Western North American Naturalist 63(4), ©2003, pp. 440–451

ATTRIBUTES ASSOCIATED WITH PROBABILITY OF INFESTATION BY THE PIÑON IPS, *IPS CONFUSUS* (COLEOPTERA: SCOLYTIDAE), IN PIÑON PINE, *PINUS EDULIS*

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ABSTRACT.—We examined attributes of piñon pine (*Pinus edulis*) associated with the probability of infestation by piñon ips (*Ips confusus*) in an outbreak in the Coconino National Forest, Arizona. We used data collected from 87 plots, 59 infested and 28 uninfested, and a logistic regression approach to estimate the probability of infestation based on plot- and tree-level attributes. Piñon pine stand density index was a good predictor of the likelihood of infestation by piñon ips at the plot level, and a cross-validation analysis confirmed that the model correctly classified 82% of the cases. Diameter at root collar and piñon dwarf mistletoe infestation level were good predictors of individual tree infestation, and a cross-validation analysis indicated that the model correctly classified 72% of the cases. Results suggest that the occurrence of piñon ips infestations may be related to stress factors associated with increased stocking and piñon dwarf mistletoe infestations.

Key words: Ips confusus, *piñon ips, bark beetles,* Pinus edulis, *piñon pine.*

Piñon-juniper woodlands are the most widely distributed forest type in the western United States. Covering about 19 million ha in the West (Evans 1988), these woodlands are the most common vegetation types in Arizona and New Mexico. Piñon-juniper woodlands provide habitat for many wildlife species, serve as watersheds, offer numerous wood products and recreational opportunities, and have ritual and ceremonial importance for Native Americans.

The piñon ips, *Ips confusus* (LeConte), is an important disturbance agent in these woodlands. Primary hosts are piñon (*Pinus edulis* Englem) and single-leaf piñon (*Pinus monophylla* Torrey & Fremont), but other pines are also recorded as hosts. The piñon ips is a small, cylindrical, brown bark beetle, 4–6 mm in length, 1.5–2.0 mm wide, and is characterized by the specific arrangement of 5 spines in the declivity of each elytron. In piñon ips and 4 other closely related species, the 3rd spine, which is the largest, has a notch on the ventral side. In the western United States the insect occurs in southern California, Arizona, New Mexico, west Texas, Nevada, Utah, Colorado, and Wyoming. It also occurs in Baja California Norte and Chihuahua in Mexico (Wood and Bright 1992). In the Southwest the insect has at least 3–4 generations a year. Adults overwinter from about November to March in colonies in the basal portion of standing trees (Chansler 1964). In the spring new host trees are initially attacked by male beetles, which excavate a nuptial chamber and are then joined by females attracted by a male-produced pheromone. After mating, each female constructs an egg gallery where oviposition takes place. After hatching, the larvae feed on the inner bark, and pupation occurs in a pupal chamber under the bark (Furniss and Carolin 1977, Wood 1982, Eager 1999).

Endemic populations of this insect invade and kill scattered, stressed piñons. Substantial tree mortality is often observed with increased insect population levels. Population increases can result from the availability of recently downed or uprooted trees, which provide suitable habitat for insect population growth. Predisposing agents such as drought or infestations of piñon mistletoe (*Arceuthobium divaricatum* Engelmann) are also believed to increase the likelihood of piñon ips attack (Wilson and Tkacz 1992).

Wilson and Tkacz (1992) observed increased piñon ips–caused mortality of piñon in stands with many trees between 17.8 and 27.9 cm in diameter at root collar and total basal areas between 22.9 and 45.9 $m^2 \cdot ha^{-1}$ in an outbreak

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in the Apache-Sitgreaves National Forest, Arizona. They also noted that many trees killed had heavy infestations of piñon dwarf mistletoe. Aside from this study, no data are available on stand and tree conditions that increase the susceptibility to piñon ips attack and mortality.

In this study we examine stand and tree characteristics associated with the occurrence of piñon ips infestations in an outbreak area in the Coconino National Forest, Arizona, and develop simple models to estimate the probability of infestation by piñon ips.

METHODS

In the spring of 1997, an outbreak of piñon ips was detected south of the Twin Arrows area of the Coconino National Forest, ca. 32 km southeast of Flagstaff, Arizona (Fig. 1). Numerous piñons began to fade as a result of piñon ips attacks. Piñon ips populations appeared to have increased in uprooted trees left in place after land-clearing operations in combination with an area-wide drought. An aerial survey estimated the affected area at 5260 ha (USDA Forest Service unpublished data). This survey was used to delineate our study area. We conducted our sampling July–August 1997. All plots were resurveyed in October 1998, whereupon we recorded any mortality that may have occurred since initial plot installation.

Plot Establishment

The study area is centered at 111°18′45″W longitude, 35°03′45″N latitude in the Elliott Canyon 7.5-minute quadrangle. We established fixed-radius plots on line transects across the affected area. Ten transects, spaced ca. 0.8 km apart, were placed perpendicular to both sides of Forest Service Road 126 that bisects the study area. Nine transects comprised 9 plots spaced 60.4 m apart, with the 10th transect composed of 6 plots, for a total of 87 plots. Plots had a radius of 8.01 m, an area of 0.02 ha, and at least 1 live or ips-killed piñon. At each plot we recorded the following information for all trees: species, diameter at root collar, and status (live, ips-killed, or other dead). Only trees ≥2.54-cm diameter at root collar were sampled. The only other tree species present in the study area was Utah juniper, *Juniperus osteosperma* (Torrey) Little. With this information we calculated average diameter at root collar, number of trees and basal area per hectare for piñon, for juniper, and for both species combined. We calculated a metric stand density index for piñon, juniper, and both species combined by adding the stand density contribution of each individual tree following Long and Daniel (1990). We modified their formula by substituting diameter at root collar for diameter at breast height as follows:

Fig. 1. Study site in the eastern part of the Coconino National Forest, about 32 km (20 miles) southeast of Flagstaff, AZ, 1997.

$$\text{Stand density index} = \text{sum}\left((\text{DRC}_k) / 25\right)^{1.6}$$

where k is the diameter at root collar (cm) of the k^{th} tree in the stand.

For piñon trees an ocular estimate of crown ratio was obtained. For this estimate 2 observers inspected the tree from different directions and agreed in their estimates to within 10%. Average crown width was also obtained for all piñons by averaging the length of the longest axis and its perpendicular axis.

A piñon dwarf mistletoe infection level index was obtained for all live and recently dead piñons, which still had visible infections. Trees were evaluated on a scale of 0–3, with 1 point scored for every one-third of the crown in which mistletoe infections were visible. We then added the score for every one-third to obtain the mistletoe infection level for the tree. The mistletoe infection level index was a modification of the 6-class dwarf mistletoe rating technique developed by Hawksworth (1977). The 6-class system has been the standard dwarf mistletoe rating system for many years and is widely accepted because it works well and is easy to use. We modified the system for 2 reasons. First, the 6-class system was developed for ponderosa pine, which most commonly has a sparse crown that is relatively easy to examine for dwarf mistletoe. Piñon pines have a full, denser crown that poses increased difficulty in adequately examining for dwarf mistletoe infections. Second, in our plots we rated live trees and recently killed trees. Since infections are more difficult to detect in piñon pines and in recently dead trees, by modifying the system we could obtain more conservative ratings while still retaining the strengths of the 6-class system.

For each plot we recorded the distance from the center of the plot to the nearest most recently killed piñon outside the plot. For each ips-killed piñon in every plot, we recorded the distance to the most recently killed piñon whether it was outside or inside the plot. Ips-killed piñon pines fade from green to light yellow to bright orange within a few days. Shortly thereafter the needles begin to fall. The most recently killed tree can be determined by observing the rate of foliage discoloration and needle loss.

Established plots were termed infested if they included at least a single tree killed by piñon ips and uninfested if no ips-killed trees were present in the plot. From the 87 plots, 59 were infested and 28 uninfested.

Data Analysis

We conducted Mann-Whitney tests to examine differences in the variables measured between infested and uninfested plots; we used analysis of variance to compare characteristics of live and ips-killed trees within infested plots because it provides a framework for using the plot and tree status interaction as the error term to account for correlation effects of trees within plots.

At the plot level there are 2 possibilities: the plot is either infested or not. At the individual tree level there are again 2 possibilities: the tree is either killed or alive. At the time of measurement some ips-attacked trees had not faded in coloration completely but were clearly dying. Some bark beetles can successfully attack a portion of a tree without killing it, which is referred to as a strip attack. However, we did not observe this in our study site. Therefore, we modeled the probability of infestation at both the plot and the individual tree level, using logistic regression with 2 possible outcomes. To develop plot-level infestation probability models, we used average plot data. To develop tree-level infestation probability models, we used the individual tree data for the infested plots since these plots included both infested and uninfested trees.

Using the logistic approach, we obtain models in the following form:

$$\text{P (infestation)} = 1 / 1 + e^{b'X} ,$$

where b′X represents a linear combination of explanatory variables X with their estimated parameters b, and e is the base of natural logarithms.

For the plot-level probability of infestation model, we used logistic regression procedures in SPSS, which estimate the parameters using maximum likelihood ratios (Norušsis 1999). For the tree-level model we used PROC NLMIXED in SAS because it allows fitting the logistic regression model assuming the presence of correlation effects of trees within plots (SAS Institute 1999).

After the logistic models were formulated, we divided the plot-level data sets into 6 groups with equal numbers of infested and uninfested plots in each group. We also divided the tree-level data set into 6 groups composed of equal numbers of infested plots. We sequentially excluded each group from analysis and generated logistic models using the same independent variables. Observed values from the excluded groups were then used to obtain estimates of probability of infestation for those groups by substituting these values into the models generated. This process allowed us to examine model performance using a cross-validation framework. We then used boxplots to examine the distribution of estimated probabilities obtained from the cross validation for the uninfested and infested plots for the plot-level data and for the killed and live trees for the tree-level data.

For plot-level data and tree-level data, we used the estimated probabilities of infestation

TABLE 1. Means (± standard error of the mean) of variables measured for plots infested with *Ips confusus*, uninfested, and all plots combined, Coconino National Forest, AZ, 1997[a].

Variable	Infested	Uninfested	All
Number of plots	59	28	87
Trees per hectare—all species	592.2 (41.5) a	333.6 (36.5) b	509.0 (33.1)
Trees per hectare—piñon	370.2 (32.6) a	155.3 (23.4) b	301.1 (25.7)
Trees per hectare—juniper	224.5 (19.7) a	178.3 (26.1) a	209.6 (15.9)
Basal area—all species ($m^2 \cdot ha^{-1}$)	27.8 (1.9) a	18.4 (2.4) b	24.8 (1.6)
Basal area—piñon ($m^2 \cdot ha^{-1}$)	7.0 (0.7) a	2.5 (0.7) b	5.6 (0.5)
Basal area—juniper ($m^2 \cdot ha^{-1}$)	20.8 (1.8) a	15.9 (2.3) a	19.2 (1.4)
Percent basal area in piñon	30.7 (2.9) a	26.6 (6.5) b	29.4 (2.9)
Stand density index—all species	496.7 (31.6) a	325.3 (39.1) b	441.5 (26.2)
Stand density index—piñon	155.5 (14.0) a	58.8 (14.3) b	124.4 (11.6)
Stand density index—juniper	341.2 (27.9) a	266.5 (37.2) a	317.1 (22.6)
Diameter at root collar (cm)—all species	20.5 (0.7) a	21.3 (1.5) a	20.7 (0.7)
Diameter at root collar (cm)—piñon	14.0 (0.5) a	11.9 (1.1) a	13.3 (0.5)
Diameter at root collar (cm)—juniper	32.9 (1.9) a	31.2 (2.6) a	32.4 (1.5)
Piñon crown ratio (%)	69.5 (2.1) a	79.7 (2.9) b	72.8 (1.8)
Piñon crown width (m)	2.5 (0.1) a	2.4 (0.2) a	2.4 (0.1)
Piñon mistletoe infection level	0.9 (0.1) a	0.3 (0.1) b	0.7 (0.1)
Distance to nearest attacked tree (m)	15.5 (0.8) a	17.6 (1.5) a	16.2 (0.7)
Residual basal area — all species ($m^2 \cdot ha^{-1}$)	22.9 (1.9) a	18.4 (2.4) a	21.4 (1.5)
Residual basal area — piñon ($m^2 \cdot ha^{-1}$)	2.1 (0.4) a	2.5 (0.7) a	2.2 (0.4)
Percent residual basal area in piñon	10.3 (2.1) a	26.6 (6.5) b	15.6 (2.6)

[a]For each variable, means followed by different letters are significantly different according to a Mann-Whitney test ($P > 0.05$). Type I error was not maintained across all variables.

from the cross-validation analysis and assigned them to an uninfested or live category if the probability was <0.5 and to an infested or killed category if the probability was 0.51 to 1. We then conducted a cross-tabulation analysis using the observed and the predicted categories to estimate percentage of correct classification.

To examine model behavior, we substituted a range of potential values into the final plot- and tree-level models. With model behavior information for the plot-level data, we determined the piñon stand density index level at which the probability of infestation approaches 0.5 and then examined differences in stand conditions for plots with piñon stand density index above and below that level using Mann-Whitney tests.

RESULTS

Plot-level and Tree-level Differences

On infested plots (Table 1) we found significantly more trees per hectare (including all species), more piñon trees per hectare, greater basal area per hectare (all species), greater piñon basal area per hectare, higher percent basal area represented by piñon, higher stand density index (all species), higher piñon stand density index, lower average piñon crown ratio, and higher mistletoe infection level. After the outbreak had subsided, there were no differences in total residual basal area or piñon residual basal area, but the percent basal area in piñon was much lower in infested plots (Table 1). Within infested plots, ips-killed trees were significantly larger in diameter at root collar, had higher mistletoe infection level, smaller crown ratios, and longer crown widths (Table 2). The mistletoe infection level was a conservative measurement because we were not able to record it for dead trees with no foliage.

The largest numbers of piñons observed across all plots including live and dead trees were in the 10.2-cm size class, with decreasing numbers observed with increasing diameter classes (Fig. 2). The distribution of live and killed trees by diameter classes within infested plots indicates that few trees were killed by piñon ips in the 5.1-cm-diameter class, one-third of the trees were killed in the 10.2-cm-diameter class, close to one-half of the trees were killed in the 15.2-cm-diameter class, and for all other diameter classes more trees were killed than live with the exception of the largest class where only 2 trees were observed (Fig. 3). In sum, the proportion of killed trees increased with increasing size classes. No plot-level or

TABLE 2. Means (± standard error of the mean) for live and *Ips confusus*-killed trees in infested plots, Coconino National Forest, AZ, 1997[a].

Variable	Live	*Ips confusus*-killed
Number of trees	215	209
Diameter at root collar (cm)	9.5 (0.5) a	17.0 (0.6) b
Mistletoe infection level	0.6 (0.1) a	1.4 (0.1) b
Nearest attacked tree	6.7 (0.2) a	6.3 (0.3) a
Crown ratio (%)	66.9 (1.5) a	63.7 (1.6) b
Crown width (m)	1.9 (0.1) a	3.0 (0.1) b

[a]For each variable, means followed by different letters are significantly different according to analysis of variance ($P > 0.05$).

TABLE 3. Logistic regression coefficients, standard error, and significance for constants and explanatory variables for predicting the probability of infestation by *Ips confusus* at the plot and individual tree level.

Model Variable	B	Standard error	Significance
PLOT LEVEL			
Constant	–0.910	0.445	0.041
Piñon pine metric stand density index	0.018	0.005	0.001
TREE LEVEL			
Constant	–2.461	0.402	0.001
Diameter at root collar	0.378	0.059	0.001
Mistletoe infection level	0.556	0.152	0.001

tree-level differences were observed in relation to the proximity of the plot or tree to previously infested trees (Tables 1, 2).

Probability of Plot-level Infestation

We tested average crown ratio of piñon, average crown width of piñon, average mistletoe infection level, average diameter at root collar for all species, average diameter at root collar for piñon, total basal area, piñon basal area, percent basal area in piñon, trees per hectare, piñons per hectare, stand density index (all species), and piñon stand density index as explanatory variables of the probability of infestation. Of these, piñon stand density index was the single best explanatory variable, with increasing stand density index associated with increased probability of infestation as indicated by the positive logistic regression coefficient (Table 3). Based on the probabilities of infestation for the infested and uninfested plots obtained from the cross-validation analysis, piñon stand density index exhibited good discriminatory power, as there is no overlap in the observations between the 25th and the 75th percentiles (Fig. 4). The median probability of infestation was 0.83 for infested plots and 0.44 for uninfested plots. The cross-tabulation analysis indicated that the model correctly classified 82% of the plots. Substituting values of stand density index from 25 to 600 (with intervals of 10) into the model demonstrates that the probability of infestation approaches 0.5 with piñon stand density index of 50, surpasses 0.8 with piñon stand density index of 150, and is asymptotic to 1 with piñon stand density index of 350 (Fig. 5). The mean ± (standard error of the mean) for observed values of piñon stand density index was 124.4 (11.6). The interquartile range was 116.8 with 50% of the observations between the values of 46.9 and 163.7. In our data there were 25 plots with piñon stand density index <50 and 62 plots with piñon stand density index >50. Plots with piñon stand density index >50 exhibited increased stocking, larger average diameter at root collar, higher percentage of piñon, reduced average piñon crown ratio, increased average piñon crown width, and increased mistletoe infection level (Table 4).

Probability of Tree-level Infestation

The following variables were tested as explanatory variables for the probability of infestation at the individual tree level: diameter at root collar, mistletoe infection level, average crown width of tree, and crown ratio. Of the variables examined, the combination of diameter at root collar and mistletoe infection level was the best explanatory variable; both variables had positive logistic regression coefficients, indicating that increased diameter at root collar and mistletoe infection level are associated with increased probabilities of infestation (Table 3). The probabilities of infestation obtained for individual tree mortality from the cross-validation analysis revealed that although the median between the 2 groups is quite different, 0.69 for the killed trees and 0.26 for the live trees, there is overlap in the observations between the 25th and 75th percentiles between the 2 groups (Fig. 6). The cross-tabulation analysis indicated that the

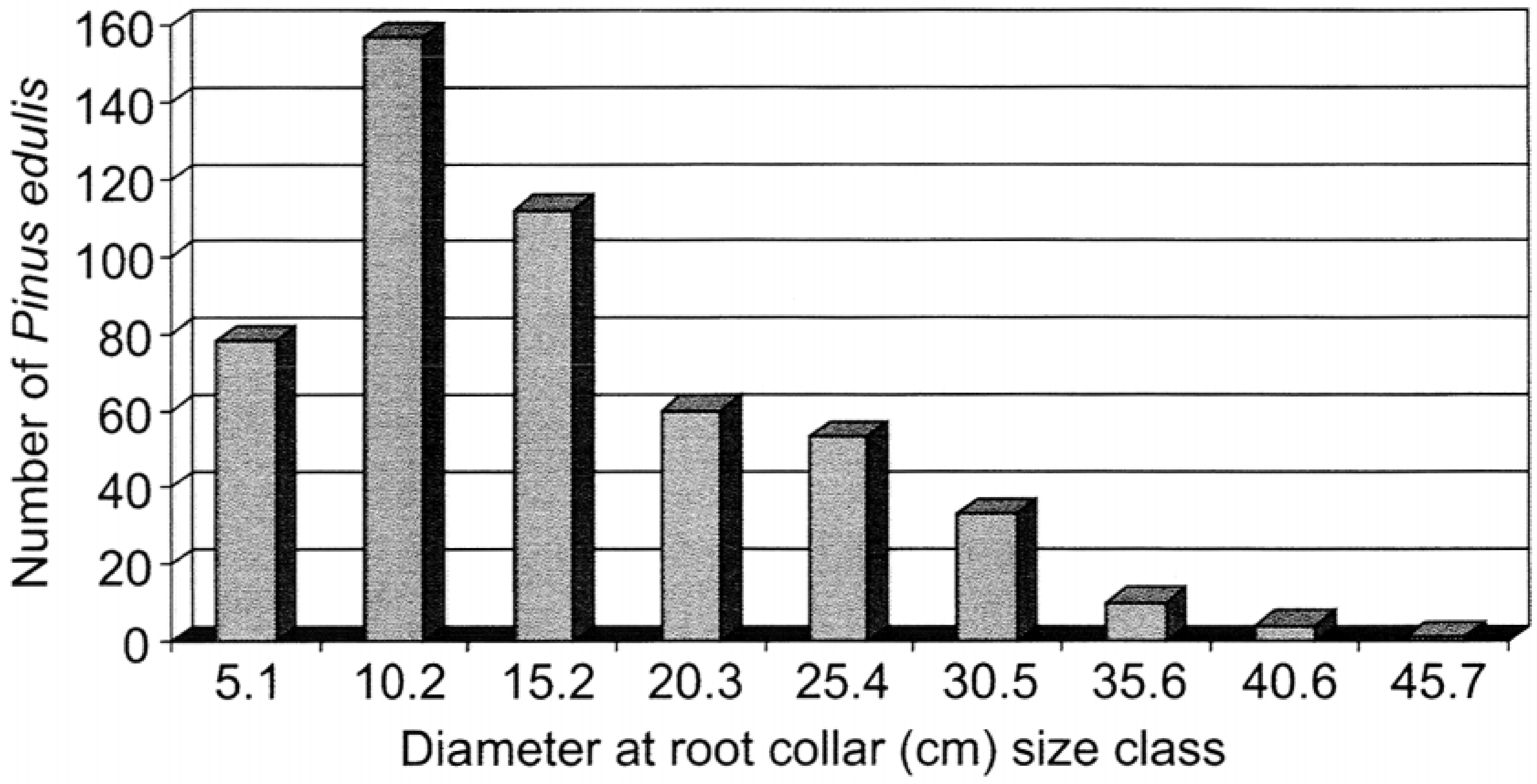

Fig. 2. Total number (live and *Ips confusus*–killed) of *Pinus edulis* in each diameter at root collar size class (cm) across all plots. Diameter at root collar of each size class indicates the upper limit of the class, Coconino National Forest, AZ, 1997.

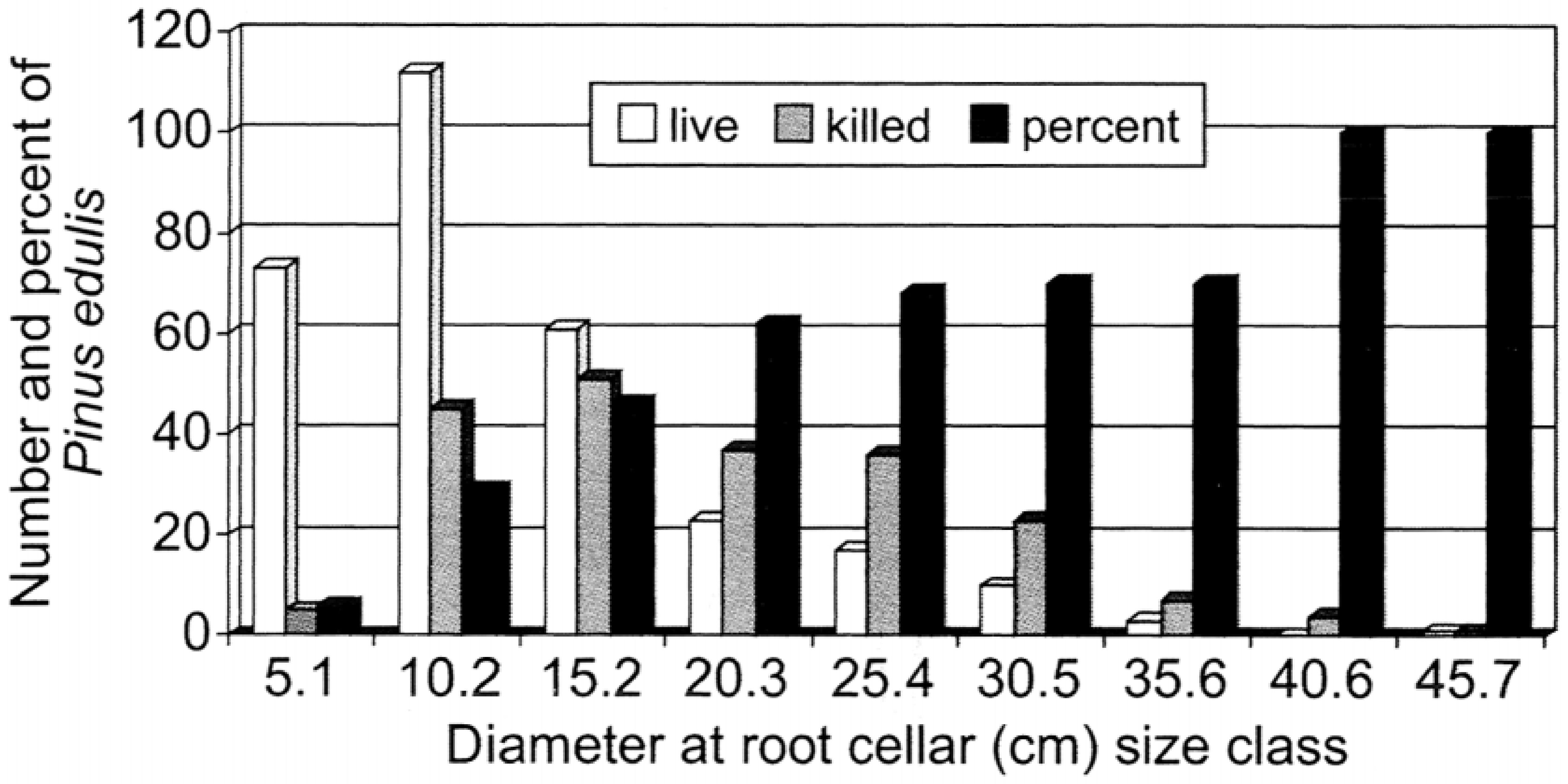

Fig. 3. Number of live and *Ips confusus*–killed *Pinus edulis* in infested plots in each diameter at root collar (cm) size class and percent of trees killed by *Ips confusus* in each size class. Diameter at root collar of each size class indicates the upper limit of the class, Coconino National Forest, AZ, 1997.

model correctly classified 72% of the cases. Model behavior obtained by using a range of diameters at root collar of 3–25 cm and mistletoe infection levels of 0–3 demonstrates how the probability of infestation increases as both variables increase (Table 5).

DISCUSSION

Results indicate that high stand density levels of piñon make stands more susceptible to piñon ips infestations. Anhold and Jenkins (1987) showed that in stands composed of >80% lodgepole pine (*Pinus contorta* Douglas), those with a metric stand density index between 313 and 625 exhibited increased mortality levels caused by mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Anhold et al. (1996) proposed management guidelines based on stand density index to reduce lodgepole pine stand susceptibility to mountain pine beetle. Other studies with mountain pine beetle have recognized that high stocking levels in ponderosa pine (*Pinus ponderosa* Lawson) are often associated with bark beetle–caused mortality (Schmid and Mata 1992, Schmid et al. 1994,

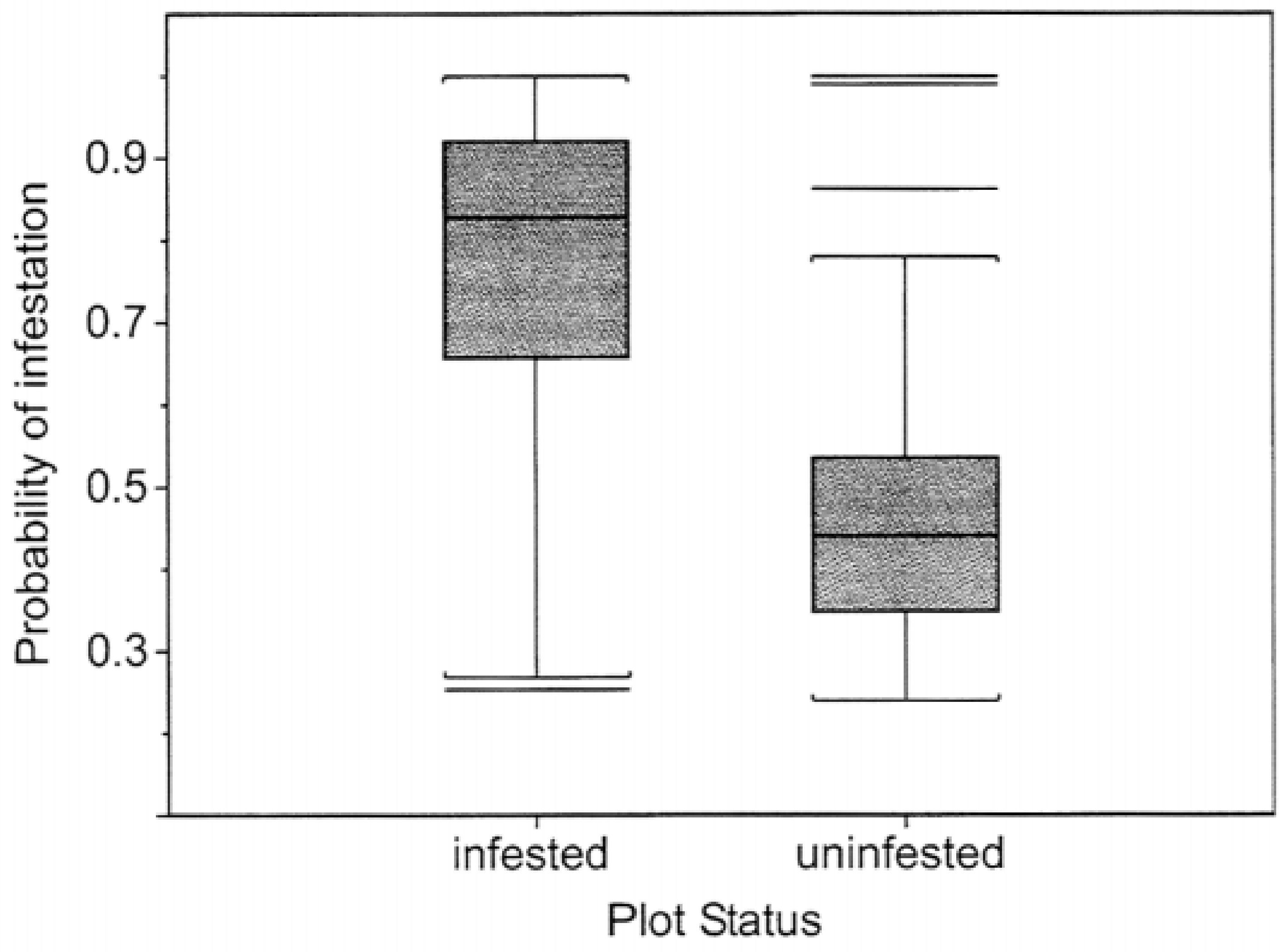

Fig. 4. Distribution of the probability of plot-level infestation by *Ips confusus* for infested and uninfested plots obtained from cross-validation analysis. Lower and upper ends of the box represent the 25th and 75th percentiles, respectively, the line inside the box represents the median, whiskers of the box represent the largest and smallest values not considered outliers, and lines outside the whiskers represent outliers.

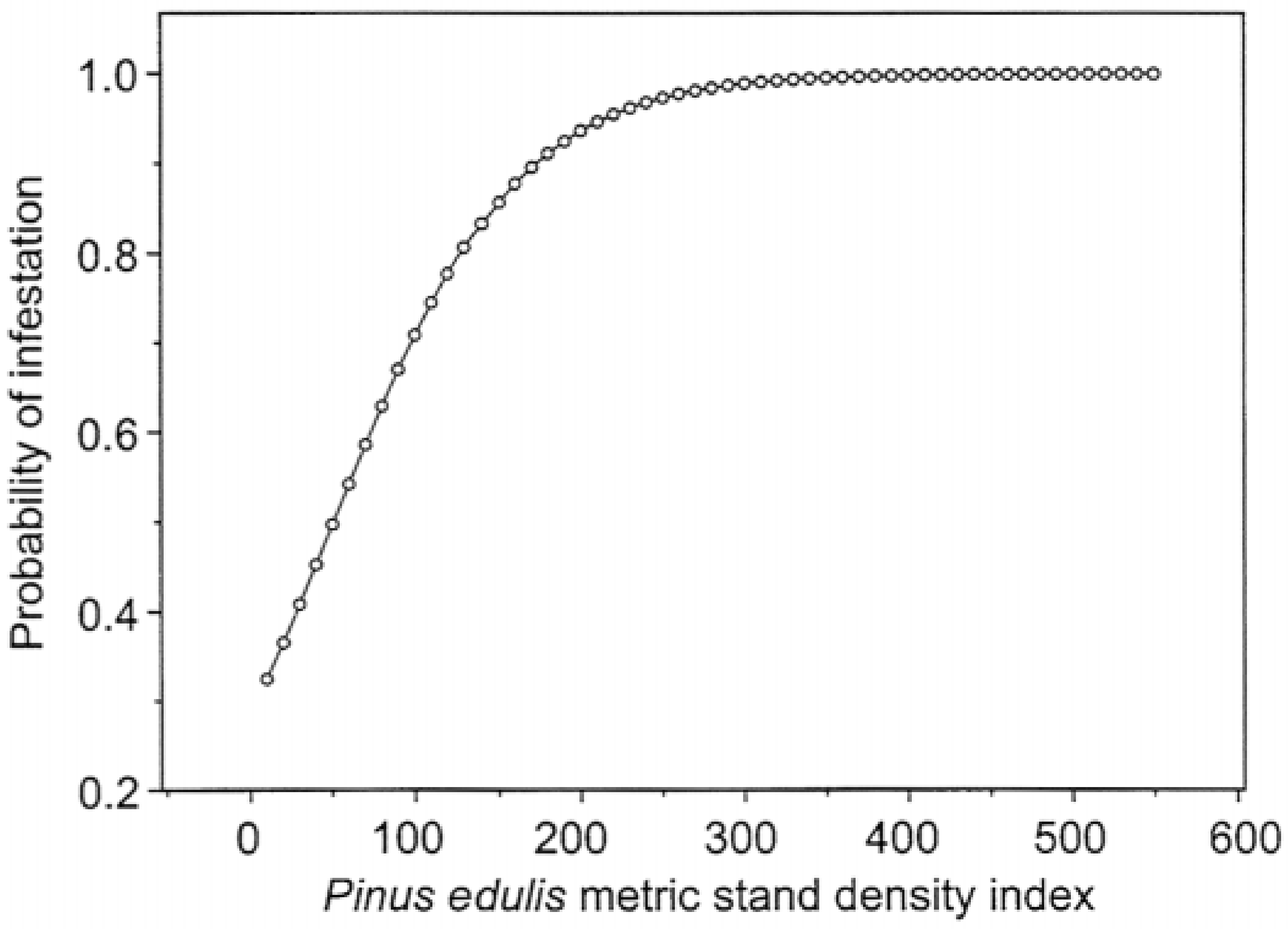

Fig. 5. Probability of plot-level infestation as a function of *Pinus edulis* stand density index as modeled with logistic regression.

Olsen et al. 1996). Furthermore, bark beetle mortality has been associated with reduced growth rates caused by increased stocking levels in ponderosa pine (Sartwell 1971, Sartwell and Stevens 1975, Negrón 1997, Negrón et al. 2000), lodgepole pine (Shrimpton and Thompson 1983), and *Picea glauca* (Moech) Voss (white spruce; Hard et al. 1983, Hard 1985). Reduced growth rates may result in weakened trees. Such trees may be unable to mobilize carbohydrates and other resources needed for defensive mechanisms, thereby increasing their susceptibility to insects (Waring and Pitman 1980, Christiansen et al. 1987). Alternatively, Amman et al. (1988a, 1988b) and Amman and Logan (1998) have suggested that reductions in stand densities by partial cutting result in reduced mountain pine beetle attacks to lodgepole pine because they alter the microclimate by increasing insolation, light intensity, and wind movement, and by reducing humidity. However, considering the intense heat, solar radiation, and xeric environment that characterize piñon-juniper woodlands, it is unlikely that these microclimate changes affect piñon ips significantly.

Total basal areas, piñon basal areas, and percent basal areas represented by piñon were all significantly higher in infested plots. Piñon basal area represented only 29% of the basal area across all plots, the remainder being juniper. Still, results for this study indicate that piñon ips infestation is likely to be more prevalent in stands with piñon stand density index >50. Basal area, stand density index, and percent basal area levels obtained in this study are consistent with others reported in the literature. Smith and Schuler (1988) examined piñon-juniper woodlands in north central New Mexico, southeastern and southwestern Colorado, and Arizona (north of the Mogollon Rim) and reported mean total basal area of 25.0 $m^2 \cdot ha^{-1}$; mean stand density index for all species combined, for piñon only, and juniper only of 540, 248, and 276, respectively; and mean percent basal area in piñon of 43. Our data are also consistent with those of Barger and Ffolliott (1972), who reported a density of 333.1 trees per hectare and a total basal area of 14.6 $m^2 \cdot ha^{-1}$ for a stand south of Flagstaff, which was dominated by Utah juniper.

Although Utah juniper constituted the majority of the basal area in the study site, piñon stand density index was a good predictor of the likelihood of infestation. Other studies have related host availability to the likelihood of bark beetle infestation or the amount of potential mortality caused by bark beetles (Sartwell 1971, Safranyik et al. 1974, Sartwell and Stevens 1975, Schmid and Frye 1976, Furniss et al. 1979, 1981, McCambridge et al. 1982, Reynolds and Holsten 1994, 1996, Negrón 1997, 1998, Negrón et al. 1999, 2000). However, in these studies the host species was the dominant species on the sites.

TABLE 4. Means (± standard error of the mean) for selected variables characterizing plots with *Pinus edulis* metric stand density index <50 and >50, Coconino National Forest, AZ, 1997[a].

Variable	SDI < 50	SDI > 50
Number of plots	25	62
Trees per hectare—all species	292.6 (31.2) a	596.2 (39.7) b
Trees per hectare—piñon	104.8 (10.8) a	380.2 (30.4) b
Basal area—all species ($m^2 \cdot ha^{-1}$)	19.4 (2.6) a	27.0 (1.9) b
Basal area—piñon ($m^2 \cdot ha^{-1}$)	1.0 (0.1) a	7.4 (0.6) b
Percent basal area in piñon	13.9 (5.3) a	35.6 (3.1) b
Stand density index—all species	327.6 (40.7) a	487.5 (31.2) b
Stand density index—piñon	25.3 (3.1) a	164.4 (13.1) b
Diameter at root collar (cm)—all species	22.7 (1.6) a	19.9 (0.7) a
Diameter at root collar (cm)—piñon	9.9 (0.9) a	14.6 (0.5) b
Piñon crown ratio (%)	81.1 (3.8) a	69.4 (1.8) b
Piñon crown width (m)	1.9 (0.2) a	2.6 (0.1) b
Piñon mistletoe infection level	0.2 (0.1) a	0.9 (0.1) b
Distance to nearest attacked tree (m)	17.1 (1.5) a	15.8 (0.8) a
Residual basal area—all species ($m^2 \cdot ha^{-1}$)	19.2 (2.6) a	22.3 (1.8) a
Residual basal area—piñon ($m^2 \cdot ha^{-1}$)	0.7 (0.1) a	2.8 (0.5) b
Percent residual basal area in piñon	12.3 (5.4) a	16.9 (3.0) b

[a] For each variable, means followed by different letters are significantly different according to a Mann-Whitney test ($P > 0.05$). Type I error was not maintained across all variables.

Foxx and Tierney (1987) suggested that piñon roots might reach 6 m below the ground but that juniper roots can attain even greater depths. Schuler and Smith (1988) proposed that these differences in rooting habits between juniper and piñon might cause intraspecific competition for moisture that may be greater than interspecific competition between piñons and junipers. This may explain why piñon stand density index is a good predictor of infestation, even when piñon represents a minor portion of site occupancy.

At the individual tree level, the probability of infestation increased with increasing diameter at root collar and mistletoe infection level. In our study site the smallest tree attacked was 4.3 cm, the largest 41.7 cm. The largest piñon observed was 45.2 cm. We also observed increased proportions of piñon ips–killed trees with increasing diameter at root collar size classes. Wilson and Tkacz (1992) confirmed that >50% of the trees with diameter at root collar between 17.8 and 27.9 cm were attacked by piñon ips, whereas <50% of trees smaller than 17.8 were attacked. Tree size influences the susceptibility to attack by piñon ips, and our data suggest that preference is exhibited for larger-diameter classes in the stand.

Dwarf mistletoe infection level was another important factor in determining the likelihood of attack by piñon ips: as mistletoe infection level increases, so also does the likelihood of attack. Stevens and Hawksworth (1984) stated that the nature of the relationship between primary bark beetles and dwarf mistletoes was at the time poorly understood. The statement remains true, as the knowledge base of this relationship is still limited. The bulk of the evidence suggests that there may be a positive relationship in ponderosa pine between mistletoe infestations by the southwestern mistletoe, *Arceuthobium vaginatum* (Willdenow) Presl subsp. *cryptopodium* (Engelmann) Hawksworth & Wiens, and mountain pine beetle and roundheaded pine beetle, *Dendroctonus adjunctus* Blandford. McCambridge et al. (1982) reported increased mortality of ponderosa pine caused by mountain pine beetle in trees infected with the southwestern dwarf mistletoe in northern Colorado. Stevens and Flake (1974) indicated that trees infected with this mistletoe were common in an area affected by an outbreak of the roundheaded pine beetle in the Sacramento Mountains, New Mexico. In another study from the same area, Negrón (1997) reported average dwarf mistletoe ratings (Hawksworth 1977) that were twice as high in plots infested by roundheaded pine beetle compared to uninfested plots. However, in lodgepole pine, studies seem to show no relationship between infections by the lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelmann) and mountain pine beetle attacks. Hawksworth and Johnson (1989) maintain that this may be the case because mistletoe-infected trees tend to have thinner phloem

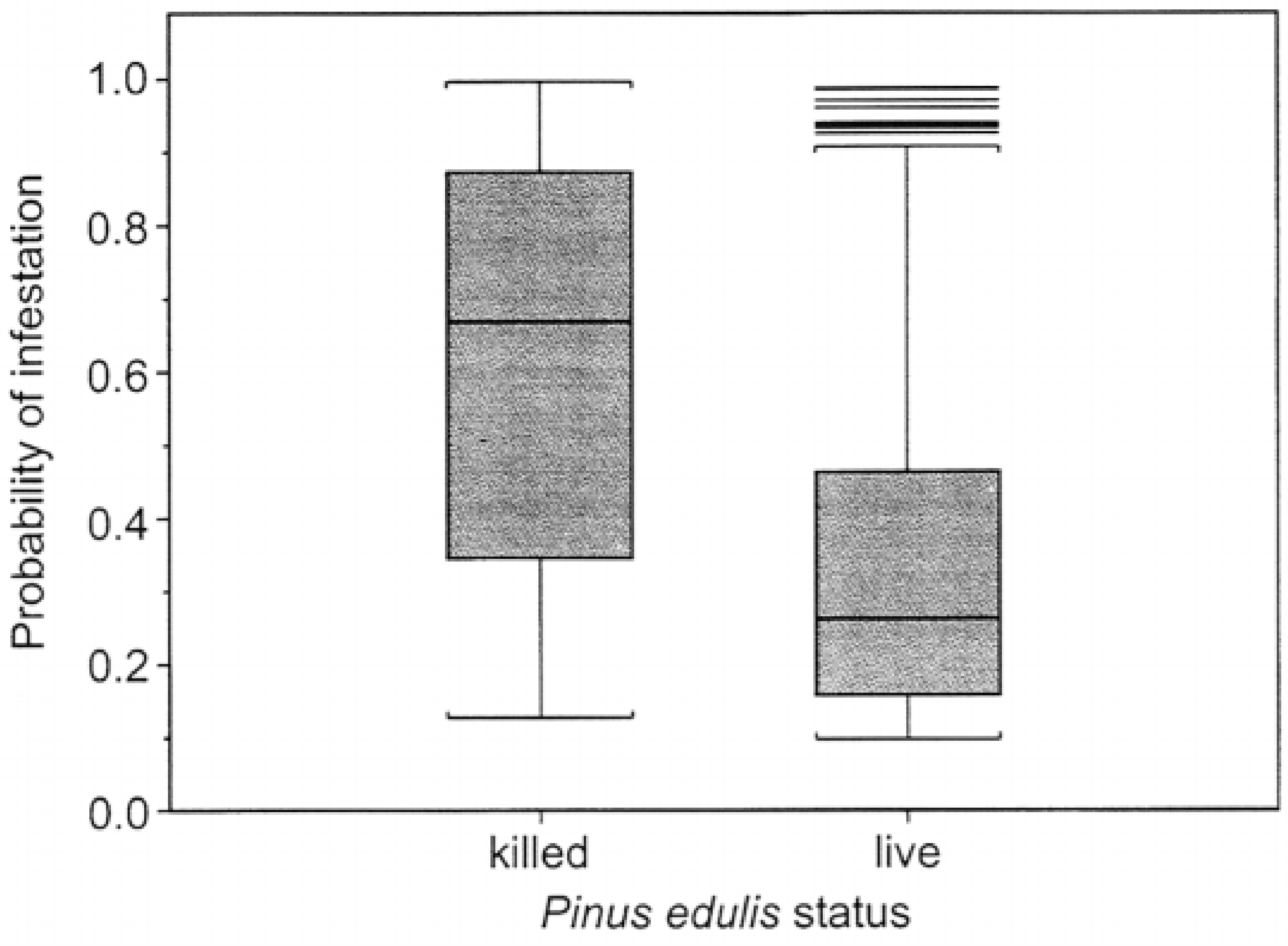

Fig. 6. Distribution of the probability of tree-level infestation by *Ips confusus* for killed and live trees obtained from cross-validation analysis. Lower and upper ends of the box represent the 25th and 75th percentiles, respectively, the line inside the box represents the median, whiskers of the box represent the largest and smallest values not considered outliers, and lines outside the whiskers represent outliers.

TABLE 5. Probability of tree-level infestation as a function of *Pinus edulis* diameter at root collar (DRC), and mistletoe infection level as modeled with logistic regression.

DRC	Mistletoe infection level[a]			
(cm)	0	1	2	3
3	0.12	0.19	0.29	0.41
4	0.13	0.21	0.32	0.45
5	0.15	0.24	0.35	0.49
6	0.17	0.27	0.39	0.53
7	0.19	0.30	0.42	0.56
8	0.22	0.33	0.46	0.60
9	0.25	0.36	0.50	0.63
10	0.27	0.40	0.54	0.67
11	0.31	0.43	0.57	0.70
12	0.34	0.47	0.61	0.73
13	0.37	0.51	0.64	0.76
14	0.41	0.54	0.68	0.78
15	0.44	0.58	0.71	0.81
16	0.48	0.62	0.74	0.83
17	0.52	0.65	0.77	0.85
18	0.55	0.68	0.79	0.87
19	0.59	0.72	0.81	0.88
20	0.63	0.75	0.84	0.90
21	0.66	0.77	0.86	0.91
22	0.69	0.80	0.87	0.92
23	0.72	0.82	0.89	0.93
24	0.75	0.84	0.90	0.94
25	0.78	0.86	0.91	0.95

[a]See text for explanation of mistletoe infection index.

according to Roe and Amman (1970). Amman (1972) indicated that thicker phloem in lodgepole pine contributes to increased survival of the mountain pine beetle. As a consequence, mistletoe-infested lodgepole pines may not serve as adequate hosts for mountain pine beetle because they may lack the necessary phloem. Furthermore, Hawksworth et al. (1983) found little relationship between dwarf mistletoe intensity and phloem thickness in lodgepole pine in Colorado.

Infections of dwarf mistletoe have a variety of effects on the host, including reductions in tree height and diameter growth rates, increased mortality, and decreased seed production (Hawksworth and Shaw 1984). Hawksworth (1961) showed reductions in mean radial growth for the last 5 years in severely infected ponderosa pines. This suggests that as infections intensify within the tree and vigor declines, its susceptibility to bark beetle attack may increase. At the plot level we observed increased mistletoe infection levels in the piñon ips–infested plots. Higher mistletoe infection levels in infested plots may be a function of increased stocking densities, which may facilitate tree-to-tree movement of dwarf mistletoe.

The piñon-ips outbreak reduced total and piñon basal area. All observed mortality occurred in piñon, and the percent basal area of piñon in infested stands decreased from 30% to 10%. This resulted in a reduction of piñon in basal area in affected areas to the same levels found in unaffected stands. Piñon mortality associated with piñon-ips outbreaks may or may not be compatible with management objectives. Widespread mortality can result in an accumulation of fuels that may considerably increase fire hazard. Piñon trees are highly valued as wildlife habitat and as a source of nuts for human consumption. On the other hand, tree mortality can also result in openings where herbaceous production is increased, which is a benefit to livestock, deer, and elk.

Although piñons are shade intolerant, establishment of piñon regeneration is most common under the shade of older trees that moderate the environment for seedlings. Premature exposure to extreme sun and heat can scald and kill seedlings (Gottfried 1987). Therefore, piñon regeneration may be negatively affected when overstory piñons are killed by ips infestations.

Results of this study suggest that piñon stand density index is a good predictor of stand susceptibility to piñon ips in our study area. This increased susceptibility may be due to reduced vigor of trees in dense stands. At the individual tree level, piñon ips appears to prefer larger-diameter trees and those with intensifying dwarf mistletoe infection. Dwarf mistletoe infection may increase susceptibility to piñon ips by causing additional stress on the tree. The simple models presented in this study can help identify areas and trees that may be susceptible to piñon ips mortality when populations of this insect increase. Where ips-caused mortality may be of concern, management techniques that include thinning to reduce piñon stand density index below 50 will reduce the likelihood of tree mortality. Since trees with severe mistletoe infections in the larger-diameter classes are more likely to be attacked, they may be good candidates for removal if the overall management objectives can be achieved.

Because our models were developed using data from a small area, extrapolation to other localities areas must be done with discretion. The important variables observed in our study will likely be of equal importance in other sites, but values may vary with changing forest conditions. Nevertheless, our models may be useful stepping-stones for the development of biological models that may be applicable to larger geographical areas (Hedden 1981).

ACKNOWLEDGEMENTS

We thank the following individuals: Yvonne Bonser, Brian Madland, Kristen Miller, Justin Selvik, and Erika Wiltenmuth for field assistance and data collection; Frederick W. Smith and Linda A. Joyce for reviews of earlier versions of the manuscript; Rudy King for statistical support; and the anonymous reviewers whose comments greatly improved the manuscript. This study was a cooperative effort between the USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, and the USDA Forest Service, Forest Health Protection, Region 3, Flagstaff, Arizona.

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Received 28 January 2002
Accepted 26 August 2002