

PROBABILITY OF INFESTATION AND EXTENT OF MORTALITY MODELS FOR MOUNTAIN PINE BEETLE IN LODGEPOLE PINE FORESTS IN COLORADO

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Abstract—The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a significant agent of tree mortality in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests throughout western North America. A large outbreak of mountain pine beetle caused extensive tree mortality in north-central Colorado beginning in the late 1990s. We use data from a network of plots established in 2006–2007 on the Sulphur Ranger District of the Arapaho and Roosevelt National Forests to develop simple probability of infestation and extent of mortality models using classification and regression trees, respectively. A classification tree indicated that when live lodgepole pine basal area was equal to or greater than 59.3 ft²/acre pre-outbreak, the probability of infestation increased. A second classification tree added lodgepole pine mean diameter as a second splitting variable. The rate of correct classification for both models was greater than 0.79. Two regression trees also used live pre-outbreak lodgepole pine basal area as a splitting variable and indicated increasing basal area killed with increasing live lodgepole pine basal area. These simple models use readily available data from forest inventories and can be used to identify stands, based on forest stand conditions, where mountain pine beetle is more likely to occur and the potential extent of lodgepole pine tree mortality should an outbreak occur.

Keywords: *Dendroctonus ponderosae*, *Pinus contorta*, bark beetles, risk and hazard rating

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INTRODUCTION

The mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) is a major disturbance agent in coniferous forests of western North America (Negrón and Fettig 2014). It is distributed from southern British Columbia, Canada, south to Baja California, Arizona, and New Mexico and east to the Black Hills of South Dakota (Wood 1982). However, as a result of climate change its range has extended to the north of British Columbia and the east into Alberta (Fauria and Johnson 2009; Robertson et al. 2009). In addition, the insect was recently reported in Nebraska (Costello and Schaupp 2011). Within its range, about 15 species of pines (*Pinus* spp.) are known to be hosts, but preferred ones include lodgepole pine (*Pinus contorta* Dougl. ex Loud.), sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* P. Lawson and C. Lawson), and limber pine (*Pinus flexilis* E. James) (Negrón and Fettig 2014).

Bark beetles are integral components of forest ecosystems that help regulate forest structure and composition (Kayes and Tinker 2012). Tree mortality associated with endemic bark beetle infestations influences critical ecological processes such as creating small-scale disturbances and accumulation of coarse woody debris that characterize functioning ecosystems (Harmon et al. 1986; Klutsch et al. 2014; Lundquist and Negrón 2000). Eruptive populations, however, can affect large landscapes resulting in timber losses and safety hazards in high value areas such as campgrounds, recreational areas and rights of way, among other challenges for land managers.

In Colorado, mountain pine beetles emerge from previously infested trees towards the end of July and early August (McCambridge 1964; Tishmack et al. 2005). The beetles attack new trees in synchronized large numbers mediated by insect-produced aggregation pheromones. These “mass attacks” overcome the defensive mechanisms of the tree, the most important being resin production, which is released at the time of insect attack (Raffa and Berryman 1983). Adults lay eggs from which larvae hatch in a few days and develop through the summer. The larvae overwinter, and in the following spring, the insects pupate and later emerge from the trees, thus completing the life cycle. The insect exhibits primarily a 1-year life cycle, but this can take 2 years in cooler, higher elevations and northern latitudes (Gibson et al. 2009; Safranyik and Carroll 2006).

Large epidemics have been occurring across the western United States since the 1990s (Negrón and Fettig 2014). In Colorado, about 3.4 million acres have been affected by MPB from 1996 to 2013, reaching its peak in yearly mortality in 2008 with populations declining after that (Colorado State Forest Service 2015). The outbreak affected primarily lodgepole pine, although ponderosa pine forests were also impacted (West et al. 2014).

Under endemic conditions, MPB attacks primarily trees that are under stress as a result of root disease, dwarf mistletoe infections, lightning strikes, or other stressors. Eruptive populations prefer to attack large-diameter trees growing in overstocked stands. Trees growing under these conditions exhibit reduced vigor and compromised defensive mechanisms while still providing the thick phloem that contributes to population increases (Amman 1972; Waring and Pitman 1985).

Stand hazard rating systems used to identify stands more likely to be infested by MPB or to experience potential mortality, or both, are useful tools for forest managers and forest health specialists in support of forest plans and management projects. Published rating systems for this purpose have been developed for MPB in lodgepole pine forests, but are primarily for use in the Intermountain Region (e.g., Amman et al. 1977) or Canada (e.g., Shore and Safranyik 1992). Although a number of studies have examined tree mortality from the recent outbreak in Colorado (Collins et al. 2012; Klutsch et al. 2009), no published data is available describing stand or tree attributes, or both, that make a stand more likely to be infested by MPB or the extent of mortality that could occur once a stand is infested. This type of information would help identify stands more likely to be affected when MPB populations increase. The information could also be used in forest simulation models such as the Forest Vegetation Simulator and for preparing risk maps (Krist 2017). Klutsch et al. (2009) published data from north-central Colorado indicating that during the recent outbreak, the density and basal area of live overstory lodgepole declined by 62 percent and 71 percent in stands affected by MPB, respectively. In this paper we revisit the data published by Klutsch et al. (2009) and use it to develop simple models to estimate the probability of infestation and the potential extent of mortality in affected lodgepole pine forests in Colorado.

METHODS

The data used here come from a study conducted by Klutsch et al. (2009) that examined stand conditions and the accumulation of coarse woody debris in MPB-affected, unmanaged stands in north-central Colorado. The study was conducted during the summers of 2006 and 2007 in the Sulphur Ranger District, Arapaho and Roosevelt National Forests, Colorado. Lodgepole pine covers about 45 percent of the 442,000 acres within the District, with an approximate elevational range of 8,200–11,500 ft. Engelmann spruce (*Picea engelmannii* [Parry]) and sub-alpine fir (*Abies lasiocarpa* [Hook.] Nutt. var. *lasiocarpa*) make up 25 percent of the tree cover and are the predominant trees at higher elevations, on north slopes, and along streams.

We used a geographic information system in combination with vegetation cover maps to randomly select plot locations within the lodgepole pine forest type. Plots were distributed throughout the study area with a minimum distance from any roads of one-quarter of a mile, and plots were separated from one another by at least the same distance. Plots were one-twentieth of an acre fixed-radius plots, and we established a total 170 plots in MPB-infested stands and 51 plots in uninfested stands.

Site data collected from each plot included elevation, aspect, and percent slope measured at plot center. For each plot tree equal to or greater than 5 inches d.b.h. (diameter at breast height), we recorded species, d.b.h., and whether the tree was live, killed by MPB (including successfully infested trees if present), or dead due to other causes. In the original publication by Klutsch et al. (2009), all trees equal to or greater than 1-inch d.b.h. were included, but a cut off of 5-inches d.b.h. is used here as it is more consistent with forest management applications.

Currently infested trees were identified by the presence of boring debris at the base of the tree, pitch tubes, and life stages inside the tree. Previously MPB-killed trees were identified by foliage discoloration, remaining pitch tubes in the bark, emergence holes, and the presence of egg galleries under the bark.

From the tree data collected, we calculated basal area, tree density, and mean and quadratic mean diameter for all trees, for lodgepole pine only and for non-host species, and percent lodgepole pine basal area. Lodgepole pine stand density index (SDI) was calculated using the summation procedure, which represents individual tree utilization of the site (Long and Daniel 1990; Stage 1968). We calculated percent of maximum SDI using 690 as the maximum value (Long 1985).

We examined the differences in stand characteristics between infested and uninfested plots with a Wilcoxon rank sum test and a Chi-square test for aspect (categorized into four cardinal directions). Although tree mortality had diminished at the time of our study, we acknowledge that the outbreak had not fully collapsed at the time of our sampling. Additional tree mortality likely occurred in the infested plots after our sampling and may have occurred in plots that were not infested at the time of measurement. However, our infested plots included tree mortality that occurred early in outbreak development, and therefore represent conditions initially selected by the MPB.

Classification and regression trees (CART), a statistical technique developed by Breiman et al. (1984), were used to construct probability of infestation and extent of mortality models in terms of basal area killed by MPB. Classification trees were developed to estimate the probability of infestation based on stand conditions, and regression trees were used to estimate the extent of MPB-caused tree mortality in infested plots. The analysis was conducted using R (R Development Core Team 2008) and the “rpart” package (version 4.1-10) available for CART analysis (Therneau et al. 2015).

For classification trees, CART performs a binary recursive partitioning of the data set based on predictor variables into the most pure class memberships possible (Verbyla 1987). When the response variable is continuous, homogenous clusters with reduced variances are produced. The results are easy to use dichotomous tree diagrams. These diagrams have predictor variables as splitting rules and also have class memberships (infested or uninfested stands) at the end nodes for classification trees or average of the response variable (tree mortality) for regression trees (Breiman et al. 1984). Classification trees are cross-validated during the model construction phase by dividing the data set into 10 subsets. Nine subsets are then used for model construction and the 10th subset is used for validation. This procedure is repeated until all subsets have been used for model construction and for model validation. The cross-validation estimates of classification accuracy, or percent of cases correctly classified, obtained from each validation run are averaged, which results in an overall cross-validation estimate. The highest cross-validation estimate of classification accuracy is used to select the best model.

The cross-validation estimate is a nearly unbiased estimate of how well the model will perform with a new sample of cases from the same population.

Previous studies examining probability of infestation and extent of mortality caused by bark beetles have applied CART methodology for other beetle species including spruce beetle (*Dendroctonus rufipennis* Kirby) (Reynolds and Holsten 1994; 1996) in Alaska, roundheaded pine beetle (*Dendroctonus adjunctus* Blandford) in New Mexico (Negrón 1997) and Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in Colorado (Negrón 1998).

RESULTS

Average stand characteristics were, for the most part, similar in infested and uninfested plots (table 1). Uninfested plots had significantly higher trees per acre of non-host species while infested plots had significantly higher lodgepole pine basal area, percent of lodgepole pine basal area, lodgepole pine SDI, and lodgepole pine percent of maximum SDI. By definition, MPB-killed trees only occurred in the infested plots. We observed no differences between infested and uninfested plots in elevation or percent slope, and infested and uninfested plots were distributed equally among north, east, south, and west facing slopes (Chi-square = 3.40, $df = 3$, $P = 0.3348$).

We identified two classification trees to estimate the probability of infestation by MPB in lodgepole pine stands (fig. 1). The first tree had one split using lodgepole pine basal area as the splitting variable and two terminal nodes; stands with a basal area equal or greater than 59.3 ft²/ac exhibiting a higher probability of infestation of 0.61 (fig. 1a). A second tree had three splits and four terminal nodes (fig. 1b). The first split was the same as indicated for the first tree. The second splitting variable was lodgepole pine mean diameter with no infested stands having a mean lodgepole pine diameter of less than 7.2 inches being attacked by MPB. The third split was also on lodgepole pine basal area, but in this case, the split was basal area less than 44.1 ft²/ac having a higher probability of infestation of 0.39. Both trees had a true positive classification rate greater than 0.8 with the true negative classification rate from 0.57 to 0.83 for the 1-split tree and the 3-split tree, respectively. The 1-split tree had an overall accuracy rate of 0.79, and the 3-split tree had an overall accuracy rate of 0.82 (table 2).

Two regression trees were identified to estimate the extent of mortality in infested plots (fig. 2). The first tree had a single split using two terminal nodes with stands having a lodgepole pine basal area equal to or greater than 106.5 ft²/ac exhibiting an average basal area killed of 104.1 ft²/ac (fig. 2a). The second tree added a second split; when lodgepole pine basal area was equal or greater than 175.6 ft²/ac, the average lodgepole pine basal area killed was 134.0 ft²/ac (fig. 2b). The R^2 for the 1-split model is 0.40 and for the 2-split model it increases to 0.47.

Table 1—Means (standard error) of stand characteristics for infested and uninfested plots. Uninfested plots had a higher TPA of non-host species; infested plots had higher lodgepole pine BA, percent of lodgepole pine BA, lodgepole pine SDI, and lodgepole pine percent of maximum SDI. No differences were observed for the rest of the variables. Only infested plots had MPB-caused tree mortality.

Variable	Infested plots (n = 170)	Uninfested plots (n = 51)	P
All species d.b.h. (inches)	9.1 (0.1)	8.7 (0.3)	0.08
PICO d.b.h. (inches)	9.5 (0.2)	9.0 (0.3)	0.11
Non-host d.b.h.	8.5 (0.2)	8.2 (0.3)	0.35
All species QMD (inches)	9.5 (0.1)	9.1 (0.3)	0.10
PICO QMD (inches)	9.9 (0.2)	9.2 (0.3)	0.09
Non-host QMD (inches)	8.9 (0.2)	8.6 (0.4)	0.49
All species TPA	311.6 (11.0)	307.1 (21.5)	0.88
PICO TPA	248.5 (11.6)	219.2 (23.1)	0.08
Non-host TPA	63.2 (7.1)*	87.8 (13.1)*	0.04
All species BA (ft ² /acre)	143.1 (4.1)	133.4 (11.8)	0.09
PICO BA (ft ² /acre)	113.2 (3.6)*	94.7 (11.4)*	0.001
Non-host BA (ft ² /acre)	30.0 (3.6)	38.7 (6.3)	0.09
Percent PICO BA	82.3 (1.9)*	71.7 (4.1)*	0.02
MPB-killed BA (ft ² /acre)	78.8 (3.2)	0 (0)	—
All species SDI	268.3 (7.4)	253.2 (20.4)	0.16
PICO SDI	211.7 (6.9)*	178.9 (20.0)*	0.004
Percent of maximum PICO SDI ^a	30.7 (1.0)*	25.9 (2.9)*	0.004
Elevation	9,508.0 (53.3)	9,575.5 (80.7)	0.34
Percent slope	25.5 (1.1)	24.1 (1.8)	0.72
Aspect category (no. of plots)	E: 36, N: 57, S: 40, W: 37	E: 5, N: 20, S: 14, W: 12	0.33 ^b

Abbreviations: d.b.h. = diameter at breast height, QMD = quadratic mean diameter, TPA = trees per acre, BA = basal area, SDI = stand density index, PICO = lodgepole pine, MPB = mountain pine beetle.

Means with asterisks are significantly different between infested and uninfested plots, Wilcoxon rank sum test, $P < 0.05$.

^a Based on maximum Stand Density Index of 690.

^b Chi-square test.

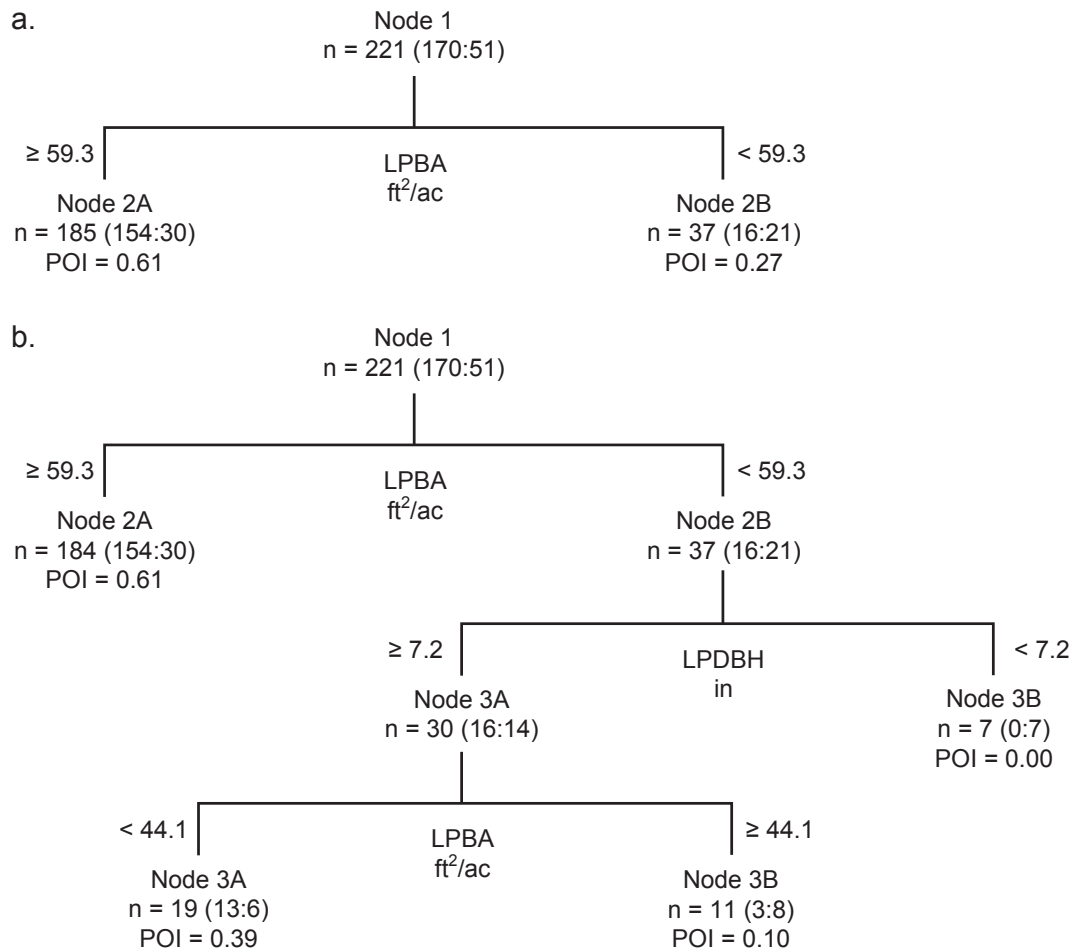


Figure 1—Classification trees to estimate the probability of infestation by mountain pine beetle in lodgepole pine forests. Numbers in parentheses indicate the number of infested and uninfested plots, respectively. The first tree (a) uses lodgepole pine basal area as a splitting variable with a higher level associated with a higher probability of infestation. The second tree (b) adds a split based on lodgepole pine mean stand d.b.h., with larger trees associated with a higher probability of attack and another split based on lodgepole pine basal area with a lower level associated with a higher probability of attack. Abbreviations are LPBA = lodgepole pine basal area, LPDBH = lodgepole pine mean diameter, POI = probability of infestation, n = number of plots. Arapaho-Roosevelt National Forest, CO, 2006–2007.

Table 2—Cross-validation statistics for classifications trees for estimating the probability of infestation by mountain pine beetle.

Model	True positive rate ^a	True negative rate ^b	Accuracy rate ^c	Error rate (1-accuracy) ^d
1-split	0.84	0.57	0.79	0.21
3-split	0.82	0.83	0.82	0.18

^a Proportion of actual positive cases that are correctly classified, true positive rate. Between 0 (worst) and 1 (best).

^b Proportion of actual negative cases that are correctly classified, true negative rate. Between 0 (worst) and 1 (best).

^c Proportion of correct positive and negative classifications. Between 0 (worst) and 1 (best).

^d Proportion of incorrect positive and negative classification. Between 0 (best) and 1 (worst).

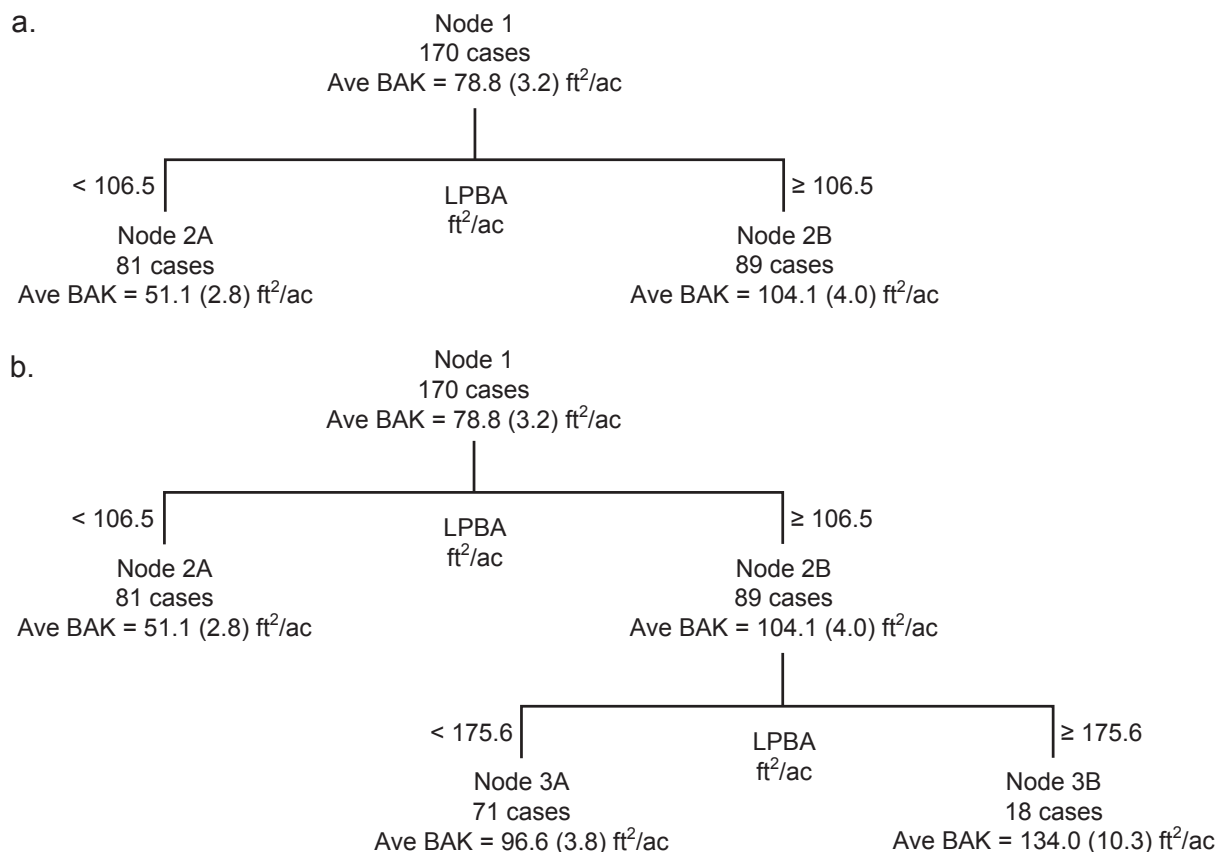


Figure 2—Regression trees to estimate the extent of lodgepole pine tree mortality caused by mountain pine beetle in infested plots in lodgepole pine forests based on lodgepole pine basal area. Abbreviations are LPBA = lodgepole pine basal area and BAK = basal area killed. Numbers in parentheses indicate standard error of the mean. The first tree (a) has one split and two terminal nodes and the second tree (b) has two splits and three terminal nodes. Higher basal area was always associated with higher tree mortality. Arapaho-Roosevelt National Forest, CO, 2006–2007.

DISCUSSION

Our study resulted in simple classification tree models to estimate the probability of infestation by MPB in lodgepole pine stands. We were also able to develop regression trees to estimate the extent of expected mortality in an infested stand. Lodgepole pine basal area was significantly higher in the infested plots and it was the most important splitting variable for identifying stands with a higher probability of infestation and a higher anticipated mortality level. Increased stand density has been well-documented to be associated with increased MPB infestations and tree mortality in lodgepole pine (Anhold and Jenkins 1987; Anhold et al. 1996; Mitchell et al. 1983; Shore and Safranyik 1992; and see Fettig et al. 2007).

Lodgepole pine mean d.b.h. was not significantly different between infested and uninfested plots, but rather it was the other splitting variable used in the second classification tree. Mean d.b.h. for the infested and uninfested stands was greater than 9 inches. Amman et al. (1977) indicated that susceptibility to MPB infestation increased with a mean d.b.h. greater than

8 inches. Although differences in mean or quadratic lodgepole pine d.b.h. were not significant between our infested and uninfested plots, plots with larger mean lodgepole pine d.b.h. were more likely to be infested. Mountain pine beetle is known to prefer larger diameter lodgepole pine trees for infestation (Mitchell and Preisler 1991). Phloem thickness increases with tree diameter and is directly related to higher brood production (Amman 1972; Shrimpton and Thomson 1985).

The probability of infestation model with two terminal nodes separates stands into what could be considered, for practical purposes, stands more likely and less likely to be infested by MPB. When trees of suitable size for MPB to attack are available, this simple classification may suffice for use in forest planning or other practical purposes. The second classification tree has four terminal nodes and adds stand lodgepole pine mean d.b.h. as another splitting variable. This second model provides a small increase in classification accuracy, but perhaps more importantly, it improves the correct classification rate of true negative cases. Its use would be more complicated and perhaps not warranted considering that the proper use of these models is for general guidelines in identifying stands more likely to be infested, but it would be up to the user, their objectives, and desired level of precision that would determine the most appropriate model to use.

The regression trees used to estimate the extent of mortality should an infestation occur also included lodgepole pine basal area as a splitting variable. The first model with two terminal nodes can classify stands into a potential high extent of mortality and a potential low extent of mortality. Adding a second split, also based on lodgepole pine basal area, creates what could be considered three potential extent of mortality classes. A lodgepole pine basal area less than 107 ft²/ac would represent low potential mortality; basal area greater than or equal to 107 ft²/ac but less than 176 ft²/ac would represent medium potential mortality; and basal area greater than or equal to 176 ft²/ac would represent a high potential mortality level. As with the probability of infestation, the model to be used would depend on user objectives.

The basal area level where the probability of infestation increases (59.3 ft²/acre) is lower than the level where the extent of mortality splits into lower and higher potential mortality classes in the infested plots (106.5 ft²/acre). This was also the case in a study with roundheaded pine beetle in Utah, where the probability of infestation increased with a ponderosa pine basal area of 250 ft²/ac and the extent of mortality split was at 310 ft²/ac (Negrón et al. 2000). In a study in Colorado with MPB in ponderosa pine, the probability of infestation increased with a basal area of 74 ft²/ac, and although a regression tree for the extent of mortality was not presented, the mean basal area in infested plots was 107 ft²/ac (Negrón and Popp 2004). Other studies with lodgepole pine do not indicate a basal area level where the probability of infestation increases; however, thinning studies have indicated that basal area to reduce mortality levels ranges from about 87 ft²/ac (Mitchell et al. 1983) to 100 ft²/ac (McGregor et al. 1987). These levels are close to or slightly lower than the level identified from our data. It is possible that the basal area levels that increase the probability of infestation by bark beetles are lower than the level at which the extent of mortality increases. This question warrants further examination.

Determining the probability of infestation and estimating potential mortality continues to be important for land managers as management strategies are developed and implemented. Rating systems are rarely validated and some that have been tested using independent data sets have not shown a high predictive ability (Bentz et al. 1993). That being the case, rating systems still provide guidelines useful to forest managers, as the objective is to identify stands where MPB can cause tree mortality. Moreover, the ratings are to be used under the umbrella of multiple use management objectives.

Management Application

The models presented in this study offer thresholds that could help forest managers and forest health specialists identify areas where MPB populations are more likely to cause tree mortality and to what extent. The models are based on variables commonly available in forest inventory databases and provide an easy to use tool. Stands could be evaluated for probability of infestation or extent of potential mortality, or both, based on lodgepole pine basal area. Probability of infestation could be simply classified as high when lodgepole pine basal area is equal to or greater than 59.3 ft²/acre or classified as low when lodgepole pine basal area is below 59.3 ft²/acre. For extent of mortality potential, two (low or high) or three classes (low, medium, and high) based on existing live lodgepole pine basal can be used. These simple models can be used as general guidelines for determining susceptibility to MPB and incorporated into forest planning or project areas, or both.

REFERENCES

- Amman, G.D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *Journal of Economic Entomology*. 65: 138–140.
- Amman, G.D.; McGregor, M.D.; Cahill, D.B.; [et al.]. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. Gen. Tech. Rep. INT-GTR-36. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 19 p.
- Anhold, J.A.; Jenkins, M.J. 1987. Potential mountain pine beetle (Coleoptera: Scolytidae) attack of lodgepole pine as described by stand density index. *Environmental Entomology*. 16: 738–742.
- Anhold, J.A.; Jenkins, M.J.; Long, J.N. 1996. Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. *Western Journal of Applied Forestry*. 11: 50–53.
- Bentz, B.J.; Amman, G.D.; Logan, J.A. 1993. A critical assessment of risk classification systems for the mountain pine beetle. *Forest Ecology and Management*. 61: 349–366.
- Breiman, L.; Friedman, J.H.; Olshen, R.A.; [et al.]. 1984. *Classification and regression trees*. New York: Chapman & Hall. 358 p.
- Collins, J.J.; Rhoades, C.C.; Battaglia, M.A.; [et al.]. 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. *Forest Ecology and Management*. 284: 260–268.
- Colorado State Forest Service. 2015. 2015 Report on the health of Colorado's forests: 15 years of change. Fort Collins, CO: Colorado State Forest Service; Colorado State University. 27 p.
- Costello, S.L.; Schaupp, W.C., Jr. 2011. First Nebraska State collection record of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae). *Coleopterists Bulletin*. 65: 21–23.
- Fauria, M.M.; Johnson, E.A. 2009. Large-scale climatic patterns and area affected by mountain pine beetle in British Columbia, Canada. *Journal of Geophysical Research*. 114(G1): 1–19.
- Fettig, C.J.; Klepzig, K.D.; Billings, R.F.; [et al.]. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management*. 238: 24–53.
- Gibson, K.; Kegley, S.; Bentz, B. 2009. Mountain pine beetle. Forest Insect and Disease Leaflet 2. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. https://www.fs.usda.gov/Internet/fse_documents/fsbdev2_042835.pdf [Accessed February 2, 2017].
- Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; [et al.]. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*. 15: 133–302.
- Kayes, L.J.; Tinker, D.B. 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. *Forest Ecology and Management*. 263: 57–66.
- Klutsch, J.G.; Beam, R.D.; Jacobi, W.R.; [et al.]. 2014. Bark beetles and dwarf mistletoe interact to alter downed woody material, canopy structure, and stand characteristics in northern Colorado ponderosa pine. *Forest Ecology and Management*. 315: 63–71.

- Klutsch, J.G.; Negrón, J.F.; Costello, S.L.; [et al.]. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management*. 258: 641–649.
- Krist, F. 2017. 2013–2027 National insect and disease risk map. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team. <https://www.fs.fed.us/foresthealth/technology/nidrm.shtml#NIDRMReport> [Accessed February 2, 2017].
- Long, J.N. 1985. A practical approach to density management. *The Forestry Chronicle*. 61: 23–27.
- Long, J.N.; Daniel, T.W. 1990. Assessment of growing stock in uneven-aged stands. *Western Journal of Applied Forestry*. 5: 93–96.
- Lundquist, J.E.; Negrón, J.F. 2000. Endemic forest disturbances and stands structure of ponderosa pine (*Pinus ponderosa*) in the Upper Pine Creek Research Natural Area, South Dakota, USA. *Natural Areas Journal*. 20: 126–132.
- McCambridge, W.F. 1964. Emergence period of Black Hills beetles from ponderosa pine in the central Rocky Mountains. Res. Note RM-RN-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.
- McGregor, M.D.; Amman, G.D.; Schmitz, R.F.; [et al.]. 1987. Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. *Canadian Journal of Forest Research*. 17: 1234–1239.
- Mitchell, R.G.; Preisler, H.K. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *Forest Science*. 37: 1390–1408.
- Mitchell, R.G.; Waring, R.H.; Pitman, G.B. 1983. Thinning lodgepole pine increases the vigor and resistance to mountain pine beetle. *Forest Science*. 29: 204–211.
- 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. *Canadian Journal of Forest Research*. 27: 1634–1645.
- Negrón, J.F. 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. *Forest Ecology and Management*. 107: 71–85.
- Negrón, J.F.; Fettig, C.C. 2014. Mountain pine beetle, a major disturbance agent in US Western coniferous forests: A synthesis of the state of knowledge. *Forest Science*. 60: 409–413.
- Negrón, J.F.; Popp, J.B. 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. *Forest Ecology and Management*. 191: 17–27.
- Negrón, J.F.; Wilson, J.; Anhold, J.A. 2000. Stand conditions associated with roundheaded pine beetle (Coleoptera: Scolytidae) infestations in Arizona and Utah. *Environmental Entomology*. 29: 20–27.
- R Development Core Team. 2008. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. <http://www.R-project.org>. [Accessed February 7, 2017].
- Raffa, K.F., Berryman, A.A., 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs*. 53: 27–49.
- Reynolds, K.M.; Holsten, E. 1994. Classification of spruce beetle hazard in Lutz spruce (*Picea X lutzii*) stands on the Kenai Peninsula, Alaska. *Canadian Journal of Forest Research*. 24: 1015–1021.

- Reynolds, K.M.; Holsten, E. 1996. Classification of spruce beetle hazard in Lutz and Sitka spruce stands on the Kenai Peninsula, Alaska. *Forest Ecology and Management*. 84: 251–262.
- Robertson, C.; Nelson, T.A.; Jelinski, D.E.; [et al.]. 2009. Spatial-temporal analysis of species range expansion: The case of the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Biogeography*. 36: 1446–1458.
- Safranyik, L.; Carroll, A.L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L.; Wilson, B., eds. *The mountain pine beetle: A synthesis of biology, management, and impacts on lodgepole pine*. Victoria, Canada: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Center: 3–66
- Shore, T.L.; Safranyik, L. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Inf. Rep. BC-X-336. Victoria, BC: Forestry Canada, Pacific Forestry Centre. 12 p.
- Shrimpton, D.M.; Thomson, A.J. 1985. Relationship between phloem thickness and lodgepole pine growth characteristics. *Canadian Journal of Forest Research*. 15: 1004–1008.
- Stage, A.R. 1968. A tree-by-tree measure of site utilization for grand fir related to stand density index. Res. Note. INT-RN-77. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 7 p.
- Therneau, T.; Atkinson, B.; Ripley B. 2015. rpart: Recursive partitioning and regression trees. R package version 4.1-10. <https://cran.r-project.org/web/packages/plotmo/index.html>.
- Tishmack, J.; Mata, S.A.; Schmid, J.M. 2005. Mountain pine beetle emergence from lodgepole pine at different elevations near Fraser, CO. Res. Note RMRS-RN-27. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 5 p.
- Verbyla, D.L. 1987. Classification trees: A new discrimination tool. *Canadian Journal of Forest Research*. 17: 1150–1152.
- Waring, R.H.; Pitman, G.B. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66: 889–897.
- West, D.R.; Briggs, J.S.; Jacobi, W.R.; [et al.]. 2014. Mountain pine beetle-caused mortality over eight years in two pine hosts in mixed-conifer stands of the southern Rocky Mountains. *Forest Ecology and Management*. 334: 321–330.
- Wood, S.L. 1982. The bark and ambrosia beetles (Coleoptera: Scolytidae) of North and Central America, a taxonomic monograph. *Great Basin Naturalist*. Memoir No. 6. 1359 p.

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