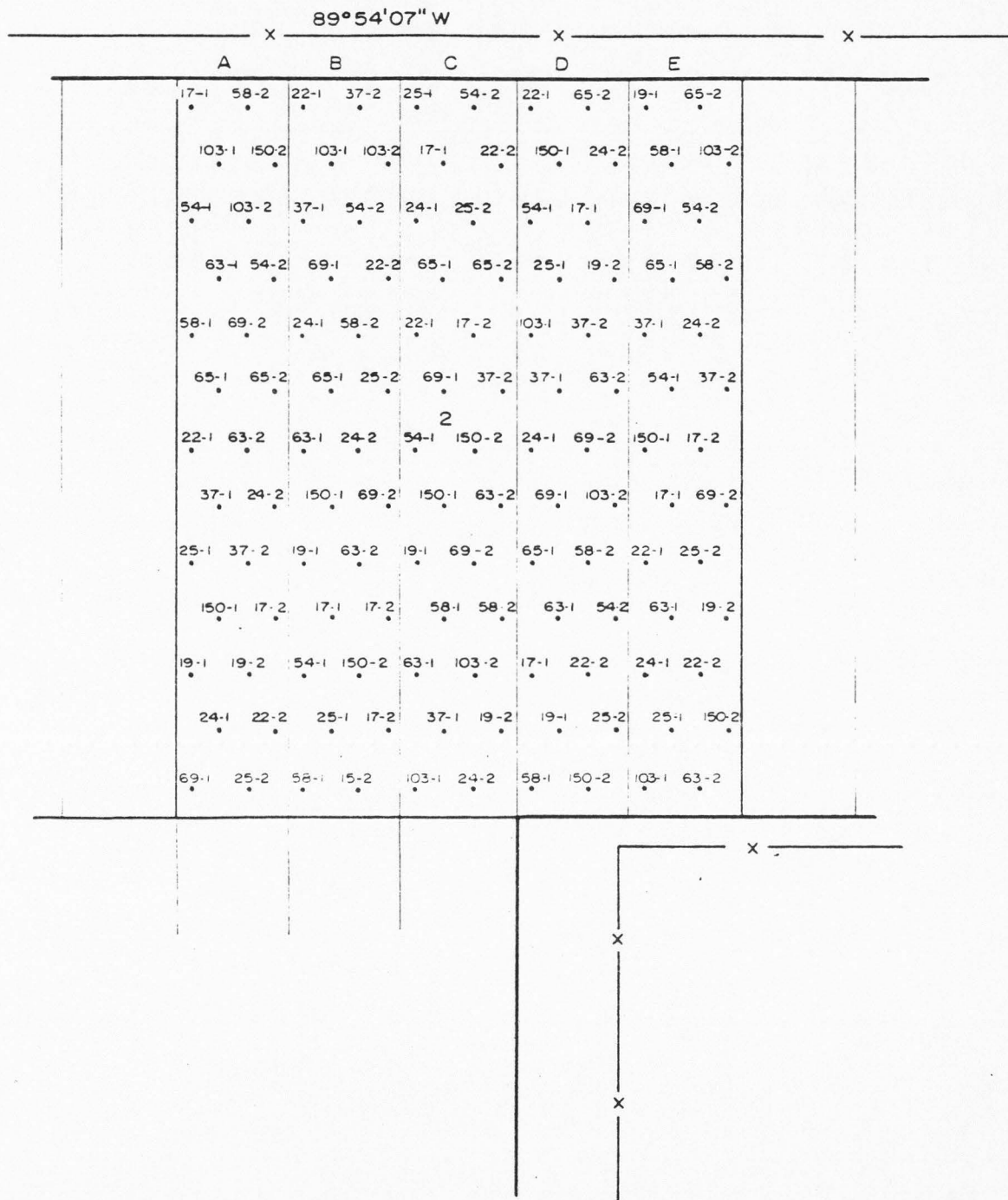


Figure 2. Detail of block two from Figure 1. Map shows letters used in labeling subblocks and numbers used to identify individual trees.

Relationship Between Cone Color and Clone

Steinhoff (1972) studied the genetic basis for cone color in western white pine and identified five cone colors ranging from green to purple. However, I found it difficult to distinguish the intermediate colors from each other. Therefore, in this study, cones are classified as green, purple or intermediate (cones having various combinations of green and purple coloration).

Cone color is a consistent trait within a clone, so each clone can be placed into one of the three cone color classes. Classification was done in mid-summer when color is easily recognizable.

Field Data Collection

By late summer cone beetle-attacked cones are distinguished by their shrunken, dried and withered appearance. Each summer during 1978 to 1981 the total number of cones and total number of cone beetle attacks were recorded for every tree in the eight complete blocks. Similar data furnished by the U.S.F.S. Intermountain Forest and Range Experiment Station enabled 5 years of data to be included in this study.

Several techniques were used for field data collection. The most often employed was ground counting using binoculars. Each tree had to be viewed from many angles to insure accurate counts. Periodically trees were climbed and numbers obtained were compared to ground counts. During the final summer of counting a cherry picker rig was used to make counts on some trees. This proved to be the safest and most accurate method, but was costly and time consuming.

The field data collection portion of this study represented the greatest expenditure of time and effort. Field data was collected and recorded with assistance from my wife, Vesna.

Data Analysis

A completely randomized design with unequal numbers was used. Data were analyzed using analysis of covariance. Total cone number was the independent variable and the total number of attacked cones the dependent variable. The analysis tested for significant differences in adjusted attack rate between clones and between colors of cones.

Laboratory Procedures

Rearing and handling insects

Collections of beetle-infested cones containing overwintering adults were made in the fall of 1980. The cones were stored at normal outside temperatures until January 1, when they were placed in a refrigerator at 40°F (4.4°C).

When needed for experiments, cones were removed from the refrigerator and placed in 5 gallon ice cream cartons covered with cheesecloth. In 3-5 days, beetles began to emerge from cones, then continued to emerge for up to 1 week. Twice daily, beetles were removed from cages, placed individually in gelatin capsules, grouped in petri dishes and returned to refrigeration until enough insects were collected for a given experiment. Gelatin capsules were used to avoid problems with tarsal wounding occurring when beetles are stored together in petri dishes.

Olfactometer

An arena-type multiple choice olfactometer similar to that used by Wood and Bushing (1963) was used in the study (Figure 3). The apparatus consisted of a quarter circle of 1/2 inch (1.27 cm) plywood 15 inches (38.10 cm) in diameter. Into this were cut three 5 inch (12.70 cm) diameter holes. Cylindrical plastic was cut into 4 inch (10.16 cm) lengths and fitted with a permanent bottom and a removable top. A 1/4 inch (0.64 cm) diameter air inlet hole was drilled in one side and a 1 inch (2.54 cm) diameter outlet hole was drilled opposite it on the other side. These cylinders functioned as sample receptacles and were placed into the three holes in the plywood. One end of each of three pieces of tygon tubing was placed into the receptacle holes and the other into a hair dryer motor powering the air stream. Air streams when passed over the desired samples converged at a single point. This was the point where beetles were released.

Desired samples were placed in two receptacles and an odorless air stream through the third functioned as a control. Beetles were released in groups of 10 and tallied as to sample choice. Ten trials of 10 insects each, using two samples and a control equalled one experiment. After each 20 insects were tested sample and control locations were changed. All insects were sexed after testing and appropriate numbers were recorded.

Using this approach a series of experiments was performed. The experiments tested the response of beetles to air streams containing the following sample choices:

Experiment 1. Crushed cones were tested versus control.

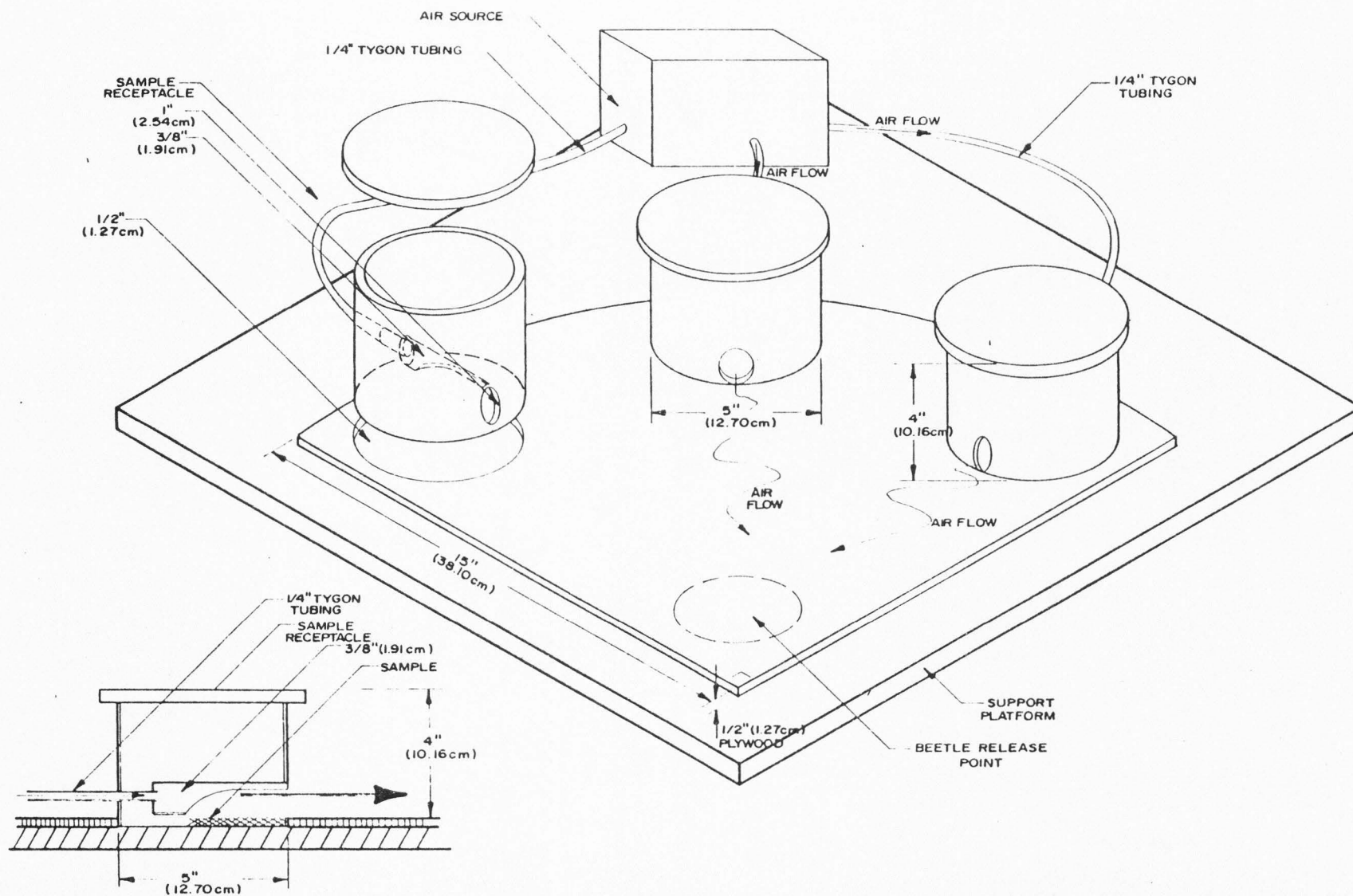


Figure 3. Diagram of olfactometer used in laboratory experiments. Adapted from Wood and Bushing (1963).

- Experiment 2. Crushed cones were tested versus crushed foliage and control. In experiments 1 and 2 cone color was not considered.
- Experiment 3. Green cones were tested versus purple cones and the control.
- Experiment 4. Male beetles and female beetles were placed in separate containers and tested versus the control.
- Experiment 5. Male beetles feeding in purple cones were tested versus male beetles feeding in green cones and the control.
- Experiment 6. Female beetles feeding in purple cones were tested versus female beetles feeding in green cones and the control.

Data analysis

Data were analyzed using contingency table analysis and the chi square distribution. This analysis was appropriate because each experiment consisted of the same number of trials with one of three possible outcomes. The probability of any particular outcome was the same from one trial to the next and each trial was independent of the others. The χ^2 statistic was used to test for responses differing significantly from probabilities expected by chance alone.

Often, in any one experiment, large numbers of beetles failed to respond to olfactory stimuli. These insects were excluded from the analysis.

Dissections

One hundred cones of each cone color were dissected during the

summer of 1981 to determine if numbers or survival of beetles differed as a function of cone color. Mean numbers of cone beetles present in cones of different colors were recorded and mean comparisons were made.

Cones were cut longitudinally using a cone cutter. Scales of the cut cones were pulled apart and total number of living and dead beetles present were counted and recorded.

RESULTS

This study was conducted to determine if a relationship existed between cone color and/or clone in western white pine and attacks by the mountain pine cone beetle. Field measurements were taken from 1977 to 1981 to assess the relationship in a field setting. Laboratory experiments were conducted to determine if cone beetles were affected by volatile substances in the oleoresin of foliage or cones of different colors. Laboratory dissections evaluated the number and survival of cone beetles as a function of cone color.

Field Measurements

Data were collected relating to the number of cones produced and the number of cone beetle attacks on each study tree during 1977, 1978, 1980 and 1981. The seed orchard design (Figures 1 and 2) facilitated grouping individual tree measurements into clonal groups. Clones were then grouped into cone color classes.

In 1979 cone production was very low and severe cold during the winter prior to cone maturation further reduced cone numbers. Few cones were available for attack in 1979 so cone production and beetle attack measurements were omitted from the analysis.

In 1981 an insecticide test was being conducted concurrently with this study. Trees used in the spray test, and those contaminated with the chemicals were not measured in the cone beetle/cone color study during 1981. The resulting reduction in sample size is evident in Tables 1, 2, 3, 4, 11, and 19.

The data obtained from field measurements were summarized by clone and clones were grouped into cone color classes (Tables 1, 2, and 3). Observation of the data in these tables indicated wide variation in cones produced, cones attacked, percentage of cones attacked and in number of sample trees measured. These differences existed between cone colors and between clones within cone color classes. Also obvious is the wide variation in all measurements from year to year.

The differences in number of cone beetle attacks between clones within cone color classes was of interest. Within the green cone color class cones of clones 25 and 19 were attacked by cone beetles at a consistently higher level than other green cone clones (Table 1). In addition, both of these clones produced more cones than other green cone clones. There were fewer sample trees measured in clone 25 and clone 86. Clone 86 and 20 were attacked at lower levels than most other green cone clones and clone 20 had a large sample tree size.

Intermediate cone clones showed similar differences in cone beetle attack levels (Table 2). Clone 17 had the highest level of attack of intermediate colored cone clones. Clone 37 also displayed high attack levels especially in 1977 and 1978. The sample size in clones 63 and 150 was much smaller than the other two intermediate cone clones. The few trees measured in clone 150 displayed very high levels of cone production.

Clones composing the purple cone color class showed corresponding differences in number of cone beetle attacks (Table 3). Of particular interest was the high attack level displayed in clone 24 during each year of the study. High levels of cone production were displayed by purple cone clones 22, 69 and 103. Clone 21 produced an unusually low

Table 1. Number of cones produced on trees of green-coned clones during 4 years and number attacked by mountain pine cone beetle.*

	Number trees	Cones produced		Cones attacked		Percent cones attacked
		Total	Mean	Total	Mean	
<u>Clone 19</u>						
1977	68	1576	23.18	1094	16.09	69.42
1978	75	3684	49.12	2460	32.80	66.78
1980	75	6524	86.99	5	0.07	0.07
1981	39	1494	38.31	49	1.26	3.30
Total		13278	51.67	3608	14.04	27.17
<u>Clone 20</u>						
1977	52	458	8.81	139	2.67	30.31
1978	54	627	11.61	308	5.70	49.12
1980	51	2330	45.69	0	0	0
1981	22	286	13.00	2	0.09	0.70
Total		3701	20.68	449	2.51	12.13
<u>Clone 25</u>						
1977	16	352	22.00	286	17.88	81.25
1978	17	443	26.06	313	18.41	70.65
1980	16	1553	97.06	1	0.06	0.06
1981	8	258	32.25	5	0.63	1.94
Total		2606	45.72	605	10.61	23.22
<u>Clone 45</u>						
1977	52	421	8.10	210	4.04	49.88
1978	46	1023	22.24	491	10.67	48.00
1980	44	1784	40.55	0	0	0
1981	22	244	11.09	2	0.09	0.82
Total		3272	19.95	703	4.29	20.25
<u>Clone 86</u>						
1977	19	282	14.84	138	7.26	48.94
1978	16	391	24.44	143	8.94	36.57
1980	18	990	55.00	0	0	0
1981	4	40	10	0	0	0
Total		1703	29.88	281	4.93	16.50

*1979 omitted due to cone crop failure.

Table 2. Number of cones produced on trees of intermediate-coned clones during 4 years and number attacked by mountain pine cone beetle.*

	Number trees	<u>Cones produced</u>		<u>Cones attacked</u>		Percent cones attacked
		Total	Mean	Total	Mean	
<u>Clone 17</u>						
1977	73	1099	15.05	1050	14.38	95.50
1978	70	1743	24.90	1447	20.67	83.00
1980	35	3577	102.20	40	1.14	1.10
1981	11	562	56.20	78	7.80	13.90
Total		6981	36.94	2615	13.84	37.46
<u>Clone 37</u>						
1977	53	961	18.13	903	17.04	93.96
1978	58	900	15.52	749	12.91	83.22
1980	57	3598	63.12	7	0.12	0.19
1981	25	236	9.44	17	0.68	7.20
Total		5695	29.51	1676	8.68	29.43
<u>Clone 63</u>						
1977	6	82	13.67	72	12.00	87.80
1978	3	65	21.67	55	18.33	84.62
1980	5	290	58.00	0	0	0
1981	3	10	3.33	0	0	0
Total		437	25.71	127	7.47	29.10
<u>Clone 150</u>						
1977	2	163	81.50	150	75.00	92.02
1978	3	226	75.33	149	49.67	65.93
1980	3	599	199.67	12	4.00	2.00
1981	0	0	0	0	0	0
Total		988	123.50	311	38.88	31.48

*1979 omitted due to cone crop failure.

Table 3. Number of cones produced on trees of purple-coned clones during 4 years and number attacked by mountain pine cone beetle.*

	Number trees	Cones produced		Cones attacked		Percent cones attacked
		Total	Mean	Total	Mean	
<u>Clone 21</u>						
1977	35	354	10.11	145	4.14	40.96
1978	32	351	10.97	108	3.38	30.77
1980	33	998	30.24	0	0	0
1981	14	102	7.29	3	0.21	2.94
Total		1805	15.83	256	2.24	14.18
<u>Clone 22</u>						
1977	76	3116	41.0	2695	35.46	86.49
1978	71	2638	37.15	1729	24.35	65.54
1980	72	7114	98.81	16	0.22	0.22
1981	33	799	24.21	25	0.76	3.13
Total		13667	54.23	4465	17.72	32.67
<u>Clone 24</u>						
1977	68	2286	33.62	2057	30.25	89.98
1978	68	2726	40.09	2077	30.54	76.19
1980	41	3723	90.80	30	0.73	0.81
1981	17	187	11.00	24	1.41	12.83
Total		8922	45.99	4188	21.59	46.94
<u>Clone 58</u>						
1977	26	337	12.96	264	10.15	78.34
1978	27	676	25.04	480	17.78	71.01
1980	25	2260	90.40	6	0.24	0.27
1981	14	662	47.29	11	0.79	1.67
Total		3935	42.77	761	8.27	19.34
<u>Clone 65</u>						
1977	13	342	26.31	213	16.38	62.28
1978	12	277	23.08	193	16.08	69.68
1980	11	821	74.64	6	0.55	0.73
1981	4	92	23.00	4	1.00	4.35
Total		1523	38.08	416	10.40	27.15

Table 3. Continued.

	Number trees	<u>Cones produced</u>		<u>Cones attacked</u>		Percent cones attacked
		Total	Mean	Total	Mean	
<u>Clone 69</u>						
1977	18	541	30.06	470	26.11	86.88
1978	18	771	42.83	559	31.06	72.50
1980	17	2259	132.88	3	0.18	0.13
1981	11	183	16.64	7	0.64	3.83
Total		3754	58.66	1039	16.23	27.68
<u>Clone 103</u>						
1977	9	171	19.00	162	18.00	94.74
1978	10	306	30.60	235	23.50	76.80
1980	13	1292	99.38	4	0.31	0.31
1981	10	562	56.20	78	7.80	13.88
Total		2331	55.50	479	11.40	20.55
<u>Clone 157</u>						
1977	5	110	22.0	88	17.6	80.00
1978	3	92	30.67	48	16.0	52.17
1980	3	134	44.67	0	0	0
1981	0	0	0	0	0	0
Total		336	30.55	136	12.36	40.47

*1979 omitted due to cone crop failure.

mean number of cones during each study year. The number of trees measured was low in clones 65, 69, 103 and 157.

Field measurement totals for cone production, and beetle attacks, for clones within the three cone color classes are summarized in Table 4. The cone production and beetle attack values were further totaled to show overall cone color totals and grand totals for the entire study. The figures thus obtained were useful in making comparisons between the cone color classes.

Values obtained for cone production, beetle attack levels, and number of sample trees all varied within the cone color classes. Cones of the intermediate color were attacked more frequently than purple or green cones in each of the 4 years studied. The greatest number of cones produced and the highest mean number of cones produced per tree were in the purple color class.

The overall totals for cone production and attack rate gave further evidence of the variability that occurred from year to year in the study. The grand totals demonstrated the amount of data evaluated in the Field Measurements portion of this paper.

The foregoing evidence indicated significant variability in the number of cones produced by clones and within the cone color classes. Analysis of covariance (ANCOV) was used to eliminate the effect a variable number of cones produced might have on the number of cones attacked by cone beetles.

The F value obtained during 1977 for differences in beetle attack rate by clone was significant at $\alpha = .01$ (Table 5). The F value for significance of the slope for χ is also significant indicating that

Table 4. Total cone production and cone beetle attack levels for each cone color class by year. Also shown are overall totals and grand totals for entire study.*

	Number trees	Cones produced		Cones attacked		Percent cones attacked
		Total	Mean	Total	Mean	
<u>Green</u>						
1977	207	3089	14.90	1867	9.02	60.44
1978	208	6168	29.65	3715	17.86	60.23
1980	204	13181	64.61	6	0.03	0.05
1981	95	2322	24.44	58	0.61	2.50
Total		24560	34.40	5646	7.91	22.99
<u>Intermediate</u>						
1977	134	2305	17.20	2175	16.23	94.36
1978	134	2934	21.90	2400	17.91	81.80
1980	100	8064	80.64	59	.59	0.73
1981	39	808	21.26	95	2.50	11.76
Total		14111	34.67	4729	11.62	33.51
<u>Purple</u>						
1977	250	7257	29.03	6094	24.38	83.97
1978	241	7837	32.52	5429	22.53	69.27
1980	215	18601	86.52	65	0.30	0.35
1981	103	2587	25.12	152	1.48	5.88
Total		36282	44.85	11740	14.51	32.36
<u>Grand total</u>						
1977	591	12651	21.41	10136	17.15	80.12
1978	583	16739	28.71	11574	19.84	69.14
1980	519	39306	75.73	130	0.25	0.33
1981	236	5717	24.22	305	1.29	5.33
Total		74413	38.58	22145	11.48	29.76

*1979 omitted due to cone crop failure.

Table 5. Analysis of covariance comparing mean number of cone beetle attacks by clone for 1977.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Equality of Adj. Cell Means	16	3,246.44	202.90	5.11**
Zero Slope	1	90,740.44	90,740.44	2,285.23
Error	573	22,752.34	39.71	

**Significant at alpha = .01.

ANCOV increased the precision of the test. A better fit was obtained using a sloped line, rather than the mean for the covariate (i.e., number of cones).

Because a significant F-value was obtained, a least significant difference (LSD) test was run, making all possible comparisons between clone means (Table 6). The attack rates in many clones differed significantly from many others. Clones 17, 37 and 86 differed the most from other clones. Clones 25, 63, 69, 103, 150 and 157 showed few differences. This probably resulted from smaller sample sizes in the clones and the larger t values required to demonstrate significance.

The F-value comparing clones in 1978 was only slightly smaller than in 1979 (Table 7). There was also less significance due to regression. The mean square error (MSE) obtained in 1978 was larger than in 1979 indicating a greater variability in the data. The LSD test for 1978 data was similar to 1977. Fewer significant differences were observed between clones 58, 63, 65 and other clones (Table 8).

In 1980 cone production increased and the cone beetle attack rate decreased dramatically (Table 4). Many individual trees had no cones

Table 6. Least significant difference t-test for adjusted mean cone beetle attack rate by clone for 1977.

Clone #	17	19	20	21	22	24	25	37	45	58	63	65	69	86	150	157	103
17																	
19	**																
20	**																
21	**																
22	**	**	*														
24		**	**	**													
25																	
37		**	**	**	**												
45	**	*	*				*	**									
58		*	*	*													
63		*	*														
65	**					**	*	**	*	**							
69		*	*								*						
86	**				*	**	*	**	*	*		**					
103												*				*	
150																	
157																	

Significant at: *alpha = .05, **alpha = .01.

Table 7. Analysis of covariance comparing mean number of cone beetle attacks by clone for 1978.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Equality of Adj. Cell Means	16	4,777.44	261.09	5.07**
Zero Slope	1	95,626.94	95,626.94	1,858.05
Error	565	29,078.39	51.47	

**Significant at alpha = .01.

attacked in 1980 (Tables 1, 2 and 3). The changes in cone production and attack rate had several effects (Tables 9 and 10). First the F-value was reduced, but still significant at alpha = .01. Secondly the variability in attack rate was reduced as observed in the smaller MSE. Finally the significance due to regression was reduced.

The significance of difference in the cone beetle attack rate was influenced almost entirely by clone 17 (Table 10). Clone 17 was attacked at the highest level of any clone in 1980, with slightly more than 1 percent of its cones attacked (Table 2). The only other significant difference was between clones 19 and 24.

During 1981 cone production dropped to the lowest level observed during the study, but the attack level increased over 1980 (Table 4). The decrease in cone production and increase in attack rate resulted in a larger significance due to regression and a larger MSE. The F-value for significant difference in the cone beetle attack level was only slightly increased over 1981 (Table 11). Again it was clone 17 that most influenced the significant difference in attack rate

Table 8. Least significant difference t-test matrix for adjusted mean cone beetle attacks by clone for 1978.

Clone #	17	19	20	21	22	24	25	37	45	58	63	65	59	86	150	157	103
17																	
19	**																
20	**																
21	**	*															
22	**																
24		**	**	**	**												
25																	
37		*	**	**	*												
45	**	**			*	**	*	**									
58									**								
63																	
65																	
69				*				**									
86	**	**	*		**	**	**	**		**		*	**				
103				*					*					**			
150																	
157																	

Significant at: *alpha = .05, **alpha = .01.

Table 9. Analysis of covariance comparing mean number of cone beetle attacks by clone for 1980.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Equality of Adj. Cell Means	16	67.74	4.23	2.13**
Zero Slope	1	20.52	20.52	10.36
Error	501	992.53	1.98	

**Significant at alpha = .01.

(Table 12). Clone 103 also differed significantly from most other clones, but the calculations are based on only 10 trees for clone 103 in 1981 (Table 3). Clones 157 (Table 3) and 150 (Table 2) did not produce cones in 1981. The degrees of freedom for equality of cell means were reduced by two (Table 11) and clones 150 and 157 were omitted from the LSD test (Table 12).

A summary of significant differences in the cone beetle attack rate by clone as obtained in LSD tests is shown in Table 13. Differences existed in the number of cone beetle attacks every year, and certain clones (e.g., 17) differed from most other clones in nearly every year. Clones 24, 45 and 86 also showed consistent differences in attack rate. Clones 150 and 157 did not differ from other clones in any year, presumably due to fewer sample trees measured in these clones.

Data for clones within the various cone color classes were summed and mean beetle attack comparisons made using ANCOV. In all cases the degrees of freedom for adjusted cell means were reduced because only three groups (green, intermediate and purple) were compared (Tables 14, 16, 18 and 19).

Table 10. Least significant difference t-test matrix for adjusted means cone beetle attack rate by clone for 1980.

Clone #	17	19	20	21	22	24	25	37	45	58	63	65	59	86	150	157	103
17																	
19	**																
20	**																
21	*																
22	**																
24		*															
25	*																
37	**																
45	**																
58	*																
63																	
65																	
69	*																
86	*																
103																	
150																	
157																	

Significant at: *alpha = .05, **alpha = .01.

Table 11. Analysis of covariance comparing mean number of cone beetle attacks by clone for 1981.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Equality of Adj. Cell Means	14	301.42	21.53	2.32**
Zero Slope	1	134.07	134.07	14.44
Error	221	2,050.88	9.28	

**Significant at alpha = .01.

In 1977 the F-value obtained in ANCOV was highly significant indicating differences in attack rate between cone color classes (Table 14). There is also a large significance due to regression. The LSD test showed that there were differences in cone beetle attack rate between all cone color classes (Table 15). The greatest difference in the number of beetle-attacked cones during 1977 was between intermediate and green-colored cones.

During 1978 results compared closely with those obtained in 1977 (Table 16). F-values for mean comparisons and regression analysis were both reduced slightly, but still very significant. The reduction in values resulted from a lower rate of cone beetle attack in 1978 than in 1977 (Table 4). In 1978 the variability in cone beetle attack rate increased as seen in the MSE (Table 16).

The LSD test in 1978 yielded results similar to 1977 with differences in number of beetle attacks existing between all cone color classes. Again the intermediate-colored cones were attacked most and

Table 12. Least significant difference t-test matrix for adjusted mean cone beetle attack rate for clones for 1981.

Clone #	17	19	20	21	22	24	25	37	45	58	63	65	69	86	103
17															
19	**														
20	**														
21	**														
22	**														
24	**														
25	**														
37	**														
45	**														
58	**					*									
63	*														
65	*														
69	**														
86	*														
103	8	**	**	**	**	*	**	**	**	**	*	*	**	*	

Significant at: *alpha = .05, **alpha = .01.

Table 13. Summary of least significant difference t-tests for clones for 1977-1981.¹

Clone #	17	19	20	21	22	24	25	37	45	58	63	65	69	86	150	157	103
17																	
19	****																
20	****																
21	****	*															
22	****	*	*														
24	*	****	**	*													
25	**																
37	**	**	**	**	**												
45	****	**	*		*	**	*	**									
58	**	*	*	*													
63	*	*	*														
65	**		*			*	*	*	*	*							
69	**	*		*					*		*						
86	****	*	*		**	**	**	**	*	**		**	*				
103	*	*	*	**	*	*	*	*	**	*	*	**	*	***			
150																	
157																	

¹Number of years that significant differences in cone beetle attack rate existed between clones is indicated by number of asterisks.

Table 14. Analysis of covariance comparing mean number of cone beetle attacks by color for 1977.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Equality of Adj. Cell Means	2	2,073.37	1,036.69	25.43**
Zero Slope	1	137,712.91	137,712.90	3,378.73
Error	573	23,355.48	40.76	

**Significant at alpha = .01.

Table 15. Least significant difference t-test matrix for adjusted mean number of cone beetle attacks by color for 1977.

	Green	Interm.	Purple
Green	.00		
Interm.	7.13**	.00	
Purple	3.12*	-4.29*	.00

*Significant at alpha = .05.

**Significant at alpha = .01.

Table 16. Analysis of covariance comparing mean number of cone beetle attacks by color for 1978.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Equality of Adj. Cell Means	2	2,519.28	1,259.64	22.80**
Zero Slope	1	145,000.86	145,000.86	2,624.36
Error	565	31,216.25	55.25	

**Significant at alpha = .01.

Table 17. Least significant difference t-test matrix for adjusted mean number of cone beetle attacks by color for 1978.

	Green	Interm.	Purple
Green	.00		
Interm.	6.67**	.00	
Purple	3.89*	-3.46*	.00

*Significant at alpha = .01.

**Significant at alpha = .05.

Table 18. Analysis of covariance comparing mean number of cone beetle attacks by color for 1980.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Equality of Adj. Cell Means	2	11.76	5.88	2.90
Zero Slope	1	40.12	40.12	19.82
Error	501	1,012.02	2.02	

Not significant at alpha = .05.

Table 19. Analysis of covariance comparing mean number of cone beetle attacks by color for 1981.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Equality of Adj. Cell Means	2	45.74	22.87	2.86
Zero Slope	1	278.11	278.11	34.85
Error	221	1,765.79	7.99	

Not significant at alpha = .05.

green-colored cones suffered the fewest number of beetle attacks. A slight increase in the difference in beetle attack rate between purple and green cone color classes occurred during 1978 as compared to 1977 (Table 17). There was a slight reduction in the beetle attack rate differences between the intermediate and purple-colored cone classes from 1977 to 1978.

In 1980 and 1981 the level of beetle attack was greatly reduced (Table 4). This resulted in F-values that were insignificant for mean attacks between cone color classes. The variability in attack level was reduced as seen in the smaller MSE values obtained. Significant F-values due to regression were obtained in both 1980 and 1981 (Tables 18 and 19). LSD tests were not run for 1980 or 1981 because of the insignificant F-values obtained.

A summary of F-values obtained in this study are shown in Table 20. The values obtained indicated strong similarities in the level of beetle attack during 1977 and 1978. Differences in beetle attack rate obtained between clones and cone color classes were similar. The MSE values were consistent indicating similar variability in the data during the 2 years.

Similarities were also evident in data from 1980 and 1981. F-values for clonal differences in cone beetle attack rate were much the same, and uniformly lower, than the preceding 2 years. There was no significant difference in beetle attacks by cone color classes in 1980 or 1981. The variability in attack levels was reduced in 1980 and 1981 being slightly higher in 1981. The decrease in variability resulted from the increase in cone production and decrease in number

Table 20. F-values and level of significance for differences in beetle attack rate by clone and cone color for each year.¹

1977		1978		1980		1981	
Clone	Color	Clone	Color	Clone	Color	Clone	Color
5.11**	25.43**	5.07**	22.80**	2.14**	N.S.	2.32**	N.S.

¹1979 omitted due to poor cone crop.

**Significant at alpha = .01.

N.S. = Not Significant.

of beetle attacks. A significant amount of the variability in the level of attack was explained by variability in cone production as seen in significant F-values obtained for regression each year.

Olfactometer Experiments

The objective of this portion of the study was to determine if cone beetles were affected by volatile substances in the oleoresin of western white pine. Cone beetle responses to foliage and cones of different colors were tested in a series of six experiments (Tables 21-26). The olfactometer as pictured in Figure 3 was used in the experiments. In each experiment, contingency table analysis was used to test for independence of response between male and female beetles. The independence chi square value obtained is listed below each table. Differences in the total number of beetles responding to particular substances in a given experiment were tested using the multinomial distribution. The goodness of fit chi square thus obtained is listed below each table.

Beetle responses to an air stream containing odors of crushed cones were tested against an odor-free air stream in Experiment 1 (Table 21). The goodness of fit chi square obtained was significant, indicating a significant response of beetles to the volatile substances emanating from macerated cones. In Experiment 1, cone color was not considered. The independence chi square indicated no significant difference in response between males and females.

In Experiment 2 all three sample receptacles were utilized. The response of beetles to macerated cones, macerated foliage and to an

Table 21. Responses of beetles to macerated cone versus an odor-free air stream was tested in Experiment 1.

	Male	Female	Total
Cone	17	8	25
Air Only	2	3	5

Independence $\chi^2 = 1.42$

H_0 : Cone = Air $\chi^2 = 13.34^{**}$

****Significant at alpha = .01.**

Table 22. Responses of beetles to macerated cones versus macerated foliage versus an odor-free air stream were tested in Experiment 2.

	Male	Female	Total
Cone	19	20	39
Foliage	8	17	25
Air	5	6	11

Independence $\chi^2 = 1.79$

H_0 : Cone = Foliage = Air $\chi^2 = 15.68^{**}$

****Significant at alpha = .01.**

Table 23. Response of beetles to macerated green cones versus macerated purple cones versus an odor-free air stream was tested in Experiment 3. Beetles responding to cones of either color were combined prior to sexing.

	Male	Female	Total
Green			21
	22	30	
Purple			31
Air	4	6	10
Independence $\chi^2 = 0.018$			
H ₀ : Green = Purple = Air $\chi^2 = 10.68^{**}$			

**Significant at alpha = .01.

Table 24. Experiment 4 was a replication of Experiment 3 above.

	Male	Female	Total
Green			38
	32	43	
Purple			37
Air	4	2	6
Independence $\chi^2 = 1.28$			
H ₀ : Green = Purple = Air $\chi^2 = 24.51^{**}$			

**Significant at alpha = .01.

Table 25. Response of beetles to green cones containing feeding male beetles versus purple cones containing feeding males versus an odor-free air stream was tested in Experiment 5.

	Male	Female	Total
Male/Green			6
	9	4	
Male/Purple			7
Air	1	0	1
Independence $\chi^2 = 0.44$			
H ₀ : Green = Purple = Air		$\chi^2 = 4.42$	

Table 26. Response of beetles to green cones containing feeding female beetles versus purple cones containing feeding female versus an odor-free air stream was tested in Experiment 6.

	Male	Female	Total
Female/Green			6
	6	8	
Female/Purple			8
Air	1	1	2
Independence $\chi^2 = 0.036$			
H ₀ : Green = Purple = Air		$\chi^2 = 3.5$	

odor-free air stream were tested (Table 22). A significant goodness of fit chi square was obtained. The significance resulted from a greater response to cone odor and a lesser response to the odor-free air stream than was expected by chance alone. The response of beetles to macerated foliage did not differ significantly from values expected by chance alone. No significant difference existed between males and females, as shown by the low independence chi square value.

Beetle responses to odors emanating from macerated purple cones, green cones and an odor-free air stream were tested in Experiment 3 (Table 23). Cones of intermediate color were not available for any of the olfactometer experiments. The goodness of fit chi square obtained was significant. The bulk of contribution to the chi square came from greater response to purple cones and lesser response to the odor-free air stream.

Beetles responding to purple and to green cones were combined prior to sexing and no distinction was made between sexes responding to purple versus green cones. The independence chi square obtained in evaluating response based on sex was insignificant.

The same experimental conditions tested in Experiment 3 were used in Experiment 4 (Table 24). The goodness of fit chi square was significant. The difference resulted from greater response to cone odor than to the odor-free air stream. There was no significant difference in response to green or purple cones. Difference in response based on sex was not significant.

Experiments 5 and 6 were conducted to determine if cone odors were altered by feeding beetles, sufficiently to affect the response of the beetles being tested. In Experiment 5, male beetles were allowed

to feed for 24 hours in purple and green cones at the same time. The cones containing the feeding beetles were then placed in sample receptacles and tested as before against an odor-free air stream. The conditions were repeated in Experiment 6 using cones containing feeding, female beetles. Neither the results from Experiment 5 (Table 25) nor those from Experiment 6 (Table 26) were significant regarding response to olfactory stimuli or differences based on sex. Experiments 5 and 6 were both hindered by too few beetles available for testing.

Laboratory Dissections

Laboratory dissections were performed to meet two objectives. The first was to see if the number of beetles that completed development in infested cones differed between cone color classes. The second was to determine if the survival of brood beetles differed with cone color. Laboratory dissections of infested cones were done during late summer after beetle development was complete.

The results of the dissections are shown in Table 27. Analysis of variance (ANOV) was conducted to evaluate differences in mean number of beetles completing development or in mean number of beetles surviving. The F-value obtained for number of beetles is not significant (Table 28). This indicated no difference existed in number of beetles that completed the life cycle in different colored cones.

The F-value obtained evaluating beetle survival is also not significant (Table 29). There appeared to be no difference in the

Table 27. Results of laboratory dissections showing numbers of brood beetles and number surviving in cones and different colors.

	Green		Intermediate		Purple	
	# beetles	# alive	# beetles	# alive	# beetles	# alive
	173	82	115	76	105	10
	14	0	38	12	81	11
	62	21	64	27	115	79
	33	4	80	19	43	12
	21	6	32	18	47	34
	30	10	168	79	65	38
	31	3	147	43	85	25
	110	77	23	13	91	71
	111	71	41	11	155	52
	152	93	103	41	91	21
Sum	734	367	811	339	878	353
$\bar{X}/10$ cones	73.4	36.7	81.1	33.9	87.8	35.3
S	28.3	13.4	24.8	12.8	28.3	13.0
\bar{X}/Cone	7.34	3.67	8.11	3.39	8.8	3.53

Table 28. Analysis of variance comparing mean number of brood adults dissected from cones of different colors.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Cone Color	2	1,038.50	519.25	0.22
Error	27	63,820.90	2,363.74	
Total	29	64,859.40		

Table 29. Analysis of variance comparing number of living brood adults dissected from cones of different colors.

Source of variance	D.F.	Sum of sq.	Mean sq.	F-value
Cone Color	2	1,019.80	509.90	0.55
Error	27	24,935.10	923.50	
Total	29	23,915.30		

Note: F-values obtained from lab dissections are not significant.

number of eggs laid, or in larval or pupal development, as indicated by the number of beetles reaching the adult stage. The survival rate of adult cone beetles was also unaffected by the color of cone in which development occurred.

DISCUSSION

Field Measurements

The level of attack by the mountain pine cone beetle was shown to differ significantly between clones of western white pine. This indicated a genetic influence associated with host selection and oviposition by the cone beetle. Certain clones (e.g. 17, 19, 24 and 25) were attacked at a consistently higher rate than others (e.g. 20, 21 and 58). Hoff (1978), studying western white pine in the Sandpoint Seed Orchard, was first to suggest a genetic influence related to beetle attack.

Genetic variability in western white pine has been well studied and it is interesting to speculate how this variability may affect preferential attack by the mountain pine cone beetle. Bingham and Squillace (1957) found that a combination of microsite and heredity caused certain individuals to be either early or late in flowering. It is possible that those trees initiating growth and cone elongation early in spring become attractive to beetles earlier in the season and are thus attacked sooner and at a higher rate.

In addition to phenological variability, morphological factors may be involved. Characteristics such as branch angle, needle length, cone scale width (Barnes 1967) and the amount of foliage (Squillace and Bingham 1953) have all been shown to be under genetic control. If the primary attraction of cone beetles involves visual cues, morphological factors such as these may affect differences in attack. Squillace and

Bingham (1958) also noted elevational differences in growth rate in western white pine. Clones selected from lower elevations may be expected to grow faster, reaching a position of dominance prior to other clones. Henson (1962) found that dominant trees are more likely to be attacked by the white pine cone beetle.

Biochemical variability in monoterpene levels in oleoresin varies significantly between clones (Hanover 1966a, 1966c, 1971). Hanover (1966b) found this variability to be under strong genetic control and to be independent of site or climate. Primary host attraction in cone beetles may likely involve olfactory cues resulting from volatile terpenes. This has been shown to be the case with other scolytids, including D. pseudotsugae (Rudinski 1962). Clonal variability in terpenes may offer a likely explanation for the differences observed in beetle attack levels between clones.

Clonal lines in the seed orchard were derived from parent trees in natural stands located throughout northern Idaho. Representatives of these clones will display the same variability in phenological, morphological, physiological and biochemical factors as the parent trees. Some combination of one or more of these factors caused preferential attack by the mountain pine cone beetle. Further study would be required to identify the factor(s) of greatest importance.

Cone color in western white pine is another factor shown to be under genetic control (Steinhoff 1974). This study has shown that cone color also affects cone beetle attack levels. Cones of the intermediate and purple colors were attacked at higher levels than green colored cones during 1977 and 1978. In 1980 and 1981 no difference in attack rate by cone color existed. It may be, however, that the

clonal effect is most important. The clones comprising the cone color classes may be the actual source of preferential attack.

However, cone color could play a role when considered in relation to what is known about the cone beetle attack sequence. Cone color can be involved in primary host orientation, and may precede orientation based on volatile terpenes, or other genetically determined factors. Henson (1962, 1964a) found that cone beetles fly when the temperature is high, during mid-day, orienting to a point source of light. They then fly horizontally, landing on any dark object. This puts beetles on exposed branches of dominant trees. Trees having dense, luxuriant foliage are more heavily infested (Dale and Schenk 1979). Cone color may have a bearing on host orientation of this type. Long range host orientation may involve a silhouette perception of a dark form against a light sky. Dark cones (purple or intermediate) would be most visible against blue-green foliage or a blue sky. This hypothesis is supported by the fact that more attacks occur on exposed branches of dominant trees. Attacks are also greater in open stands (Barnes et al. 1964, Schenk and Goyer 1967, Dale and Schenk 1979) where silhouette perception is maximized.

Temperature may also be a factor influencing the cone color effect. Henson (1962) found that cone beetles fly to regions of higher temperature. Sturgeon and Mitton (1980), studying Abies concolor (Gord. and Glend.) Lindl., found that dark cones attain higher internal temperatures. The higher temperatures attained by purple or intermediate cones of western white pine could influence cone beetle attack. This effect would be greatest at close range and involved in secondary host orientation. The silhouette reaction would bring cone beetles close to darker

cones and the higher temperature perceived would further affect beetle oviposition behavior.

The present dissertation study indicated that dark cone color increased the likelihood of a cone being attacked. However, possible negative effects of dark cone color cannot be overlooked. Higher temperatures attract cone beetles, but severe temperatures are disadvantageous. Bedard (1966) studied C. lambertiana and reported that internal cone temperatures greater than 48°C were lethal. Maximum air temperature in Sandpoint, Idaho can reach 40°C, positively influencing adult beetle oviposition behavior. But air temperatures of 40°C would probably result in internal cone temperatures greater than the upper lethal limit. This would adversely affect brood development and result in increased mortality. Bedard (1966) found that convection cooled cones sufficiently to reduce brood mortality. Based on this information, dark colored cones on the lower branches of the south-facing side of the tree are least likely to be attacked and would suffer the greatest brood mortality. Cones on exposed branches in the upper crown are most likely to be attacked. Air circulation is also greatest in the upper crown and convective cooling is most efficient. Therefore, brood development is enhanced in cones on exposed branches of dominant trees. The possible selective advantage to beetles ovipositing in the larger trees on exposed branches is apparent. Results of this study indicated that the attractive effect of dark cone color outweighs any possible negative influence on brood development. Dark cones were attacked more frequently and brood survival was not reduced.

Further study to determine the exact role, if any, of cone color to attacks by the mountain pine cone beetle are needed. Laboratory

studies using colors as attractants would be useful in separating the visual and olfactory cues, and in determining the exact sequence of stimuli causing cone beetle attacks. Some ovipositing adults may attack up to four cones (Morgan and Mailu 1976). Knowledge of how feeding and prior oviposition affect host orientation in subsequent attacks would be of interest.

Painter (1958) developed terms useful in describing the effects of genetic variability on plant resistance to insects. He hypothesized three mechanisms: 1) preference or non-preference, 2) antibiosis, and 3) tolerance. Attack by the mountain pine cone beetle on cones of western white appears to be an example of preference or non-preference. The interaction of several host genetic factors, including cone color, appear to be involved. Also involved are several site and climatic factors including elevation, stand density, aspect, maximum temperatures, and air currents.

The variability in pine cone production is an extremely important factor regulating cone beetle population densities. It plays an important role in cone beetle behavior. In this study considerable variation in cone production occurred from year to year, from tree to tree, and between the various clones (Tables 1-4). Eis (1976) also reported wide annual variations in western white pine cone crop size. He concluded that weather, most importantly water deficit, was the primary factor involved. Rehfeldt et al. (1971) also associated water stress with western white pine cone production variations. They found that cone production in western white pine followed cycles of approximately 4 years. In this study some cones were produced each year. This is in line with the study by Franklin et al. (1974) of several

western conifers. In their study western white pine was the most consistent cone producer with total crop failure being rare. Puritch (1972) suggested that cone crop periodicity was due to interactions of tree metabolism, climate, and biotic agents, including squirrels and insects. This study demonstrated that host genotype also plays an important role in cone production in western white pine. Differences in cone production by clone are evident in Tables 1-3. Certain clones (e.g. 19, 69 and 150) produced consistently more cones than others. The effects of variation in cone production on the level of the cone beetle population are evident in Figure 4. Cone production and beetle attack are erratic (Barnes et al. 1964), but large crops typically suffer lower percentage losses to seed and cone insects (Schenk and Goyer 1967). As seen in Figure 4, damage is greatest when small crops follow large ones because cone beetle numbers build up when food is abundant. During years when small crops are produced competition and lack of food causes high mortality and few new beetles are produced. This situation has been reported previously for eastern white pine (Henson 1961a, 1964b; Morgan and Mailu 1976), red pine (Mattson 1971, 1978), pinyon pine (Forcella 1980) and western white pine (Hoff 1978). The phenomenon indicates coevolution of seed and cone insects and conifer cone production. Feeding by seed and cone insects could have resulted in the aperiodic nature of cone production.

Numerous infested cones were collected in the orchard in the fall of 1978. These cones were used as a source of beetles for laboratory testing. Removal of the cones helped reduce the beetle population and decrease cone losses. The cones were removed prior to the small crop

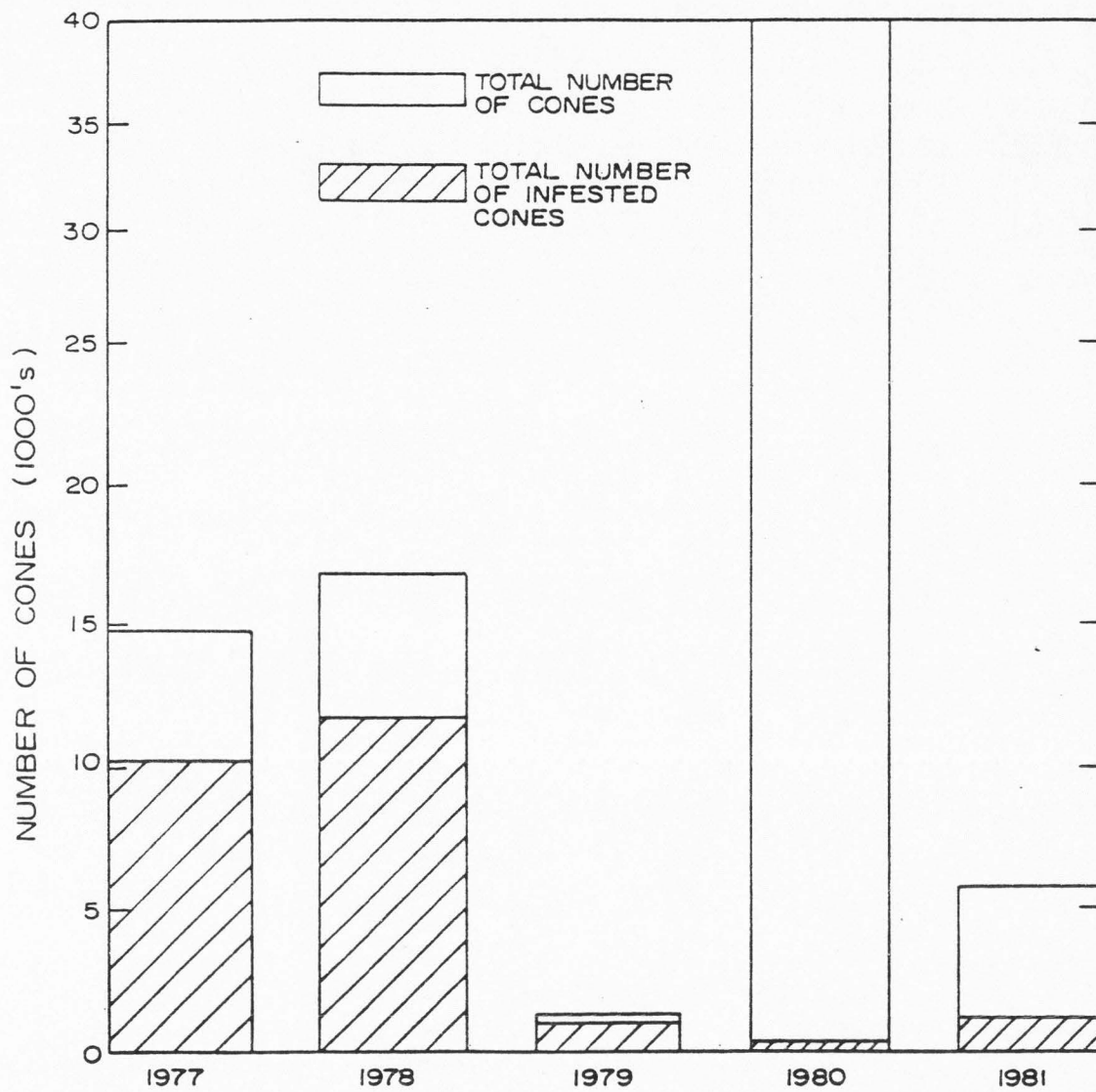


Figure 4. The relationship between cone production in western white pine and attacks by the mountain pine cone beetle in the Sandpoint Seed Orchard, Idaho.

during 1979 and the reduction in beetle population had little effect on the results of this study.

The hypothesized preferential attack behavior of cone beetles is expected to occur only when cones are abundant. In years when cone production is low, and beetle numbers are high, host preference is overridden by food shortage, and the majority of cones are utilized by cone insects. This was the case in 1979 when nearly the entire crop was destroyed. In the 2 years when cones were abundant and beetle numbers were high, the greatest amount of preferential attack was observed. In 1977 and 1978 the most significant differences in attack rate between clones and cone color classes occurred (Table 19). A bumper crop was produced in 1980. One would expect preferential attack to be most dramatic in such a year since food and oviposition sites were essentially unlimited. This, however, was not the case in 1980 or in 1981 due to the low populations produced in 1979. In both years clonal attack rate differences were reduced, and cone color class attack rate differences were not significant.

At least two factors may be of importance in the results obtained during 1980 and 1981. The first is the reduction in the number of beetles in both years, and the sampling of fewer trees in 1981. The second factor relates to the opportunistic attack behavior of cone beetles. Cone beetles normally fly only as far as is necessary to find a suitable host. Therefore the location of the brood cone from which beetles emerged affected the cones they will attack. In natural stands this phenomenon was observed repeatedly. Trees producing heavy, yearly cone crops harbor a population of cone beetles attacking cones of the same tree, generation after generation. Migration away from trees of

this type occurred only when the tree did not produce sufficient cones. A situation such as this may have affected 1980 and 1981 results. Genetic preference to cone beetle attack likely occurs. But trees producing annual cone crops will be attacked more consistently, regardless of other genetic factors affecting cone beetle attacks.

The importance of long term studies involving seed and cone insects is apparent. The cycling of the cone beetle population related to pine cone production is an important consideration. The duration of the field measurements portion of this study strengthens the validity of its results. Observations and analyses of attack rates, and behavior were made for 5 years under varying levels of cone beetle numbers and of cone production.

Olfactometer Studies

The response of walking beetles to olfactory stimuli is a complex process, involving central nervous system integration of multiple inputs (Kennedy 1978). One must be aware of the limitations, and of the possible ambiguities that may result from describing behavior in nature based on laboratory olfactometer studies. Such studies may not distinguish various responses or may elicit responses that would not be observed in nature.

In this study cone beetles responded to cone odor in a moving air stream. No significant response to air alone was observed. The possibility of anemotaxis was further eliminated by alternating receptacle positions. Other studies have substantiated the fact that anemotaxis in scolytids does not occur. These studies include those by Wood and Bushing (1963) with Ips confusus, Jantz and Rudinski (1965)

with Dendroctonus pseudotsugae and Francia and Graham (1967) with Trypodendron lineatum.

Greater response was elicited from cone odor than from odor emanating from crushed foliage. This indicates that cone odor is a host attracting factor operating at close range. Once the suitable host tree is located, cone odor may be important in helping the cone beetle locate the appropriate attack site. Locating the attack site may also be facilitated by geotropic and chemotropic responses. Positive responses to odors support the hypothesis that volatile monoterpenes are involved in host orientation. It may be that differences in monoterpenes between clones are important factors in beetle attacks related to host genotype.

Flight does not appear to be a prerequisite to olfactory response. Beetles responded positively to olfactory stimuli having never flown. Graham (1959) and Francia and Graham (1967) found that flight altered responses to odor and light. It appeared that flight exercise was necessary to release Trypodendron beetles from photopositive domination. Kinzer et al. (1972) studied C. ponderosae and found that flight was not required for positive host attraction to occur.

There was no difference in response to odors emanating from cones of different colors. There may be no differences in the terpenes correlated with different colored cones. Certainly there is a difference in pigment content, but pigments do not appear to play a role in beetle olfactory attraction. Further study into the differences on monoterpenes present in cones of different colors would be of interest. Cone color appears to be involved only as a visual stimulus.

Differences in beetle attack rate between clones probably resulted from variation in monoterpenes that are not reflected in cone color classes.

The results of this study do not indicate significant, positive response differences between cone beetle sexes to cone odors. There was insufficient evidence to indicate whether pheromones are involved in attraction to attack sites. Results of this study agree with those of Henson (1961b), in which no attraction was found between Conophthorus sexes in olfactometer studies. Henson found sexual differences regarding aggregation, with greater thigmotropism occurring among females during or following dispersal.

Researchers, working with other genera of scolytids, have found significant differences existing between sexes in their response to odors. Rudinski (1962) found a different response sequence occurring between male and female D. pseudotsugae. Sex specific responses were also reported by Wood and Bushing (1963) in Ips beetles with fewer males responding to olfactory stimuli.

Kinzer et al. (1972) found significant attraction of male Conophthorus to feeding females. From their study they suggested that females make the initial attack and pheromones are emitted which attract males. In a previous study, however, Kinzer et al. (1970) had found that mating occurred prior to attack, and prior to feeding. Schaeffer (1964) also described mating occurring prior to emergence from overwintering sites in Conophthorus. Pheromone production is likely involved, but there is still the question of how the attacking female orients to the host. From their studies Kinzer et al. (1970) hypothesized that primary host attraction is by females to host odor, and males are secondarily attracted by the odors emanating from the feeding

female. This hypothesis is consistent with their observations of the female initiating attack, but is not consistent with results of this study. Stimuli other than pheromones may, however, be involved in beetle communication between sexes (e.g. stridulation). If females are the sex responsible for primary host orientation one would expect significantly greater response by females to odors used in the olfactometer studies. This, however, was not the case. In no olfactometer experiment was there a significant difference in response between sexes to a particular odor. There were several uncontrolled factors which may have affected responses of beetle sexes in the laboratory. These included the insect's physiological condition, especially whether it had fed or mated. It is also possible that odors were too concentrated under the conditions of olfactometer testing. Further testing is required before definitive conclusions related to the occurrence and function of pheromones can be made.

In all olfactometer experiments many beetles failed to respond to stimuli. These insects were eliminated from analysis. This is not an unusual situation and other researchers have reported similar findings. Henson (1961b, 1962) reported 5-50 percent of his Conophthorus beetles had to be eliminated before aggregation tests. Strong thigmotropism displayed before dispersal may have caused the beetles to remain in contact groups, and they were not in the proper physiological condition to respond. Schaeffer (1964) studied Conophthorus and concluded that increased respiration occurring in insects held in room light led to exhaustion, and non response. Kinzer et al. (1972) had only a 50 percent response of Conophthorus beetles in their tests. They concluded physiological differences were the cause. Similar levels of non response

were reported by Wood and Bushing (1963) and Seybert and Gara (1970) studying Ips.

Dissections

From counts made of adult beetles in attacked cones of different colors it was concluded that no difference existed in life cycles or survival in cones of different colors. Once a cone was attacked development of egg, larval, pupal and adult stages proceeded unaffected by cone color. Using counts of adults to determine if mortality to immatures occurred is justified based on previous work by Morgan and Mailu (1976). They found only small mortality of immature stages of Conophthorus within cones while making life table studies. An excellent opportunity for further study in this area would be to subject developing broods to varying temperature regimes to assess temperature effects on brood development in cones of different colors. This work could be done in the laboratory and in the field. In the field, attacks could be induced on cones of different colors and different crown locations. Temperature and brood development measurements could be made and evaluated. Similar studies could be conducted in the laboratory subjecting attacked cones to varying temperatures.

Results of laboratory dissections reduced the possibility that antibiosis or tolerance mechanisms of plant resistance were in operation.

CONCLUSIONS

Results of this study demonstrate that host selection and attack by the mountain pine cone beetle does not occur at random, but is influenced by host tree genotype and/or cone color.

The influence of the genotype is evident by observing that certain clones are consistently attacked at a higher rate than other clones. Host factors of importance in preferential attack by cone beetles include volatile terpenes, growth rate, and amount of foliage. Various site and climatic factors are also involved. The variation in attack rate among clones comprising cone color groups may have affected differences in attack rate observed between cone color groups.

Cone color may be of importance when considered in relation to what is known about cone beetle emergence and attack sequence. Previous research has indicated that initial host selection is based on perception of a silhouette formed by the host tree against a light sky. Cone beetles orient to the terminal portion of exposed branches in the upper crown (Henson 1962). If this is the initial long range mechanism of host orientation then dark cone color may accent this response. Dark cones were shown to be attacked at a higher rate than light colored cones.

Variability in the numbers of cones produced in an area is the most important factor regulating cone beetle population size. Results of this study showed that host preference is also affected by the number of cones available for attack in a given year. In years when

abundant cones are available and beetle populations are high host preference is most marked.

Initial cone beetle flight is into the wind. As proximity to the host increases olfactory stimuli become increasingly important. Results from olfactometer studies showed the existence of host emanated olfactory stimuli affecting beetle response at close range. Olfactory cues must be of importance in separation of host silhouettes from those of other conifers. When the cone beetle has landed on a suitable host, olfactory stimuli combined with geotropic and chemotactic cues are probably used to locate the attack site on the developing cone.

Once the cone has been attacked oviposition and brood development proceeded uninfluenced by host genotype or cone color. The results do not demonstrate the existence of physiological genetic resistance in western white pine to attacks by the mountain pine cone beetle. The mechanism involved appears to be one of host preference.

Further studies should be aimed at determining the particular set of host factors responsible for preferential attack by cone beetles. Laboratory analysis revealing the presence and functioning of pheromones and their effect on beetle behavior would be of great value. Flight studies further elucidating cone beetle emergence and attack behavior are also suggested.

The importance of basic research in forest entomology lies in its application to management systems. Results of this study must be evaluated and incorporated into existing and planned rust resistant western white pine seed orchard management plans.

It is not recommended that selection of orchard trees be based on the genetic preference displayed by cone beetles in their attack

behavior. Rust resistance is the primary criterion for selection. In addition cone production and general growth characteristics must also be considered. Where possible, however, genotypes showing excessive predisposition to cone beetle attack should be avoided. Likewise those showing resistance to beetle attack and meeting other criteria should definitely be used.

The proposed mechanism of cone beetle host orientation involving visual silhouette perception places the orchard manager in a dilemma. Wide spacing in orchards is advantageous to increased cone production and efficient cone collection. This study indicates that wide spacing increases the likelihood of cone beetle attack.

The relationship between cone production and cone beetle attack levels is of considerable importance. The orchard manager must consistently monitor cone beetle population size and pine cone production. The 2 year cycle of cone production in pines allows prediction of problems well in advance. Decisions can be made regarding the necessity of direct control measures, realizing that the best natural control is a cone crop failure.

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