



Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range

José F. Negrón*, John B. Popp

USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect, Fort Collins, CO 80526, USA

Received 8 June 2003; received in revised form 9 July 2003; accepted 29 October 2003

Abstract

Insect-caused tree mortality, fires, and pathogens are primary disturbance agents in forest ecosystems. The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a bark beetle that can cause extensive mortality in ponderosa pine, *Pinus ponderosa* Lawson, along the Colorado Front Range. Despite the history of outbreaks of this insect in Colorado, no models have been developed to estimate the probability of infestation. Thirty-five clusters of one infested and three baseline plots were established from 1998 to 2000 in the Arapaho-Roosevelt National Forest in north-central Colorado to develop empirical models of probability of infestation based on forest conditions. Mountain pine beetle-infested plots exhibited higher basal area and stand density index (SDI) for ponderosa pine and for all tree species combined, and higher number of ponderosa pine trees per hectare. Within infested plots, infested trees were larger in diameter at breast height and in the dominant and co-dominant crown positions. A classification tree model indicated that the likelihood of infestation by mountain pine beetle is 0.71 when ponderosa pine basal area is $>17.1 \text{ m}^2/\text{ha}$ at the stand level. A second plot-level model indicated that the probability of infestation increased with increasing ponderosa pine SDI, ponderosa pine quadratic mean diameter, and total basal area. For individual trees within infested plots the likelihood of infestation was 0.77 for dominant or co-dominant trees $>18.2 \text{ cm}$ in diameter at breast height. Results are consistent with other studies that have documented increased likelihood of infestation or enhanced mortality levels or both as a result of higher host type stocking. The simple models developed should help to guide silvicultural treatments and restoration efforts by establishing stocking levels below which mountain pine beetle-caused mortality is less likely, particularly in the dry sites and poor growing conditions characteristic of the Colorado Front Range.

Published by Elsevier B.V.

Keywords: *Dendroctonus ponderosae*; Mountain pine beetle; Bark beetles; *Pinus ponderosa*; Ponderosa pine

1. Introduction

Ecological disturbances are paramount in defining composition and structure of forest ecosystems. Fires, insects, and pathogens are primary agents of disturbance and under certain circumstances can cause

extensive tree mortality (Goyer et al., 1998). Although these ecological processes are an integral part of the natural environment, in many situations widespread tree mortality can be undesirable and in conflict with resource objectives of land managers or landowners or both.

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a bark beetle that can cause significant mortality of ponderosa pine, *Pinus ponderosa* Lawson, along the Colorado Front Range (Schmid and

* Corresponding author. Tel.: +1-970-498-1252;
fax: +1-970-498-1314.
E-mail address: jnegrón@fs.fed.us (J.F. Negrón).

Mata, 1996). This insect also attacks and kills other pine species that occur within its geographical distribution, which extends from British Columbia and western Alberta south to Baja California Norte in Mexico and throughout the western United States (Amman et al., 1989; Wood and Bright, 1992).

Rocky Mountain coniferous forests are a mosaic of stands that exhibit variation in age and history which result from the result of the interplay of fire, wind, and insects (Peet, 1981). A better understanding of the characteristics that make ponderosa pine stands more susceptible to mountain pine beetle attack will help us better understand the spatial and temporal distribution of tree mortality caused by this insect and its interaction with other disturbance agents.

High levels of ponderosa pine mortality caused by mountain pine beetle were observed along the Colorado Front Range in the mid-1970s (Schmid and Mata, 1996). Ponderosa pine mortality resulted from a mountain pine beetle outbreak that extended from about 290 km from the Colorado–Wyoming border south to Canon City, CO. About 809,000 ha of ponderosa pine forest were affected (McCambridge et al., 1982). More recently, populations have been increasing in the Colorado Front Range since 1991. From 1997 to 1999, mountain pine beetle killed about 315,800 trees and about 457,900 were killed in 2001 across Colorado. The majority of this mortality has occurred in the Front Range (Harris et al., 2001, 2002).

Approaches to manage tree-killing bark beetles have included prevention and direct suppression strategies. Prevention tactics include the use of models to identify stands that may be susceptible to infestation or high mortality levels to bark beetles (Amman et al., 1977; Hedden, 1981; Shore and Safranyik, 1992; Anhold et al., 1996; Negrón, 1997, 1998; Chojnacky et al., 2000; Perkins and Roberts, 2003). Silvicultural prescriptions can be implemented in the susceptible stands to mitigate potential bark beetle-caused mortality. Although mountain pine beetle has a history of outbreaks in ponderosa pine in Colorado, little is known about forest conditions in which the insect occurs and none have been conducted to model the probability of occurrence. McCambridge et al. (1982) examined mortality in unmanaged stands in north-central Colorado and reported that tree mortality was related to ponderosa pine basal area, tree density, and

perhaps to ponderosa pine dwarf mistletoe, *Arceuthobium vaginatum* subsp. *cryptopodum* (Engelm.) Hawksworth and Wiens, infection. Examination of susceptibility to attack in ponderosa pine has been conducted mostly in the Black Hills of South Dakota (Sartwell and Stevens, 1975; McCambridge and Stevens, 1982; Schmid and Mata, 1992; Schmid et al., 1994; Olsen et al., 1996; Obedzinski et al., 1999) and in Oregon (Sartwell, 1971; Sartwell and Dolph, 1976). In sum, these studies indicate that mountain pine beetle-caused ponderosa pine mortality is related to stand density. These studies provide valuable insight on stand characteristics and ponderosa pine susceptibility to mountain pine beetle, but may not be applicable to the Colorado Front Range ponderosa pine forests due to differences in the biotic environment and disturbance history. In this paper, we present the results of an empirical study where we model the probability of infestation by mountain pine beetle in ponderosa pine in the Colorado Front Range. The simple models are tools that land managers can use to rate stands for potential infestation by mountain pine beetle when populations rise.

2. Methods

2.1. Study site

The Colorado Front Range, located in north-central Colorado, is the easternmost range of the Rocky Mountains and extends from about 150 km south of the Colorado–Wyoming border south to Canon City, CO, by the Arkansas River. On the west it is bound by North Park, South Park, and the Continental Divide and on the east by the Great Plains (Whitney, 1983; Mast et al., 1998).

The study was conducted during the summers of 1998–2000 at the Canyon Lakes Ranger District of the Arapaho–Roosevelt National Forests in north-central Colorado (Fig. 1). The study area comprised about 60 km² centered on UTM coordinates 13T 0448800 north and 4514200 east. Elevation in the plots ranged approximately from 2600 to 2800 m. The predominant plant association type in the area is *P. ponderosa*/*Purshia tridentata* and is described in Johnston (1987). Other tree species present in our study sites included lodgepole pine, *Pinus contorta* Dougl. ex

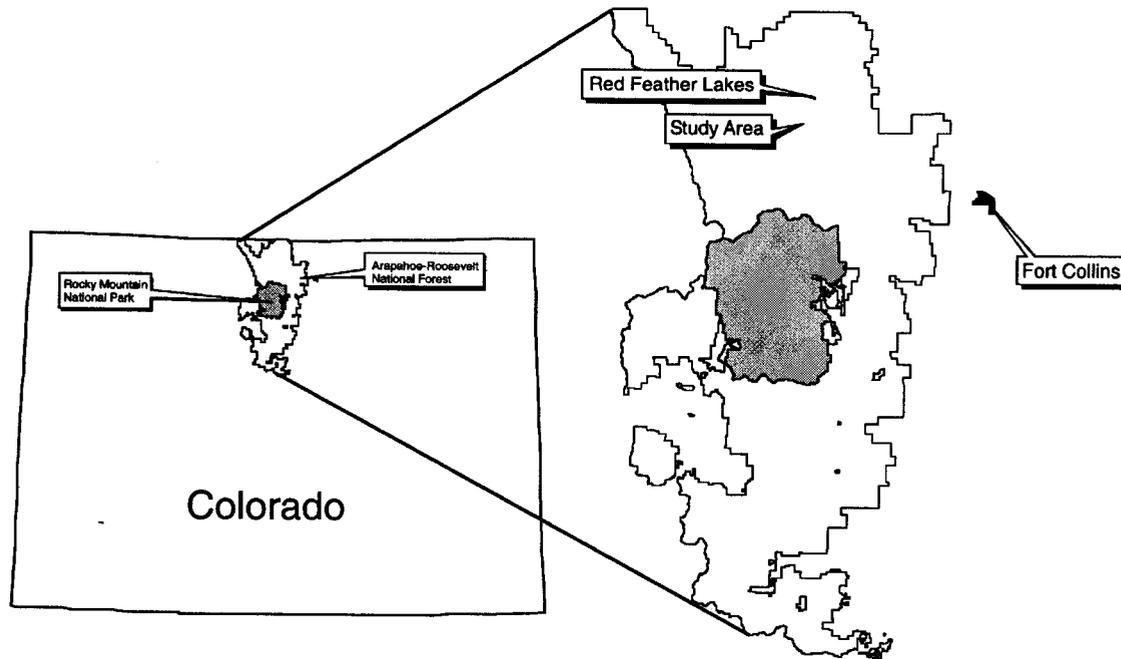


Fig. 1. Location of study area within the Canyon Lakes Ranger District, Arapaho-Roosevelt National Forests, Colorado, 1998–2000.

Loud.; Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco; limber pine, *Pinus flexilis* James, and aspen, *Populus tremuloides* Michx. This forest type fits the Peet (1981) description of xeric ponderosa pine forests which are described as a mix of old groves of large trees with dense sapling populations, younger stands with dense even-aged populations of small trees, which may be post-fire stands, and stands of mixed ages.

2.2. Plot establishment and data collection

Ponderosa pine forests along the Colorado Front Range have an irregular stocking distribution. We used a cluster sampling approach in an effort to minimize the influence of irregular stocking. We established a total of 35 clusters of four plots. Each cluster included one infested plot and three baseline plots, except one cluster that was limited to two baseline plots due to logistical constraints. Infested plots included at least one ponderosa pine killed by mountain pine beetle. Baseline plots included at least one ponderosa pine 15.2 cm in diameter or larger at 1.4 m (dbh) and no trees killed by mountain pine beetle. To determine plot center for infested plots, we would approach a group

of trees killed by mountain pine beetle and identify the trees that were initially killed by the insect within these groups. Trees initially killed were determined by the relative rate of foliage discoloration and the presence or absence of small branches. At this point, random numbers for distance and azimuth were obtained that would determine the precise location of plot center. Baseline plots were located at azimuths of 75°, 195°, and 315° from the center of the infested plot and at a distance of 40.6 m. Plots were circular and comprised an area of 0.02 ha.

For all plot trees 2.54 cm or larger at dbh, we recorded species, dbh, crown position, and dwarf mistletoe rating using the rating scale developed by Hawksworth (1977). We also recorded tree status using the following categories: live, mountain pine beetle-killed, currently infested, pitchout (unsuccessful mountain pine beetle attack), or dead from other causes.

2.3. Data analysis

We calculated mean dbh for all species combined and for ponderosa pine, quadratic mean diameter for

all species combined and for ponderosa pine, total basal area, trees per hectare, and stand density index (SDI) for all species combined and for ponderosa pine for all plots. SDI values were obtained by summation of the individual tree utilization of the site (Stage, 1968), using the following expression modified from Long and Daniel (1990):

$$SDI = \text{SUM} \left(\frac{dbh_j}{25} \right)^{1.6}$$

where dbh_j is the dbh of the j th tree in the plot.

We used classification trees (Breiman et al., 1984; Steinberg and Colla, 1992) to model the probability of infestation at both the tree and plot levels. This approach examines every level of every variable to partition the data into the most pure membership classes through binary recursive partitioning. The result is a binary tree with splitting rules used to classify the data points. A cross-validation framework is used to determine how the resulting tree would classify another sample derived from the same population. We used CART[®] (Salford Systems, San Diego, CA) to conduct the classification tree analysis. Our classification criterion was whether the plots or trees

were infested or not with the variables measured examined as potential splitting rules.

We used the Benard–van Elteren rank test to compare tree and plot mensurational information between infested and uninfested plots and trees (Norwood et al., 1989). We used cross-tabulations and chi-square analysis to test for association between live and mountain pine beetle-killed trees and crown position. Finally, we graphed the number of ponderosa pines across all plots by 5 cm diameter classes and the numbers of live and mountain pine beetle-infested trees in the infested plots by 5 cm diameter classes.

3. Results

The number of ponderosa pines across all plots by diameter classes shows the uneven-aged nature of our study site (Fig. 2). The range of ponderosa pine dbh observed was from 2.54 to 70.6 cm in dbh. The diameter class with the most trees was the 7.5 cm class and the number of trees per diameter class decreased as the diameter classes got larger. There were 76 trees equal to or larger than 2.54 cm and less

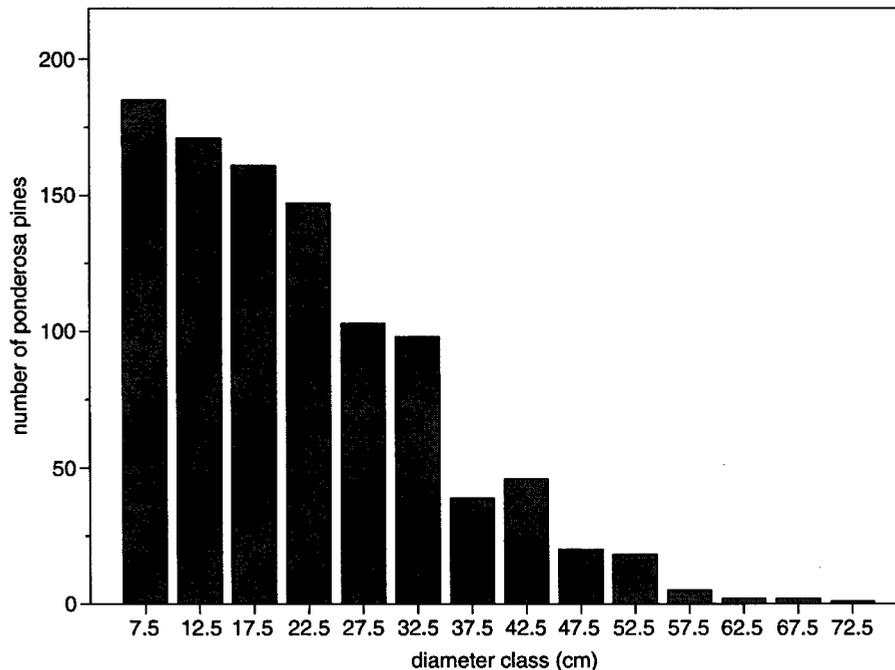


Fig. 2. Number of ponderosa pines per 5 cm diameter classes across all plots, diameters indicated are the midpoint of the size class.

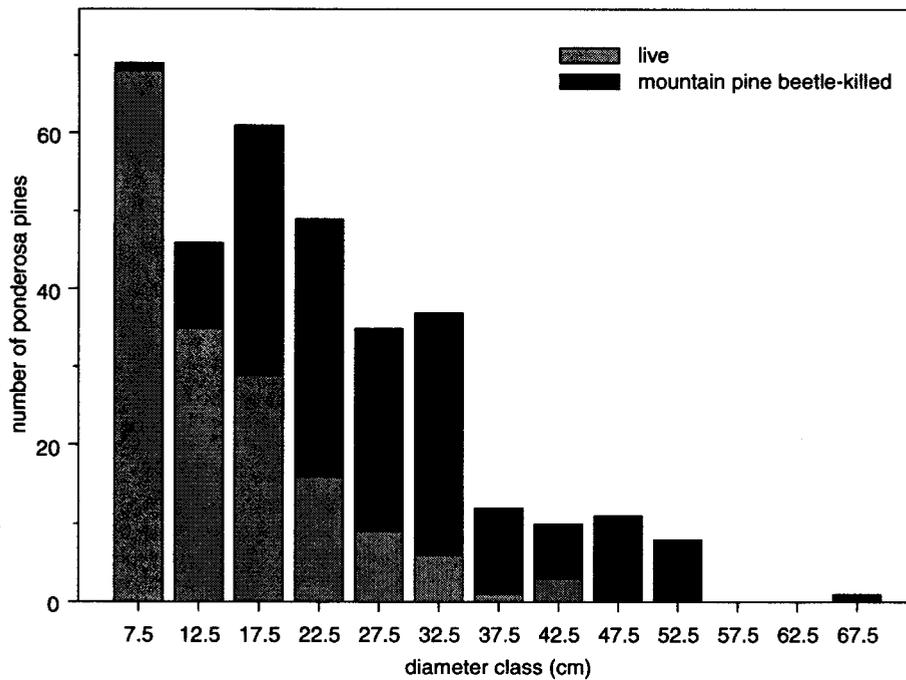


Fig. 3. Number of live and mountain pine beetle-killed ponderosa pines per 5 cm diameter classes across infested plots, diameters indicated are the midpoint of the size class.

than 5 cm in dbh that are not included in the graph so that all classes in the graph included the same size range. Mountain pine beetle-killed trees in diameter classes of 7.5 cm and larger and the proportion of mountain pine beetle-killed trees increased steadily with increasing diameter classes (Fig. 3). The smallest and largest trees killed by mountain pine beetle were 5.3 and 65.5 cm, respectively.

3.1. Classification trees—plot-level analysis

A classification tree indicated that the probability of infestation at the plot level was 0.71 when the ponderosa pine basal area was greater than 17.1 m²/ha and 0.21 with ponderosa pine basal area equal to or less than 17.1 m²/ha (Fig. 4). Cross-validation analysis estimated probability of correct classification to be 70%.

SDI was a strong competitor variable to ponderosa pine basal area in the classification tree analysis. Therefore, we removed ponderosa pine basal area as a predictor from the model construction phase and obtained a second classification tree model

(Fig. 5). The second tree used ponderosa pine SDI as the first predictor, with stands with ponderosa pine SDI less or equal to 273.1 having a probability of infestation of 0.2. The second split was made on quadratic mean diameter of ponderosa pine, with a value greater than 21.4 cm exhibiting a probability of infestation of 0.73. The last split was made on total basal area, with stands of total basal area greater than 29.2 m²/ha, exhibiting a probability of infestation of 0.78. Cross-validation analysis estimated probability of correct classification to be 66%.

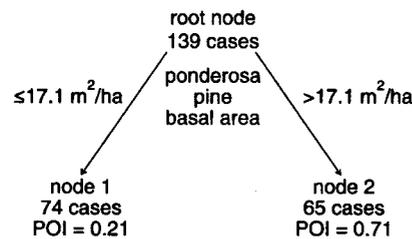


Fig. 4. Classification tree for estimating probability of infestation by mountain pine beetle at the plot level using ponderosa pine basal area.

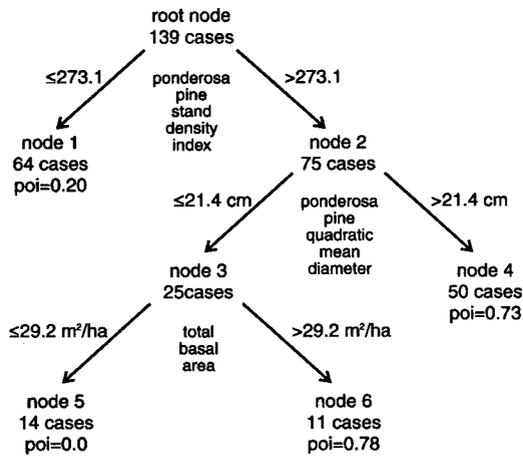


Fig. 5. Classification tree for estimating probability of infestation by mountain pine beetle at the plot level using ponderosa pine SDI, ponderosa pine quadratic mean diameter, and total basal area.

3.2. Classification trees—tree-level analysis

A classification tree model constructed for predicting the probability of infestation of individual trees within infested plots used dbh and crown position as predictor variables (Fig. 6). When dbh was equal to or less than 18.2 cm the probability of infestation by mountain pine beetle was 0.18. With trees larger than 18.2 cm, if crown position was other than intermediate the probability of infestation was 0.86. This is a essentially dominant or co-dominant tree, since only four of the trees that were included in this node were either suppressed or open grown. For trees with intermediate crown position, when dbh was less than or equal to 31.0 cm the probability of infestation was 0.42 and for trees larger than 31.0 cm the probability of infestation was 1.0. Cross-validation analysis estimated probability of correct classification to be 77%.

3.3. Plot-level comparisons

Infested plots exhibited significantly higher basal area levels and SDI both for all species combined and for ponderosa pine, higher ponderosa pine tree density, and a higher percentage of the basal area in ponderosa pine (Table 1). No differences were observed in trees per hectare for all species, diameter measurements, or dwarf mistletoe ratings.

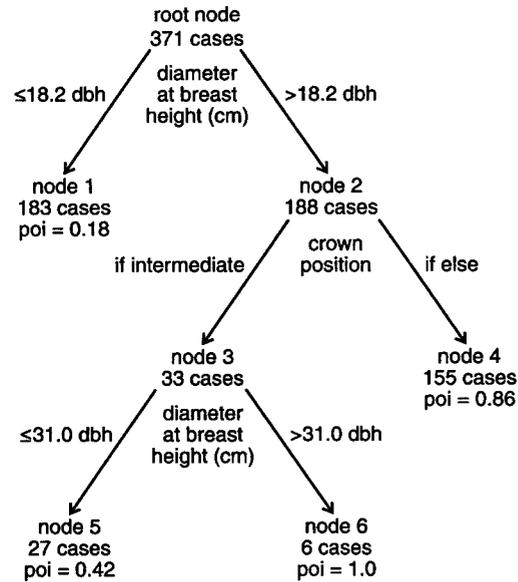


Fig. 6. Classification tree for estimating probability of infestation by mountain pine beetle at the individual tree level. Data from Table 2 presents 368 trees while the root node here presents 371; there were three trees for which data on crown position was missing and are not included in Table 2.

3.4. Tree level comparisons

Mountain pine beetle-killed trees within infested plots were significantly larger in dbh compared to live trees (Benard–van Elteren rank test, $P < 0.0001$). Mean dbh (standard error of the mean) for beetle-killed trees was 28.0 cm (0.8) and 12.8 (0.6) for live trees. A chi-square test for association between tree status and crown position was significant ($\chi^2 = 122.8$, d.f. = 4, $P < 0.001$). Mountain pine beetle killed more dominant and co-dominant trees and less intermediate, suppressed or open-grown trees (Table 2). Dwarf mistletoe infestation levels were higher in the live trees, 0.17 (0.07), than in mountain pine beetle-killed trees, 0.02 (0.02), but the infection levels were negligible (Benard–van Elteren rank test, $P < 0.0001$).

4. Discussion

Infested plots had higher stocking levels and SDI for all species and for ponderosa pine compared to

Table 1

Mean (\pm standard error of the mean) for variables for all plots combined, baseline, and infested plots, Canyon Lakes Ranger District, Arapaho-Roosevelt National Forests, Colorado, 1998–2000^a

Variable	All plots	Baseline	Infested
<i>N</i>	140	105	35
Trees per hectare for all species	630 (47)	610 (54) a	690 (100) a
Ponderosa pine trees per hectare	390 (34)	337 (30) a	545 (93) b
Total basal area for all species (m ² /ha)	22.0 (1.0)	20.1 (1.1) a	27.8 (1.9) b
Ponderosa pine basal area (m ² /ha)	17.7 (1.0)	15.3 (1.0) a	24.5 (1.8) b
Percent basal area in ponderosa pine	82.1 (2.2)	80.0 (3.0) a	89.2 (3.0) b
Quadratic mean diameter for all species (cm)	24.3 (0.8)	23.8 (1.0) a	25.9 (1.2) a
Ponderosa pine quadratic mean diameter (cm)	27.7 (0.9)	27.3 (1.1) a	28.6 (1.5) a
Mean diameter at breast height for all species (cm)	21.6 (0.8)	21.1 (1.0) a	23.0 (1.3) a
Mean diameter at breast height for ponderosa pine (cm)	25.5 (0.9)	25.3 (1.1) a	26.3 (1.6) a
Mean dwarf mistletoe rating per plot	0.07 (0.05)	0.04 (0.03) a	0.19 (0.19) a
Metric SDI for all species	413 (20)	378 (22) a	516 (40) b
Metric SDI for ponderosa pine	321 (18)	277 (19) a	448 (38) b
Maximum ponderosa pine diameter (cm)	70.6	70.6	65.5
Maximum ponderosa pine diameter of mpb-killed (cm)	65.5	Na	65.5
Maximum ponderosa pine diameter of live (cm)	70.6	70.6	44.2

^a Means within rows for baseline and infested plots followed by the same letter are not significantly different at the 0.05 level (Benard–van Elteren rank test).

uninfested plots. The first classification tree model indicates a higher probability of mountain pine beetle attack with higher ponderosa pine basal area. The second classification tree used ponderosa pine SDI as the first splitting variable with lower ponderosa pine SDI resulting in a lower probability of infestation. Total basal area was the last splitting variable, again with higher stocking resulting in a higher probability of infestation.

Various studies have linked high stocking with higher probability of infestation or higher ponderosa pine mortality levels caused by mountain pine beetle (Sartwell, 1971; Sartwell and Dolph, 1976; McCambridge and Stevens, 1982; Schmid and Mata, 1992;

McCambridge et al., 1982). Our findings are consistent with these studies although our model establishes a lower basal area level, 17.1 m²/ha, where susceptibility to mountain pine beetle in ponderosa pine increases in our study area. For the Black Hills, Sartwell and Stevens (1975) proposed 34.4 m²/ha and Schmid and Mata (1992), after additional studies, suggested a threshold of a 27.5 m²/ha. Sartwell (1971) and Sartwell and Stevens (1975) indicate that better sites could support higher stocking levels with less beetle-caused mortality than poor sites. In general, ponderosa pine stands along the Colorado Front Range are found on very poor and dry sites (Meyer, 1934; Mogren, 1956; Schubert, 1974).

Table 2

Number of live, and mountain pine beetle-killed trees observed and expected by crown position in infested plots, Canyon Lakes Ranger District, Arapaho-Roosevelt National Forests, Colorado, 1998–2000^a

	Dominant	Co-dominant	Intermediate	Suppressed	Open-grown
Live					
Observed	6	31	56	87	9
Expected	21	67	44	51	6
Mountain pine beetle-killed					
Observed	34	100	30	13	2
Expected	20	64	42	49	5

^a $\chi^2 = 122.8$, d.f. = 4, $P < 0.0001$.

How can increased stocking cause this increase in susceptibility to mountain pine beetle? Some studies have suggested that higher stand densities increase stand susceptibility because tree vigor is compromised (Larsson et al., 1983; Mitchell et al., 1983; Waring and Pitman, 1985). In Arizona, Kolb et al. (1998) reported increased physiological responses associated with resistance mechanisms in ponderosa pine with reduced basal area. These results are consistent with the tree resistance hypothesis, which proposes that tree resistance to insect attack is reduced in high-density stands due to increased competition for resources that limits resource partitioning to resistance mechanisms (Berryman, 1976). Alternatively, reduced mortality in partial cut treatments has also been attributed to changes in stand microclimate that cause beetles to avoid attacking trees within the thinned stands (Amman et al., 1988; Bartos and Amman, 1989; Amman and Logan, 1998).

The second splitting variable in the second plot-based model was ponderosa pine quadratic mean diameter. The first node of the classification tree model developed for individual trees attacked separated trees 18.2 cm and smaller dbh into a low probability of infestation node. The second splitting variable was crown position with trees in the dominant and co-dominant positions, which are also the largest diameter trees, being more likely to be attacked. Within the intermediate crown position, larger trees were also the most likely to be attacked. Characteristics of trees in infested plots indicated that mountain pine beetle-killed trees were larger in diameter than surviving trees and that tree mortality most often occurred in the dominant and co-dominant crown positions.

Sartwell and Stevens (1975) indicated that in ponderosa pine, mountain pine beetle attacks stands with average dbh in the 20.3–30.5 cm range. McCambridge et al. (1982) reported less mountain pine beetle-caused mortality of ponderosa pine with dbh below 20.3–22.8 cm. Schmid and Mata (1996) indicated that mountain pine beetle attacks, most commonly, ponderosa pine trees when dbh > 20.3 cm. Our data is in agreement with these studies in that normally, attacks occur on trees larger than around 20.3–22.8 cm.

Trees initially attacked by mountain pine beetle become focus trees that attract additional beetles. When the focus tree is fully attacked, the insects

attack adjacent trees (Geizler and Gara, 1978; Schmid and Mata, 1996). In lodgepole pine stands, it has been proposed that the larger diameter trees serve as focus trees (Cole and Amman, 1969; Mitchell and Preisler, 1991). In ponderosa pine in the Black Hills, Eckberg et al. (1994) indicate that focus trees are those with *Armillaria* spp. infections, damaged by lightning or wind or attacked previously by mountain pine beetle but not killed. Studies have suggested that mountain pine beetle in ponderosa pine does not preferentially attack the larger trees in the stand, often leaving larger diameter trees unattacked after an infestation has subsided in a stand (McCambridge et al., 1982; Olsen et al., 1996).

We did not know exactly which tree was attacked first in our infested plots. Although the larger diameter trees may not be attacked first, our data suggests that once the infestation develops and subsides a larger proportion of larger diameter trees are killed. To an unknown extent, the higher proportion of larger diameter trees killed in infested plots may be a function of stand structure. Ponderosa pine stands in the Colorado Front Range typically occur in small groups or clumps with abundant natural openings and a wide range of diameter classes present. This stand structure contrasts with the intensively managed stands that characterize the Black Hills where stands are more uniformly stocked with less variation in diameter classes.

McCambridge et al. (1982) also indicated that a higher percentage of dwarf mistletoe infected trees were killed by mountain pine beetle than uninfected trees, but the influence of dwarf mistletoe on the susceptibility to attack could not be examined due to the confounding effects of other factors such as tree diameters. In our study sites, dwarf mistletoe infections although present, were very low so they are not believed to be influencing susceptibility to attack. There are stands within the Colorado Front Range where dwarf mistletoe infections are severe and extensive. In these stands, mountain pine beetle dynamics and tree susceptibility to attack may also be influenced by dwarf mistletoe infection levels. Although some studies started to examine the interactions between bark beetles and dwarf mistletoe and their role in killing their host, much remains to be learned about these interactions (Hawksworth et al., 1983; Hawksworth and Shaw, 1984; Hawksworth and Johnson, 1989; Linhart et al., 1994).

Profound ecological changes have been well documented in ponderosa pine forests across the western United States. Various studies indicate that Pre-European settlement ponderosa pine forests were much more open and park-like in nature, a condition that was maintained by periodic surface fires that killed ponderosa pine seedlings and saplings. These patterns have changed in the late 1800s and early 1900s when land managers began aggressive fire suppression programs and grazing in forest ecosystems became widespread. The result of altering these processes has been well documented increases in stand densities and fuels. Increased stand densities are thought to make stands more susceptible to insect outbreaks and large fires (Weaver, 1951, 1955, 1959; Cooper, 1960; Fisher et al., 1987; Mutch et al., 1993; Covington and Moore, 1994; Johnson, 1994; Arno et al., 1995a,b; Brown and Sieg, 1996; Fulé et al., 1997; Brown et al., 2000).

A direct relationship between higher levels of bark beetle-caused tree mortality as a result of increased tree densities resulting from fire suppression has yet to be demonstrated for any specific location. Nevertheless, factors associated with higher stocking levels such as reduced tree vigor, a more suitable environment for insect development and spread or a combination of both likely contribute to higher susceptibility to beetle attack.

Our findings are of particular importance as communities in the Colorado Front Range embark in restoration activities, which are meant to “restore historical variability in forest structure and fire processes” (Brown et al., 2001). Our results estimate the basal area level at which ponderosa pine forests along the Colorado Front Range become more susceptible to mountain pine beetle. Results from this study should be considered in restoration efforts, particularly when thinning from below, leaving only larger diameter trees unless the stocking levels are maintained below susceptible levels that reduce the probability of infestation by mountain pine beetle. Large diameter trees growing in high-density clumps will likely be susceptible to mountain pine beetle attack when the insect populations increase. Restoration efforts cognizant of these relationships will likely be more successful in achieving their objectives. Managing stands or landscapes less susceptible to mountain pine beetle could result in maintaining a variety of resource objectives.

Acknowledgements

The authors would like to thank Keith Lingenfelter, Isabel Munck, Brett Sanborn, Chastity Sheets, and Erica Thompson for their assistance in conducting the field work; Paul Langowski and Steve Johnson, Arapahoe-Roosevelt National Forest for providing information on the location of infestations; Rudy King for statistical support; Joyce VanDeWater for preparing the figures; and to Mike Battaglia, Robert Cain, Steve Munson, Joel McMillin, and Wayne Shepperd for reviews of earlier versions of the manuscript; and the anonymous reviewers whose comments significantly improved this manuscript.

References

- Amman, G.D., McGregor, M.D., Cahill, D.B., Klein, W.H., 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the rocky mountains. General Technical Report INT-36. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, 19 pp.
- Amman, G.D., Logan, J.A., 1998. Silvicultural control of mountain pine beetle: prescriptions and the influence of microclimate. *Am. Entomol.* 44, 166–177.
- Amman, G.D., McGregor, M.D., Dolph Jr., R.E., 1989. Mountain pine beetle. For. Ins. Dis. Leaf. 2. USDA Forest Service, 9 pp.
- Amman, G.D., McGregor, M.D., Schmitz, R.F., Oakes, R.D., 1988. Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands. *Can. J. For. Res.* 18, 688–695.
- Anhold, J.A., Jenkins, M.J., Long, J.N., 1996. Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. *West. J. Appl. For.* 11, 50–53.
- Arno, S.F., Harrington, M.G., Fiedler, C.E., Carlson, C.E., 1995a. Restoring fire-dependent ponderosa pine forests in western Montana. *Rest. Mgmt. Notes* 13, 32–36.
- Arno, S.F., Scott, J.H., Hartwell, M.G., 1995b. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. Research Paper INT-481. USDA Forest Service, Intermountain Research Station, Ogden, UT, 25 pp.
- Bartos, D.L., Amman, G.D., 1989. Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestations. Research Paper INT-400. USDA Forest Service, Intermountain Research Station, Ogden, UT, 10 pp.
- Berryman, A.A., 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Entomol.* 5, 1225–1233.
- Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. *Classification and Regression Trees*. Chapman & Hall, New York, 358 pp.

- Brown, P.M., D'Amico, D.R., Carpenter, A.T., Andrews, D., 2001. Restoration of montane ponderosa pine forests in the Colorado Front Range: a forest ecosystem management plan for the city of Boulder. *Ecol. Rest.* 19, 19–26.
- Brown, P.M., Ryan, M.G., Andrews, T.G., 2000. Historical surface fire frequency in ponderosa pine stands in research natural areas, Central Rocky Mountains and Black Hills, USA. *Nat. Area J.* 20, 133–139.
- Brown, P.M., Sieg, C.H., 1996. Fire history in interior ponderosa pine forests of the Black Hills, South Dakota, USA. *Int. J. Wildl. Fire* 6, 97–105.
- Chojnacky, D.C., Bentz, B.J., Logan, J.A., 2000. Mountain pine beetle attack in ponderosa pine: comparing methods for rating susceptibility. Research Paper RMRS-26. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 10 pp.
- Cole, W.E., Amman, G.D., 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. Research Note INT-95. Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, 7 pp.
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forest since white settlement. *Ecol. Monogr.* 30, 129–164.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. For.* 92, 39–47.
- Eckberg, T.B., Schmid, J.M., Mata, S.A., Lundquist, J.E., 1994. Primary focus trees for the mountain pine beetle in the Black Hills. Research Note RM-531. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 10 pp.
- Fisher, R.F., Jenkins, M.J., Fisher, W.F., 1987. Fire and the prairie-forest mosaic of Devils Tower National Monument. *Am. Midl. Nat.* 117, 250–257.
- Fulé, P.Z., Covington, W.W., Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol. Appl.* 7, 895–908.
- Geizler, D.R., Gara, R.I., 1978. Mountain pine beetle attack dynamics in lodgepole pine, pp. 182–287. In: Beryman, A.A., Amman, G.D., Stark, R.W. (Eds.), *Proceedings of the Symposium on Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*, April 25–27, 1978, Pullman, WA. For. Wild. Range Exp. Stn., Univ. of Idaho, Moscow; USDA For. Serv., For. Ins. Dis. Res., Washington, DC; Int. For. Range Exp. Stn., Ogden, UT, 224 pp.
- Goyer, R., Wagner, M.R., Schowalter, T.C., 1998. Current and proposed technologies for bark beetle management. *J. For.* 96, 29–33.
- Harris, J.L., Mask, R., Witcosky, J., 2002. Forest insect and disease conditions in the Rocky Mountain region, 2000–2001. Renew. Res. USDA Forest Service, Rocky Mountain Region, 42 pp.
- Harris, J.L., Frank, M., Johnson, S., 2001. Forest insect and disease conditions in the Rocky Mountain region 1997–1999. Renew. Res. USDA Forest Service, Rocky Mountain Region, 39 pp.
- Hawksworth, F.G., 1977. The 6-class dwarf mistletoe rating system. General Technical Report RM-48. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 7 pp.
- Hawksworth, F.G., Johnson, D.W., 1989. Biology and management of dwarf mistletoe in lodgepole pine in the Rocky Mountains. General Technical Report RM-169. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 38 pp.
- Hawksworth, F.G., Lister, K.C., Cahill, D.B., 1983. Phloem thickness in lodgepole pine: its relationship to dwarf mistletoe and mountain pine beetle (Coleoptera: Scolytidae). *Environ. Entomol.* 12, 1447–1448.
- Hawksworth, F.G., Shaw III, C.G., 1984. Damage and loss caused by dwarf mistletoes in coniferous forests of western North America. In: Wood, R.K.S., Jellis, G.J. (Eds.), *Plant Diseases: Infection, Damage, and Loss*. Blackwell Scientific Publications, Oxford, pp. 285–297.
- Hedden, R.L., 1981. Hazard-rating system development and validation: an overview, pp. 9–12. In: Hedden, R.L., Barras, S.J., Coster, J.E. (Eds.), *Proceedings of the Symposium on Hazard-rating Systems in Forest Pest Management*, August 1–July 31, 1980, Athens, GA. General Technical Report WO-27. USDA Forest Service, 169 pp.
- Johnson, M., 1994. Changes in southwestern forests: stewardship implications. *J. For.* 92, 16–19.
- Johnston, B.C., 1987. Plant associations of Region 2: potential plant communities of Wyoming, South Dakota, Nebraska, Colorado, and Kansas. USDA Forest Service, R2-ECOL-87-2, 429 pp.
- Kolb, T.E., Holmberg, K.M., Wagner, M.R., Stone, J.E., 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. *Tree Physiol.* 18, 375–381.
- Larsson, S., Oren, R., Waring, R.H., Barrett, J.W., 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *For. Sci.* 29, 395–402.
- Linhart, Y.B., Snyder, M.A., Gibson, J.P., 1994. Differential host utilization by two parasites in a population of ponderosa pine. *Oecologia* 98, 117–120.
- Long, J.N., Daniel, T.W., 1990. Assessment of growing stock in uneven-aged stands. *West. J. Appl. For.* 5, 93–96.
- Mast, J.N., Veblen, T.T., Linhart, Y.B., 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *J. Biogeogr.* 25, 743–755.
- McCambridge, W.F., Hawksworth, F.G., Edminster, C.B., Laut, J.G., 1982. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. Research Paper RM-235. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 7 pp.
- McCambridge, W.F., Stevens, R.E., 1982. Effectiveness of thinning ponderosa pine stands in reducing mountain pine beetle-caused tree losses in the Black Hills—preliminary observations. Research Note RM-144. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 3 pp.
- Meyer, W.H., 1934. Growth in selectively cut ponderosa pine forests of the Pacific Northwest. USDA Tech. Bull. No. 407, 66 pp.
- Mitchell, R.G., Preisler, H.K., 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *For. Sci.* 37, 1390–1408.

- Mitchell, R.G., Waring, R.H., Pitman, G.B., 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.* 29, 204–211.
- Mogren, E.W., 1956. A site index classification for ponderosa pine in northern Colorado. Number 5. *Sch. For. Range Manage.*, Colorado A&M College, Fort Collins, CO, 2 pp.
- Mutch, R.W., Arno, S., Brown, J., Carlson, C., Omar, C., Peterson, J., 1993. Forest health in the Blue Mountains: a management strategy for fire-adapted ecosystems. General Technical Report PNW-310. USDA Forest Service, Pacific Northwest Research Station, Portland, OR, 14 pp.
- Negrón, J.F., 1997. Estimating probabilities of infestation and extent of damage by the roundheaded pine beetle in ponderosa pine in the Sacramento Mountains, New Mexico. *Can. J. For. Res.* 27, 1936–1945.
- Negrón, J.F., 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. *For. Ecol. Manage.* 107, 71–85.
- Norwood, P.K., Sampson, A.R., McCarroll, K., Staum, R., 1989. A multiple comparisons procedure for use in conjunction with the Benard–van Elteren Test. *Biometrics* 45, 1175–1182.
- Obedzinski, R.A., Schmid, J.M., Mata, S.A., Olsen, W.K., Kessler, R.R., 1999. Growth of ponderosa pine stands in relation to mountain pine beetle susceptibility. General Technical Report RMRS-GTR-28. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 13 pp.
- Olsen, W.K., Schmid, J.M., Mata, S.A., 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *For. Sci.* 42, 310–327.
- Peet, R.K., 1981. Forest vegetation of the Colorado Front Range. *Vegetatio* 45, 3–75.
- Perkins, D.L., Roberts, D.W., 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *For. Ecol. Manage.* 174, 495–510.
- Sartwell, C., 1971. Thinning ponderosa pine to prevent outbreaks of mountain pine beetle, pp. 41–52. In: Baumgartner, D.M. (Ed.), *Proceedings of the Precommercial Thinning of Coastal and Intermountain Forests in the Pacific Northwest*, February 3–4, 1971, Pullman, WA. *Coop. Ext. Serv., Dep. For. Range Manage.*, Washington State Univ., Pullman, WA, 109 pp.
- Sartwell, C., Stevens, R.E., 1975. Mountain pine beetle in ponderosa pine: prospects for silvicultural control in second-growth stands. *J. For.* 73, 136–140.
- Sartwell, C., Dolph Jr., R.E., 1976. Silvicultural and direct control of mountain pine beetle in second-growth ponderosa pine. Research Note PNW-268. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, 8 pp.
- Schmid, J.M., Mata, S.A., 1992. Stand density and mountain pine beetle-caused tree mortality in ponderosa pine stands. Research Note RM-515. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 4 pp.
- Schmid, J.M., Mata, S.A., Obedzinski, R.A., 1994. Hazard rating ponderosa pine stands for mountain pine beetles in the Black Hills. Research Note RM-529. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 4 pp.
- Schmid, J.M., Mata, S.A., 1996. Natural variability of specific forest insect populations and their associated effects in Colorado. General Technical Report GTR-275. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 14 pp.
- Schubert, G.H., 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. Research Paper RM-123. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 71 pp.
- Shore, T.L., Safranyik, L., 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Information Report BC-X-336. Pacific and Yukon Region, For. Canada, 12 pp.
- Stage, A.R., 1968. A tree-by-tree measure of site utilization for grand fire related to stand density index. Research Paper INT-77. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, 7 pp.
- Steinberg, D., Colla, P., 1992. CART: a supplementary module for SYSTAT. SYSTAT, Evanston, IL, 292 pp.
- Waring, R.H., Pitman, G.B., 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66, 889–897.
- Weaver, H., 1951. Fire as an ecological factor in the southwestern ponderosa pine forests. *J. For.* 49, 93–98.
- Weaver, H., 1955. Fire as an enemy, friend, and tool in forest management. *J. For.* 53, 499–504.
- Weaver, H., 1959. Ecological changes in the ponderosa pine forest of the warm springs Indian reservation in Oregon. *J. For.* 57, 15–20.
- Whitney, G., 1983. *Colorado Front Range: A Landscape Divided*. Johnson Books, Boulder, 164 pp.
- Wood, D.L., Bright Jr., D.E., 1992. A catalog of Scolytidae and Platypodidae (Coleoptera). Part 2. Taxonomic Index Volume A. *Great Basin Nat. Mem.*, Number 13. Brigham Young University, Provo, UT, 833 pp.