INVESTIGATION OF HOST SELECTION BY MOUNTAIN PINE BEETLE
(DENDROCTONUS PONDEROSAE) HOPK. IN LODGEPOLE PINE
(PINUS CONTORTA) DOUGL.

by

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In 1983 the United States Forest Service agreed to support a Research Assistantship under the direction of Dr. Michael J. Jenkins. This project was designated to study the relationship between the mountain pine beetle (Dendroctonus ponderosae Hopk.) and lodgepole pine (Pinus contorta Dougl.). The work contained in this thesis is a result of this project.

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Thomas James Eager
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Investigation of Host Selection by Mountain Pine Beetle
(Dendroctonus ponderosae) Hopk. in Lodgepole Pine
(Pinus contorta) Dougl.

by
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Utah State University, 1986

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Department: Forest Resources

Lodgepole pines Pinus contorta (Douglas) were treated by girdling to assess the response by an endemic population of mountain pine beetle Dendroctonus ponderosae (Hopkins) (Coleoptera: Scolytidae). Capture in 'sticky traps' indicated that the beetles were attracted while in flight towards the wounded trees. A significant difference in the landing rates of bark beetles between the treated and untreated trees indicated that the beetles were able to distinguish wounded from non-wounded trees while still in flight. Pressure chamber readings demonstrated that water stress developed in the girdled trees when compared to the non-girdled trees.

(68 pages)
INTRODUCTION

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera:Scolytidae) is one of the most serious insect pests found in the forests of western North America. This native insect species is an integral part of many forest ecosystems including those with high economic and social values.

The geographic range of the mountain pine beetle includes much of the pine forests throughout western Canada, down into the Sierras and Rocky Mountains and south into the Sierra Madre range of northern Mexico (Fig. 1). Recorded hosts of the mountain pine beetle include such native species as *Pinus contorta*, *P. lambertiana*, *P. monticola*, *P. ponderosa* and *P. albicaulis*. Infestations and successful broods have also been reported on secondary hosts such as *P. coulteri*, *P.edulis* and *P.monophylla* (Furniss and Carolin 1977).

The genus *Dendroctonus* (literally "tree-killer") also contains the important pest species southern pine beetle (*Dendroctonus frontalis*), western pine beetle (*D. brevicomis*) and the douglas-fir beetle (*D. pseudotsugae*) which fulfill a similar ecological role in their native ranges. All of the members of this group are considered 'primary' bark beetles, that is they are able to overcome a relatively healthy tree's defense system and kill it. The members of Scolytidae are one of the few groups of insects that are able to bore through a tree's bark in order to
Fig. 1. Distribution of the mountain pine beetle in western North America.
feed upon the energy and nutrient rich interior.

Much of the Rocky Mountain region is currently in the midst of widespread destruction of lodgepole pine stands due to the depredations of unprecedented mountain pine beetle populations.

In this paper I will explore various aspects of mountain pine beetle lodgepole pine interaction, particularly the phenomena known as 'primary attraction'. This will begin with a review of the literature; I will then discuss a field experiment which was conducted to shed light on some aspects of host selection by mountain pine beetle which were unclear.

REVIEW OF THE LITERATURE

The Lodgepole Pine

Lodgepole pine is one of the most important forest trees of western North America. It ranges over an area covering 5.3 million hectares and is a valuable economic resource in many areas. Lodgepole pine is particularly important in the Rocky Mountains due to its dominance of much forest acreage.

Three distinct forms of this species are widely recognized:

- **Pinus contorta** var. *contorta* - Pacific Coast form
- **P. contorta** var. *murrayana* - Sierra-Cascade form
- **P. contorta** var. *latifolia* - Rocky Mountain form

The latter form is found locally and is the form referred to in the remainder of this paper.
The lodgepole pine is described as a medium size tree 20 - 25 m high with an average D.B.H. of 36 - 75 cm at maturity. Its long, clear, cylindrical bole makes it an important timber species. The bark is fairly thin, colored orange-brown to gray and covered by thin, loosely appressed scales. The crown is short, narrow and open consisting of 2.5 - 7.5 cm needles in fasicles of two (Fig. 2).

Lodgepole pine can be a prodigious producer of seed; cones can appear as early as the tree's tenth year. The cones arise from a short stalk (sessile) on the branch and are commonly found in clusters. Heavy cone crops are said to have a periodicity of 2 - 3 years, but in many races the cones remain closed and are retained on the branch for as long as 20 years (Harlow et al. 1979).

Pfister and Daubenmire (1975) characterized four successional roles of Lodgepole pine:

**Minor seral** - A component of young even-aged stands that will be replaced by shade-tolerant associates in 50 to 200 years.

**Dominant seral** - The dominant cover type of even-aged stands having a vigorous understory of shade-tolerant species that will replace the lodgepole pine in 100 to 200 years.

**Persistent** - The dominant cover type of even-aged stands that give little evidence of replacement by shade-tolerant species.

**Climax** - The only tree species capable of growing in a particular environment - self-perpetuating.
Fig. 2. Illustration of lodgepole pine and gallery of mountain pine beetle.
Lodgepole pine attains its best development in moist, but well-drained soils on elevations of 1,500 to 11,500 ft. However, lodgepole pine is particularly noted for its adaptability to a wide variety of sites. In addition, it is a hardy and aggressive species; it is often found at extremely high stocking levels (Harlow et al. 1979) While it is a fast grower at an early stage the overstocked stand soon suffers from stagnation, reducing growth and putting the trees under stress.

To appreciate the role that mountain pine beetle plays in the ecology of lodgepole pine it is important to understand the role that other organisms play in the system. In addition to mountain pine beetle, a great number of other organisms are dependent upon the lodgepole pine.

A variety of mammals feed to varying degrees upon the foliage, inner bark [of stem and roots], and seeds of lodgepole pine. Some of these animals are casual users like the white-tail (Odocoileus virginianus) and mule deer (O. hemionus) who will feed on the needles when hard-pressed during winter. The snow shoe rabbit (Lepus americanus), red squirrel (Tamiasciurus hudsonicus), porcupine (Erethizon dorsatum), pocket gopher (Thomomys spp.) and several species of voles (Microtus spp.) feed so heavily at times they are considered important pests in certain areas (Sullivan 1985).

Mountain pine beetle are the most impressive insect consumers of lodgepole pine, but virtually every life stage
and vegetative structure is host to some form of insect life. However, the vast majority of these insects cause so little damage they are not considered pests.

Several species of sawflies (*Neodiprion* sp.) (Hymenoptera: Diprioidae) periodically have large population outbreaks, at times becoming epidemic. The larvae of sawflies are similar in appearance to caterpillars and defoliate the lodgepole pine. A large epidemic took place during the mid-1970's which covered 92,000 ha near Prince Rupert, Canada. This outbreak caused significant mortality after two years of heavy defoliation (Amman and Safranyik 1985).

Another prominent defoliater of lodgepole pine is the lodgepole pine needle miner (*Coleotechnites milleri*) (Lepidoptera:Gelechiidae). When conditions are favorable this insect can defoliate large areas of trees. However, it is very sensitive to cold winters and weather conditions are infrequently favorable to its development (Strumble 1973).

Several pathogens are prominent in the biology of the lodgepole pine. The most important of these is considered to be the dwarf mistletoe (*Arceuthobium americanum* Nutt. ex. Engel.) (van der Kamp and Hawksworth 1985). Mistletoe is particularly important because thinning stands to increase their vigor and thus better resist attack by bark beetles (Waring and Pitman 1985) can encourage the spread of this pathogen (Baranay 1975).

Lodgepole pine is subject to several stem rusts
throughout its range. All of the pine stem rusts belong to the genus *Cronartium*, in the forests of northern Utah *C. commandra* is an important pathogen. There is much variation in the degree of infection by these rusts because stand conditions and individual tree resistance varies widely (van der Kamp and Hawksworth 1985).

The most common root diseases of lodgepole pine are *Armillaria mellea*, *Polyporus Schweinitzii*, and *Verticicladiella wagnerii*. The incidence of root disease varies widely throughout the range of lodgepole pine. In certain areas (particularly those of lower site quality) occurrence of root disease makes the silviculture of lodgepole difficult if not impossible (Safranyik et al. 1974). It has been demonstrated on several occasions that in some of these areas the incidence of root diseases is intimately tied to the population dynamics of mountain pine beetle (Cobb et al. 1974, Hawksworth 1975, Gara et al. 1985).

Because there are so many organisms utilizing the resources of the living lodgepole pine, the tree has evolved several lines of defense. The first way in which members of the *Larix*, *Pseudotsuga*, *Picea* and *Pinus* genera respond to wounding is an automatic response; when the resin ducts within the phloem are severed, the resin oozes out into the wounded tissue. This is referred to in the literature as the 'preformed system' (Klement and Goodman 1967). This resin acts to physically flush out any pathogens that would try to exploit the exposed tissue.
The resin also contains toxins which chemically acts as an antibiotic which increases the protective power of the resin system.

The second form of an immediate response to wounding is common to all vascular plants. Klement and Goodman (1967) refer to this system as the 'induced response'. This is also known as the 'hypersensitive reaction' which describes the necrotic response of the tree. Like all other vascular plants when wounded, the lodgepole pine begins to consume the starches and carbohydrates that are found in the ray cells in the immediate vicinity of the wound. This 'scorched earth policy' removes the carbohydrates which the invader could feed on (Shrimpton 1984).

The wound response is self-destructive resulting in non-functional plant tissues. As a result of beetle mass attack the hypersensitive reaction can hurt the tree in two ways: first, since tissues become non-functional they cease to be able to assist in the defense of surrounding tissue. Secondly, as the wounds coalesce under the conditions of uniform distribution of attack on the bole (Berryman 1982), the necrotic tissues join and the tree effectively girdles itself (Shrimpton 1984).

If the first two lines of defense are able to withstand the initial wounding, the final defense response comes into play. The process of compartmentalization is a physical and chemical response by which the tree attempts to 'wall off' the wounded tissue (Shigo and Marx 1977).
Before the advent of European culture in the western forests the ecological role of mountain pine beetle is thought to have been as a natural thinning and 'harvesting' agent of lodgepole pine. The action of the beetle in conjunction with various fungal pathogens causes scattered mortality of lodgepole pine throughout the forest. The resulting accumulation of dead wood in the forest creates fuel for lightning ignited fires which periodically sweep through an area (Peterman 1978).

Lodgepole pine cones display varying degrees of serotinny; a fact which reveals the integral role which fire plays in this ecosystem. In addition, fire releases many of the nutrients which would otherwise be tied up in standing wood as well as clearing away competing vegetation. The lodgepole pine seeds newly released from their cones find an almost ideal environment; an open bed cleared of competing plants and high in soil nutrients (Brown 1975).

In nature the fire cycle can last variously from 20 to over 100 years (Arno 1976, Romme 1980). In addition, under certain conditions lodgepole pine forests are converted to mixed species forests and towards various climax communities dominated by alternate species (Lotan et al. 1985).

It is evident that as the lodgepole pine forests are brought under more intensive management that the mountain pine beetle must be the object of major consideration. An understanding of the basic biology and especially the
population dynamics will be essential in the manipulation of lodgepole pine forests.

The Mountain Pine Beetle

The geographic range of the mountain pine beetle coincides very nearly with the overall range of its natural hosts. The exception to this is where climatic conditions are unfavorable to its development.

Life Cycle

In the Rocky Mtns. mountain pine beetle typically produces one generation per year (univoltine). Oviposition occurs in mid-August. The eggs are laid beneath the bark in the margin between the phloem and sapwood. The adult female oviposits each egg within a small niche located on either side of the vertical "egg" gallery which has been constructed by her and her mate.

The small ovoid cream colored eggs are laid in groups on alternating sides of the gallery. The incubation period for mountain pine beetle is fairly short (usually one to two weeks) and the larvae hatch out in late August or early September. The larval form of the beetle is small, white to cream colored and maggot-like (eucephalous) and it soon begins to consume its way through the phloem, creating a distinctive gallery pattern beneath the bark (Fig. 2 and 3). The larvae of the mountain pine beetle have 4 instars, the first two of which occur in early fall. With the onset of winter the larva begins to reduce the amount of water in
Fig. 3. The larval and adult forms of the mountain pine beetle.
its haemolymph and replace it with glycol, a sugary type of antifreeze which allows the insect to withstand the extremely harsh temperature associated with its typical habitat. By the time the first freeze takes place the insect is well into diapause (Amman 1978).

In some of the more marginal areas of the mountain pine beetles range cold can cause large amounts of mortality during the winter months. It is thought that the northern (56° N latitude) and elevational limits (750 m near the northern limit, 3,650 m near the southern limit of 31° N) to its distribution are delimited by temperature conditions (Safranyik 1978).

In the spring, gradually warming temperatures cause an ever increasing amount of activity within the galleries of the mountain pine beetle. The larva begins to feed once more and goes through its final two molts. Between mid-June and mid-July the larva has transformed into the pupal stage of its existence, for the next month the insect will lie within the pupal cell which it has excavated in the bark and sapwood. It is undergoing the metamorphosis that will bring it sexual maturity as well as the adaptations (flight, locomotion and exoskeleton) that allow it to maintain itself in the outer world. The newly emerged adults are a light tan with unsclerotized (unhardened) integument (this stage is called "callow" or "teneral" adult). The young adults remain beneath the bark for a short while, feeding in smaller quantities and undergoing final sexual maturation and development of the flight
Emergence of the beetles is strictly controlled by environmental conditions. Due to the nature of mountain pine beetle host selection and colonization habits, it is vital that as large as possible populations be released simultaneously. This sudden flooding of the forest with adult beetles also serves to overwhelm the numerous predators of mountain pine beetle which have previously been unable to attack it within its cryptic habitat (with notable exceptions). The actual emergence takes place in a spell of warm, dry weather. After one to two days of sunny weather the adult beetles emerge from their galleries through holes bored out through the bark (Amman 1978).

Emergence holes are quite different in appearance than the parents entrance sites; since the tree is dead when emergence finally occurs, there is no pitch associated with the emergence holes and they look like buckshot holes in the bark. If available the young adult will utilize the emergence hole of a sibling, especially at high densities (Amman and Cole 1983). The period of emergence will last for roughly one week to ten days in a given area, the daily peak occurring around 4 P.M. in the afternoon when the temperature has reached at least 16°C (Reid 1962).

Environmental influences appear to have a profound influence on the dispersal flight. As has been noted previously, the timing of emergence and the commencement of dispersal is contingent on the weather, particularly the temperature. Once the dispersal flight is under way
dramatic increases or decreases in temperature can cause the beetle to land and wait for optimal conditions. Humidity also can effect the flight.

Wind patterns can have various effects. Very strong winds can force the beetle downwind, but the general direction of beetle flight is upwind (positive amenotaxis).

Adult mountain pine beetle are a robust, cylindrically shaped insect about 1 to 1.5 cm long. Their coloration ranges from a dark reddish tan to nearly jet black. There are no obvious differences between males and females in appearance, sexing of the insects requires a microscope to examine the last few segments of the abdomen.

During, and for a while following emergence the young adults are positively phototaxic (are attracted to light). After a short resting period on the outer bark of their home tree they take to the wing in the dispersal phase of their "host-seeking" behavior (Wood 1982).

The mountain pine beetle is associated with many organisms which either take advantage of the situation created by the beetle, or feed upon the beetle itself. Dahlsten and Stephen (1974) found that over 60 species were associated with mountain pine beetle attacking sugar pine (Pinus lambertiana).

Many mites (Acarina) are found beneath the bark within bark beetle galleries. Most of these tiny arachnids subsist mainly by feeding upon the fungi that grows within the galleries. Some mites however, feed upon the eggs of mountain pine beetle. Their impact is not considered to be
great, Amman and Cole (1983) reported 0.06% of the eggs were eaten in one study. Mites are commonly seen attached to the cuticle of the adult beetle during their dispersal when they 'hitch-hike' to the new host tree (this situation is known as 'phoresy') where they re-establish their numbers.

A major source of mortality in bark beetles are nematodes. Some of these roundworms are parasitic on the larvae, pupae and adults while other species feed upon the eggs. The effect of nematodes on the population may be quite subtle; the parasites do not often kill their hosts outright, but can have a severe debilitating effect on dispersion and reproduction (Nickle 1978).

Nematodes are thought to have potential in the biological control of bark beetles. They are very host specific and can be cultured in large numbers. An attempt to reduce population of *Scolytus scolytus* in England by spraying infested trees with a solution containing nematodes failed, but the authors felt the potential still existed (Finney and Walker 1979).

The importance of parasitism by Hymenopterans is widely recognized. Their numbers have been found to increase in proportion to bark beetle outbreaks thus providing an important check on the population (Amman and Cole 1983). Most of the adult female wasps oviposit their egg right through the bark onto a mountain pine beetle larva. The method of host location is by the wasp picking up on auditory cues made by the larva feeding beneath the
bark (Ryan 1961) or by sensing the gradient of heat generated by the metabolic heat of the beetle larva (Richerson and Borden 1972). One genera, *Roptrocerus*, actually enters the galleries of the bark beetle and oviposits directly on the larva (Dahlsten and Bushing 1970).

The rate of parasitism by wasps can be quite high. Bedard (1933) found that 54% of the brood in wind fallen and 65% of the brood in standing trees were parasitized.

While most hymenopterous parasites are very host specific, there is a large numbers of general predators of mountain pine beetle. Checker beetles (*Cleridae: Coleoptera*) have long been recognized as an important predator of bark beetles. This brightly colored insect can often be seen on the bark of a tree under attack, pouncing on the bark beetles as they land. The larvae of the clerids are also predatory and feed on the larvae of mountain pine beetle within the galleries. Amman (1970) reported that a single clerid larva (*Enoclerus sphagus*) fed upon an average of 27 mountain pine beetle larvae while completing development.

Other important insect predators of mountain pine beetle are *Temnochila* spp. (Coleoptera:Trogositidae), long legged flies (Diptera:Dolichopodidae) and hister beetles (Coleoptera:Histeridae) (Dahlsten 1982). The rapid appearance of these insects on trees under attack led Camors and Payne (1973) to speculate that some of the
Predators are attracted to the trees by pheromones produced by the bark beetles.

The other major group of bark beetle predators are birds, notably the woodpeckers (Picidae), but also flycatchers (Tyrannidae), nuthatches (Sittidae) and creepers (Certhiidae) who feed on the adult beetles during emergence and dispersal (Amman and Cole 1983). Woodpeckers are well known for their habit of digging insects from beneath the bark, but due to their small size mountain pine beetle are not a favored prey. When populations of bark beetles are at epidemic proportions woodpeckers have been reported to have increased in numbers fifty fold (Koplin 1969).

The role of pathogens in mountain pine beetle populations is not well understood. Little work has been done beyond isolation and identification of some of the protozoan and fungal diseases (Dahlsten 1982). The most work that has been done in the U.S. has been done on southern pine beetle. Sikorowski et al. (1979) made an intensive survey of diseases and found 22% mortality over a two year period.

The common insect pathogen Beauvaria bassiana, a fungal disease found in many orders of insects, has been recorded in many genera of Scolytidae (Dahlsten 1982). An attempt to control Dendroctonus micans in the Soviet Union resulted in a 40% reduction in the population (Kurashvili et al. 1974). This line of research is quite promising and a major study is currently underway by the Canadian Forest
Host Selection

Phenology

Once dispersion has been completed, location of a suitable host is required. The actual selection of the trees to be mass attacked is made by the earliest emerging female beetles which are known as pioneer beetles. The behavioral mechanism involved in host selection and when this selection occurs (the final go/no go decision) is presently unknown, although there has been much investigation in this area. The goal of this thesis is to investigate certain aspects of host selection in mountain pine beetle, particularly the aspect referred to in the literature as 'primary attraction'.

Primary attraction is the process by which the earliest emerging insects are able to locate hosts which are more easily overcome by mass attack due to some physiological weakness. It refers to cues given off by the potential host which allow the pioneer beetle to locate the trees which are under some form of stress and thus less able to defend itself.

Once a suitable host has been determined by the pioneer beetle the production of attractant pheromones begins. These aromatic chemicals serve to attract other mountain pine beetles; additional females to aid in the group or mass attack of the tree as well as males which will mate with the females. The sex ratio of the beetles
arriving at the selected tree is very nearly 1:1, the beetles are monogamous and the males search out the fresh attack sites occupied by an unclaimed female. The couple work together on the gallery and mate as soon as they are able to get inside the bark. All this while the newly attacked lodgepole pine attempts to throw off the mass attack by the production of copious quantities of 'pitch' (Amman and Cole 1983).

The action of a beetle boring into a pine tree causes a unique structure called a 'pitch tube' to be formed. The pitch tube consists of the tree's exuded resins and frass. The color of the pitch tube is an indication of the attacking beetle's success; a white tube means that the beetle has just cut into the resin system, as it gets progressively redder it indicates that the beetle are feeding on the phloem. Pitch tubes are important to forest entomologists because it helps them locate trees under attack (Smith 1966).

If a sufficient number of beetles attack the tree, the defenses of the tree are overcome and the death of the tree is assured. Ideally the production of pitch stops within 1 to 2 days of initial attack although the struggle against resistant trees may continue for some time and certain trees are able to withstand mass attack altogether. The critical factor is the interaction between the resistance of the tree and the numbers and densities of the beetle attack. On trees artificially 'baited' with synthetic
pheromones to simulate highly attracting trees, large numbers of beetles are able to overcome even those trees which are classified as resistant.

In addition to the action of the beetle's boring which physically cuts the resin ducts of the tree, the beetle introduces many pathogenic fungi and yeasts into the tree's conducting tissues. These micro-organisms are carried to the new host in a specially adapted structure on the beetle called the mycangium. Spores and mycelium are obtained from the beetle's brood tree and when introduced into the new host begin to grow through the tree's tracheal and resin duct system. The relationship is symbiotic, the beetle receives assistance in overcoming the tree's resistance and the fungi are inoculated into a new host (Reid et al. 1967).

The beetle carries a wide variety of organisms in its mycangium; yeasts, bacteria and fungi are all commonly inoculated into the tree. The most prominent of these pathogens are the blue stains (Ceratocystis spp.) which extend mycelium deep into the host's sapwood, cutting off the flow of water and staining the wood a silvery blue color (Robinson 1962).

Once all resistance to beetle activity ends the mated pair begin to construct an egg gallery in earnest. When complete, the eggs are laid by the female to provide the brood for the next years beetles.
The Chemical Environment of the Mountain Pine Beetle

The mountain pine beetle's ability to locate and congregate on a scarce resource (susceptible trees) over large expanses of forest is nothing short of remarkable. This ability is possible through the mountain pine beetle's use of pheromones to coordinate attacks on host trees.

The beetle spends only a short portion of its life outside the protective habitat of the inner bark. In addition, mountain pine beetles have no source of food other than the host tree. It is not surprising that the array of odors that this insect produces and utilizes are products of the host tree's biochemical system.

The defensive chemicals of lodgepole pine are basically oleoresins (literally fatty gums); this material along with small amounts of alcohols and esters comprise most of the materials within the tree's resin system. The oleoresin of coniferous trees may be broken down into two major constituents: monoterpenes and resin acids. The resin acids in the oleoresin serve primarily to give the oleoresin its physical properties, rate of crystallization, "stickyness" etc. The monoterpenes give oleoresin their chemical properties, primarily odor and toxicity (Smith 1964).

Terpenes are volatile C$_5$ and C$_{10}$ compounds which are produced by many plants. These aromatic substances comprise many plant odors such as peppermint and mustard 'oils'. The familiar 'piney' odor is the result of monoterpenes in the
The evolutionary function of terpenes is believed to be defensive, to protect against phytophagous organisms. However many organisms have adapted to toleration of these compounds and some have even specialized upon groups of plants with similar chemical defenses. Much of the host specificity of phytophagous insects has to do with the need for specialized insects to include these chemicals in their diets (Chapman 1982).

One of the many paradoxes regarding the lodgepole pine-mountain pine beetle relationship is the role that terpenes play. While there are toxic reactions to the terpenes displayed by the mountain pine beetle (Smith 1965), the essentially defensive chemicals produced by the tree have been adopted by the beetle and turned against the tree.

Mountain pine beetles use terpenes to locate and identify potential host trees and also use them as the precursors of their chemical messengers (Renwick 1970). Beta phellandrene is the most abundant terpene in lodgepole pine oleoresin, it is especially important because it is one of the terpenes that elicits the strongest attraction of the mountain pine beetle. Cole et al. (1981) has reported that the amount of beta phellandrene is proportionately larger in lodgepole pine with greater diameter and thicker phloem.

Another of the important terpenes found in lodgepole pine is alpha-pinene. Mountain pine beetle transforms this
chemical into trans verbonal, one of the more important pheromones produced by the insect. This pheromone is the constituent which elicits rapid and increasing response attack by attracted beetles. Other terpenes found in lodgepole pine are beta pinene, myrcene and various other fractions which have varying degrees of attractancy to the mountain pine beetle (Amman and Cole 1983) (Fig. 4).

Mountain pine beetles perceive chemical cues via their chemoreceptor system which is found primarily in their antennae. Dickens and Payne (1977) recorded varying degrees of neural impulses passing from the flagellum of the antennae to the brain in response to various odors presented to the southern pine beetle.

The effect of the terpenes attracting a consumer is termed a kairomone effect. The definition of kairomone is the chemical message that is given off by an organism of one species to an organism of another species which benefits by it. It has been called an 'evolutionary backfire', the beetle is using the defensive chemicals produced by the tree to locate and attack the tree (Nordlund et al. 1981).

The effects of pheromones and terpenes (kairomones) are synergistic. The combined odors of the tree's terpenes and the beetle's pheromones are a powerful attractant to other beetles. Cole et al. (1981) found that the greatest response was a result of combining the terpene beta phellandrene with the pheromone trans verbonal. This is referred to in the literature as the 'bouquet effect'.
Fig. 4. Ball and stick diagram of the conversion of the lodgepole pine monoterpene α-pinene to the mountain pine beetle pheromone trans-verbenol. Ball and stick diagram of myrcene, an important terpene produced by lodgepole pine.
The pheromones themselves appear to be the product of host compounds converted by the insect. Hendry et al. (1980) followed the in vivo conversion of host compounds to pheromones in the Scolytid *Ips paraconfusus* by the use of radioactive labelled host materials. The means by which these compounds are transformed is the use of the gut flora by the insect. The production of pheromones can be stopped by including antibiotics in the diet of a pre-emergent beetle (Byers and Wood 1981b).

The phenology and function of the various mountain pine beetle pheromones is quite complex and has been subject to several revisions in the literature. In addition to the chemical messages carried by pheromone production, the beetle also produces auditory signals (a series of faintly audible to super-sonic 'chirps') under certain conditions (Rudinsky and Michael 1973).

Theoretical Models of Host Selection

There have been various theoretical models proposed regarding the phenology of the colonization of host trees by scolytids. Wood (1982) divided the process into four phases: dispersal, selection, concentration and establishment. Amman and Cole (1983) used a slightly different classification dividing the process into emergence and flight, selection and infestation and finally mating and oviposition. Vite and Pitman (1968) categorized the behavior into detection and selection, attack and colonization and finally the colonization of surrounding
trees.

Since we will be looking closely at the process of tree colonization it will be expedient for us to use the terminology used by Wood. However, it is important to keep in mind that any attempt to divide a dynamic process like colonization into stages will be arbitrary; the beetles themselves do not display discrete phases in their behavior (Wood 1973). The phenology of the process begins with dispersal.

Dispersal is the least known phase of beetle behavior. This is not due to lack of study, it is because it is so difficult to study. Observational data is lacking due to the difficulty of following a single beetle as it winds its way in and out of the trees through the forest. Attempts to make such observational studies result in small sample sizes.

Most of the information we do have regarding dispersal is a result of attack patterns and laboratory experiments. From this work we have obtained information about the mountain pine beetle's physiological needs and the effects of environmental influences.

The very production of pheromones appears to be contingent on a dispersal flight of some length. Hughes (1975) found that the volatile products which constitute the mountain pine beetle's chemical messages are the result of "volatization" of lodgepole pine lipases in the gut. Apparently this process can be carried out only under the high metabolic rates associated with flight. The initial
Flight period appears to be a necessary period of physiological conditioning. Bennet and Borden (1971) have reported that the beetle must work a gas bubble out of the hindgut, an interesting finding in light of what we know about subsequent pheromone production.

It is difficult to characterize the distance of dispersal for mountain pine beetle. The conditions which are required by the beetle for dispersal (warm, dry weather) is also a time when strong upward air currents are frequent (Chapman 1967). Collections of bark beetles have been made on snow fields up to 20 km away from the nearest infestation (Furniss and Furniss 1972). However it is difficult to determine how much of this distance is covered by free flight as opposed to being carried by wind currents.

The most in-depth study of flight in the closely related Douglas fir beetle *Dendroctonus pseudotsugae* was carried out by Atkins (1961). This work examined the lipid reserves of a newly emerged beetle and using a flight mill he determined it is capable of sustained flight for up to four hours at speeds of 3.0 to 6.0 km/hour.

There are two basic theories regarding the selection phase of adult behavior. The first is that the selection of the tree to be mass attacked is the result of a reaction to an initial feeding that the pioneer beetle makes upon landing on the potential host tree. The second hypothesis is that flight is not random, but that the beetle flies towards various stimuli and then makes the final selection
based on additional cues (Payne and Coulson 1985, Wood 1982).

In this first scenario the dispersal phase of the pioneer beetles is essentially random. Random flight infers that after a dispersal flight of sufficient length to achieve the physiological changes alluded to previously, the pioneer beetle lands on the nearest available substrate. The beetle then samples the bark and the chemicals present allow the insect to determine if it will be a suitable host. It is thought that the presence of feeding stimulants in the host material causes the pioneer beetle to continue feeding, release pheromones and begin construction of the gallery (Hynum and Berryman 1980).

This theory argues that the beetle's strategy in finding a suitable host is to flood the forest with pioneer beetles and then to re aggregate them when one 'stumbles' across a suitable host. If a pioneer beetle happens to land upon a non-host or what is deemed an unsuitable host, the beetle takes off and resumes flight in a random pattern. If however, the gustatory cues found in the trial feeding elicits a positive response the aggregation/mass attack phase of the behavior is initiated by the release of the aggregating pheromones.

The second major theory in host selection is actually made up of several aspects, but they all center around the idea that initial flight is not totally random; that sensory information provides clues as to the 'best' direction for flight (that which would lead to successful
The sensory cues are believed to be of two basic kinds: visual and olfactory. Visual orientation by mountain pine beetle towards large, dark vertical objects was demonstrated by Shepard (1966). This phototaxic response is thought to aid the beetle by orienting it towards 'tree-like' objects.

The mountain pine beetle's reaction to light changes several times during the adult stage. The beetle is positively phototaxic during emergence and dispersal. They are attracted to single or spot light sources similar to that which would be encountered on the sunny days that is required for emergence to occur. Unlike many other insects they do not appear to utilize polarized light for navigation.

In a series of experiments Schonherr (1976) determined many of the beetle's preferences for visual stimulation. In the lab a series of tests established the beetle's preferences for compact patterns over diffuse patterns; vertical bars over horizontal bars and broad stripes over narrow stripes.

In the field Schonherr set out 'sticky-traps' of various colors. He found that brown and black were the preferred colored targets.

Once selection has been completed and the beetle has begun the establishment phase of behavior, there is a reversal of photo response (Graham 1959). At this point the beetle becomes negatively phototaxic and makes attempts to move away from light sources.
Mountain pine beetles have surprisingly good vision. The studies done by Shepard (1966) regarding target preference bear this out. Not only is target shape and size found to have a positive influence, but texture and color have proven to be important.

There has been no experimental work done to specifically disprove that sight does not aid a beetle in site orientation; circumstantial evidence is cited to discredit this hypothesis. Burnell (1977) produced a model that purported to explain random beetle attack patterns by the distribution of vertical substrate in the forest. He held that larger trees are not attacked because they are more susceptible or offer the beetles a favorable habitat (thicker phloem as in Amman (1978)) but simply because they offer more surface area to the beetles. He does, however, state that his studies were made under epidemic conditions where the phenomena of selection is disrupted.

Another use of sensory information for host selection is what has been termed 'primary attraction' in the literature. It is believed that the beetle is able to pick up gradients of volatiles in the air and is able to follow these 'scent plumes' towards a likely host. Light (1983) found that the insects showed a positive attraction to the host terpenes even at very small concentrations in the air.

Some workers have gone beyond simple host detection and have shown that the beetles are able to find susceptible trees. Person (1931) first hypothesized this aspect of selection in his observations regarding
lightning struck trees and the beetle's uncanny ability to locate and successfully overcome these stressed trees. He coined the term 'Primary Attraction' at a time when the phenomena of pheromones (which later was termed 'Secondary Attraction') were unknown.

Many studies have demonstrated that beetles can locate, attack and overcome stressed trees. Drought (Blackman 1924, Ferrel 1978), defoliation (Dewey et al 1974), disease (Bega et al. 1966, Partridge and Miller 1972, Lessard et al. 1985) and fire (Furniss 1965, Gara et al. 1985) are just a few of the influences that can cause stress in lodgepole pine and result in beetle attack.

However, this is not primary attraction per se. The process of primary attraction ends with the first pioneer beetle releasing its pheromone. From this point on secondary attraction and the pheromone communication of the beetle is the driving force.

It is necessary to prove that there is a differential in landing rates on the susceptible stressed tree as opposed to resistant trees in order to demonstrate that the pioneer beetles are actually navigating through the woods to find the source of an attracting odor. The belief that beetles are able to locate stressed trees has as a collarary that a stressed tree produces an odor which reveals its stressed nature.

There has been a great deal of debate in the literature as to the existence of this phenomena. Both sides of the issue can be supported with literature from
There are some very good arguments for primary attraction that are based upon the beetle's biology.

There can be no doubt that the beetles possess a finely tuned sense of "chemoreception/smalld". They are able to locate the source of their pheromones at very small levels. Light (1983) found that beetles were able to locate plume sources at concentrations around $1 \times 10^{-4} \mu g$ within a small enclosed olfactometer.

Another argument against the random flight hypothesis is that the mountain pine beetle looks like a very weak flier, that even if it were able to locate potential hosts it would most likely be unable to get there due to its ungainly flight. This is probably due to the 'bumbling' appearance that most beetles have while in flight; Coleopteran flight is certainly not as graceful as the flight of Lepidopterans or as precise as Dipterans.

However, Miller and Keen (1960) found that mountain pine beetles are able to fly surprisingly well. In field experiments they found that the beetles were able to maneuver around non-suitable substrate without landing.

Another argument for inter-flight (pre-landing) selection of suitable hosts is the way that beetles release their pheromones. Vite and Pitman (1968) found that mountain pine beetle, western pine beetle and southern pine beetle commonly release pheromones before any feeding has occurred. In fact, the production of
aggregating pheromone ceases entirely once extensive feeding begins.

They found that it was difficult to obtain an attractancy effect from the frass (fecal particles and boring dust) of the beetles, while material from the excised hind guts of females from freshly attacked trees were extremely attractive. This indicates that sustained feeding is not what causes the mountain pine beetle to release pheromones, that pheromones are released at the point of a decision made by the pioneer beetle that it has found a susceptible host.

In contrast *Ips* spp. requires feeding upon host material before release of the pheromones can occur and continued production of the pheromones are required for sustained feeding.

The apparent paradox can be explained by examining the ecological roles that each of these insects play. *Dendroctonus* spp. are considered 'tree predators', they must overcome and kill a tree which will put up at least some degree of resistance. They are in only one host per year and are in a 'do or die' situation. *Ips*, on the other hand fulfill more of a scavenger role. Their common habitat is either in slash or in the tops of fairly weakened trees. These beetles rely on a scattered ephemeral food source and a single beetle can infest several sites in one season (Byers and Wood 1981a).

The *Ips* beetles release their pheromone to locate and colonize, the suitability of a host is assured by the
requirement of prior feeding. In addition, once the host is no longer suitable (in the case of slash, once it dries out) pheromone production ceases and all the beetles migrate in search of new host sites. *Dendroctonus* attractant pheromones 'serve primarily as a signal for mutual invasion of a resistant host'. Production of the pheromone persists only as long as there is host tree resistance, once the death of the host is assured there is no longer any need for recruitment (Borden et al. 1968).

The fact that production of attractant pheromone by *Dendroctonus* spp. sometimes commences before feeding points to the probability that selection is not entirely in response to gustatory cues.

**Population Dynamics**

The unique population dynamics of the mountain pine beetle is perhaps one of the factors most responsible for the success of these organisms. The large degree of intra-species cooperation makes the study of the changes through space and over time of the state of a population intrinsic to understanding its basic biology.

The mountain pine beetle is best known to forest managers for its ability to kill large numbers of trees covering extensive areas. The insect is capable of producing large numbers of brood which can literally fill the air at emergence time. But the mountain pine beetle is also a permanent resident of the lodgepole pine stand, it is present whenever lodgepole pine makes up any significant
part of the forest canopy.

A great number of factors influence the size as well as the rate of increase or decrease within a mountain pine beetle population. The characteristics of the host stand have a great deal to do with the possibilities for brood production. Since the mountain pine beetle is a univoltine insect (with a few exceptions) the formula for its population dynamics is relatively simple: If this year's brood exceeds last year's the population is increasing. While this may sound overly simplistic, it is the basis for population monitoring.

There are two types of influences that affect populations. They are density dependent factors (disease, food supply, natality, etc.) and density independent factors (weather, fire, etc.). The interaction of these influences are what causes fluctuations in population size. At times population fluctuations appear somewhat regular and when graphed exhibit a cyclical nature. However, as noted previously populations can also expand enormously.

There has been much work done on describing the dynamics of mountain pine beetle populations. It is hoped that with this understanding, mathematical models can be formulated that will allow the forest manager to better recognize forest characteristics that encourage increases in beetle populations and better predict mountain pine beetle population trends (Berryman 1982).

The different states of a mountain pine beetle population can be classified according to rates of change
and sheer numbers of insects (Fig. 5).

An endemic population is essentially a steady state with minor cyclic fluctuations. Under these conditions the mountain pine beetle utilizes only weakened trees since the population numbers are not great enough to overcome vigorous hosts (Shrimpton and Reid 1973, Berryman 1978).

In addition the beetles can maintain a population at low levels by making what are known as 'strip attacks'. This refers to a series of attacks by a group of mountain pine beetle upon an otherwise non-susceptible host by limiting attacks to a narrow vertical strip, thus concentrating all of their efforts on a small proportion of the host tree's defense system.

These small populations can be maintained indefinitely until conditions in a given area alter to favor the mountain pine beetle. Should a number of trees become stressed for some reason or another, mountain pine beetle are able to spread out their activity thus providing optimum conditions for brood production; the numbers of beetles emerging the following year can be expanded enormously. Two conditions will allow the mountain pine beetle population to expand rapidly: large amounts of susceptible trees or large numbers of beetles which migrate from small areas of host stress and are able to overcome non-susceptible trees in the surrounding areas (Berryman 1982).

When mountain pine beetle numbers swell rapidly it is called an outbreak condition. When the beetle population
Fig. 5. Conceptual model of the population dynamics of the mountain pine beetle.
is released it can build to tremendous numbers and should the outbreak stage continue for any length of time, epidemic conditions are said to exist. In this stage the beetle population is essentially self-perpetuating, it has reached the 'critical beetle population' in which the average resistance of trees within the stand can be overcome (Thalenhorst 1958). This means that the population is large enough that the mountain pine beetle can kill just about any tree they attack just by weight of sheer numbers.

Once a population has reached the epidemic stage there is little the forest manager can do to halt its progress. A mountain pine beetle epidemic in full swing is very much like a wildfire. Eventually the epidemic ends due in part to increased disease and predation, but mainly due to exhaustion of the food resource.

These various stages in the development of mountain pine beetle populations have much to do with the insect's discrimination of possible hosts. When in the epidemic stage the mountain pine beetle has little need to carefully choose a potential host, the numbers of the beetle are so great that they can overwhelm any tree with which they come into contact. On the other hand when the population is in the endemic stage the mountain pine beetle must be very careful about which trees are selected for attack, should a wrong decision be made a significant proportion the next year's brood could be destroyed by the defenses of the tree (Berryman 1978).
It is therefore imperative that the pioneer beetles utilize every means at their disposal to make the correct choice. This is also the reason why it is necessary for the researcher to understand the state of a beetles population and how this affects the physiological conditions of its members.

Recent work by Stock and Amman (1985, 1980) has focused on the genetic diversity of mountain pine beetle. They have found that beetle populations under stress (mixed stands vs. pure, thin phloem vs. thick) are more genetically diverse. Other work by Stock et al. (1978) on the genetic diversity of Douglas fir tussock moth (Orgyia pseudotsugata McDunnough) (Lepidoptera:Lymantriidae) found that at epidemic levels, genetic diversity increases. Although no work of this nature has been completed for the mountain pine beetle, if the same relationship holds true there may be a link between genetic and the behavioral characteristics displayed at different population levels.

It is clear that the fate of the mountain pine beetle and its host are inexorably inter-twined. Although resource managers tend to consider the mountain pine beetle only when it is at the epidemic level, the life of a stand is long and the future risks to the various consumers of lodgepole pine must be weighed.

Most of the work done on mountain pine beetle has focused on the epidemic stage of the population. However, if the goal is to manage the insect at endemic levels and effectively reduce the amount of damage, it will be
necessary to understand the biology of the insect at all population levels.

Host selection is one of the factors which allows a population to expand, if a beetle population can successfully locate and colonize stressed hosts it may be able to increase its numbers and exceed a given area's critical population threshold. Once this has been accomplished it is only a matter of time before epidemic levels are reached.

With this in mind an experiment was conducted to fulfill partial requirements for a Master of Science degree. The following manuscript will be submitted to the Journal of Environmental Entomology for publication.
Mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera:Scolytidae) is one of the most important forest insects of western North America. Epidemic populations cause large amounts of mortality to important timber species such as ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*) and other primary host trees within its range.

When at epidemic population levels mountain pine beetles are present in the forest in fantastic numbers. Large numbers of trees can be killed over great acreages. Host selection at these population levels is indiscriminate, even those trees which would normally resist attack succumb to massive invasion as their defenses are overwhelmed. When populations are at low levels the mountain pine beetle maintains its numbers by confining its attacks to weakened or stressed trees. By attacking weaker trees, the insects are able to more easily overcome the defenses of the prospective host.

This propensity to attack weakened trees was first noticed by early forest entomologists who noted that trees struck by lightning were often singled out and attacked (Person 1931). Other workers found that drought (Blackman 1924), defoliation (Dewey et al. 1974), disease (Partridge and Miller 1972), and fire damage (Furniss 1965) all increase the likelihood of attack.
Berryman (1978) proposed a theoretical model which considers the means by which a small endemic population can enlarge to the epidemic state. Release of the population can occur due to changes in the condition of the stand whereby host resistance is decreased or by factors which allow the reproductive capacity of the beetle to increase.

The term 'primary attraction' was coined by Person (1931) to describe the mechanism by which the insects were able to recognize odors emanating from susceptible hosts and to follow these odor plumes to trees physiologically less able to resist attack. Subsequently Vite and Gara (1961) discovered that many members of Scolytidae produce attractant pheromones (termed secondary attraction) once a suitable host was located by the pioneer beetle.

The phenomenon of primary attraction has been hypothesized by several authors for closely related scolytid species. Heikkenen and Hrutfiord (1965) studied primary attraction in *Dendroctonus pseudotsugae* using an olfactometer in the lab. Later Heikkenen (1977) determined that the southern pine beetle *D. frontalis* also utilized primary attraction to locate artificially stressed hosts in the field. Gara et al. (1984) found that landing rates on trees infected with fungal decay were higher than on uninfected trees. However, Moeck et al. (1981) in an extensive series of experiments found no evidence of primary attraction in the western pine beetle *D. brevicomis*.

It was our intent to further explore the process of
host selection in mountain pine beetle through the use of artificially stressed hosts. The objective was to determine if the mountain pine beetle was able to locate wounded trees while in flight.

Methods

The experiment was conducted in the vicinity of Log Cabin Ridge in the Wasatch-Cache National Forest near Bear Lake, Utah in lodgepole pine stands with an endemic population of mountain pine beetle.

Three plots were established in nearly pure stands of lodgepole pine which had a mean basal area of 50.5 m$^2$/ha (stand. dev. 7.7 m$^2$/ha). Plot centers were established at random, provided there were no group infestations within 500 m. Diameter at breast height was recorded for all trees within the immediate vicinity of plot center and pairs were formed on the basis of D.B.H., crown class (suppressed, intermediate, co-dominant and dominant) as well as presence or absence of scars on the bole.

A girdling treatment was then randomly applied to one member of each pair. The treatment trees were girdled at breast height, removing the bark and phloem from a band approximately 10 cm. wide. In an attempt to reduce the amount of volatile odors released from the wound itself, one half of the treated tree wounds were sealed with polyethylene plastic and plaster.

Following treatment all of the study trees were fitted with 'sticky traps' which consisted of a 1.3 m band of
white nylon cloth gauze and then coated with a layer of 'Tanglefoot'.

In addition to the 16 pairs of trap trees, 2 trees were selected to monitor the water status throughout the test period. This pair was also matched on the basis of D.B.H. and had branches 1 m. above the ground to facilitate taking of pre-dawn moisture stress readings. One member of the pair was girdled and the other was left as an untreated control.

The traps were inspected on a daily basis during the beetle flight period. The number of trapped mountain pine beetles was noted and the insects were removed from the trap. Once a tree was actually attacked by the beetles (determined by the presence of frass and/or pitch tubes above or below the trap) the phenomena of secondary attraction was considered to have begun, and the pair was removed from the study population.

After girdling, a pre-dawn moisture stress reading was taken with a pressure bomb on the monitor pair on a weekly basis. This continued throughout the flight period.

Results

Thirty eight days after the girdling treatment was applied the beetles flight period began. It continued for approximately 10 - 12 days during which time the traps were inspected on a daily basis. At the end of the experiment total numbers of trapped beetles on the treated and untreated trees were summarized.
Due to the skewed distribution of our results, the use of a Normal theory test is inappropriate. A non-parametric test of significant differences between treatments was used, Wilcoxon's test of sum of positive ranks. This statistic ranks the differences between treatment and control and takes the sum of the ranks for the positive differences. The sum is then compared to a tabular value to obtain a p value (Hollander and Wolfe 1973).

A significant difference was found in the landing rate between treated and untreated trees. Significant differences were also recorded between the sealed wound trees and their untreated partners as well as between the unsealed girdles and their counterpart. There were, however, no significant differences between the sealed and unsealed treatments. There was also no significant difference in trap rates between the 3 plots indicating that the beetle population was fairly homogeneous over the study area.

There was no evidence to suspect that variables such as crown class, evidence of porcupine feeding and butt scars affected the landing rate.

Diameter at breast height however did have a significant effect. Trees greater than the 20 cm were landed on more frequently than those less than 20 cm in diameter.
Discussion

The results of the study demonstrate that the mountain pine beetle is able to locate wounded and stressed trees while in flight. Most of the trapped mountain pine beetles were located in the middle regions of the band indicating that they landed on the trap and were unable to free themselves. This is supported by lab tests demonstrating that pedestrian beetles will avoid walking in 'Tanglefoot'.

The results obtained by this study agree closely with the work of Gara et al. (1984) who found greater beetle landing rates on trees under natural stress (fire scars and fungal decay). Gara et al. (1984) found that the landing rates (also determined by traps on trees) were higher on those trees under stress. They concluded that the beetles were landing more frequently on the stressed trees than those with no signs of scarring or decay. Gara et al. (1984) hypothesized that the cues used by the beetle resulted from the interaction between the host and the fungal decay.

Heikkenen and Hrutfiord's work (1965) with the closely related Douglas-fir beetle (*Dendroctonus pseudotsugae*) established that the insect can distinguish between several of the important compounds found in the host (primarily alpha and beta pinene). He hypothesized that the attractancy effect of the alpha pinene served to aid the beetle in locating water stressed trees; when under water stress a mature Douglas-fir releases proportionally more
alpha pinene from its stomata.

Heikkenen (1977) also studied the effect of tree wounding on the response of the southern pine beetle *Dendroctonus frontalis*. He compared the landing rates of southern pine beetle on loblolly pines which had been girdled versus untreated controls. The results showed that landing rates were greater on the treated trees indicating that the southern pine beetle was attracted to the wounded trees while on their dispersal flight.

In contrast to these studies, work done by Hynum and Berryman (1980) suggested that the mountain pine beetle is unable to distinguish susceptible from nonsusceptible hosts by olfactory cues. They found that landing rates on dead and living lodgepole pine and non-host Douglas-fir were not significantly different. Their data suggest that the mountain pine beetle lands on objects at random, and only after sampling the substrate by feeding are they able to determine the suitability of the object. Hynum and Berryman (1980) contend that it is the presence of chemical feeding stimulants in the bark that causes the beetle to begin construction of the gallery (Raffa and Berryman 1982a). In a follow-up paper Raffa and Berryman (1982b) were unable to find any physiological differences between susceptible and resistant lodgepole pine other than localized wound response in the form of quantity of resin flow.

This theory of non-oriented flight was supported by a model of attack patterns proposed by Burnell (1977). The
model assumed that pioneer beetles attack the available bark substrate in a forest on a random basis. A further assumption is made that all trees have an equal likelihood of being mass attacked regardless of their physiological condition or the state of the mountain pine beetle population.

Objections to the random flight theory were raised by Amman and Cole (1983), who suggested that the experimental design as described by Hynum and Berryman (1980) was flawed. Small sample sizes and failure to account for the visual orientation towards large objects, as demonstrated by Shepard (1966), could explain the results obtained by Hynum and Berryman (1980). Amman and Cole (1983) also reported that predictions of attack patterns made by Burnell (1977) based on his random attack distribution model were not fulfilled.

A model explaining the epidemiology of the southern pine beetle proposed by Coulson et al. (1985) was based on the incidence of lightning struck trees as providing a highly susceptible host tree. Once located, these trees were colonized and were able to sustain large numbers of brood, sometimes establishing large infestation centers around the lightning struck tree. These centers then acted as a springboard releasing large numbers of dispersing beetles into the surrounding stand.

The girdled treatment in our study can be compared to a tree struck by lightning. In both cases large amounts of volatiles are released into the air by the wounding of the
bark, phloem and cambium. In addition, the disruption of the phloem causes a rapid decrease in the amount of carbohydrates supplied to the tree's root system resulting in a decline in the root's ability to supply water and nutrients to the crown. This decline was illustrated by the increase in water stress in the crown of the treated monitor tree.

It is important to emphasize that our study was conducted in a stand with an endemic beetle population. When mountain pine beetle populations reach epidemic levels, host selection is indiscriminate; the beetles are able to overcome even the most resistant tree by sheer weight of numbers. However, at the endemic level it is important that pioneer beetles quickly find and colonize susceptible host trees. It is under these conditions that the phenomena of primary attraction is most likely to occur. In the field it has been demonstrated repeatedly that the beetles are able to locate stressed and wounded hosts.

It appears that the phenomena of primary attraction is not an all or nothing event. It almost assuredly occurs when the population is at a low level and damaged or wounded trees are in the vicinity. The question is how strong is the beetle's ability to locate a stressed host. Gara et al. (1984) found that mountain pine beetle are able to locate trees infected by root disease via olfactory cues, but what degree of infection is needed for this to occur?
More information is needed regarding the interplay of host stress and beetle response, especially mechanisms by which beetles locate weakened trees. Future work should examine varying degrees of host stress induced by non-physical methods and how the beetle reacts to these levels.
Fig. 6. The development of water stress in treated and untreated lodgepole pines.
Fig. 7. Landing rates of mountain pine beetle on treated and untreated lodgepole pines.
Table 1. Statistical analysis of landing rates on treated and untreated lodgepole pines

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<td>32</td>
<td>b</td>
<td>0.91</td>
<td>40.0</td>
</tr>
</tbody>
</table>

a Wilcoxon test for unequal treatments
b Kruskal-Wallis test for one-way layout
c (S) signifies plastic sealed girdle


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