

Attack Pattern of *Platypus koryoensis* (Coleoptera: Curculionidae: Platypodinae) in Relation to Crown Dieback of Mongolian Oak in Korea

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ABSTRACT The ambrosia beetle, *Platypus koryoensis* (Murayama), vectors the Korean oak wilt (KOW) pathogen, *Raffaelea quercus-mongolicae* K.H. Kim, Y.J. Choi, & H.D. Shin, in Korea, which is highly lethal to Mongolian oak, *Quercus mongolica* Fisch., and is considered a major threat to forest ecosystem health. We characterized the attack pattern of *P. koryoensis* along the lower trunk of 240 Mongolian oaks in relation to tree decline symptoms on Mt. Uam in Gyeonggi-Do Province, Korea during June–July 2009. For each tree, we recorded diameter at breast height (dbh) (DBH) and *P. koryoensis* entrance hole density at two heights along the lower trunk (near groundline and at 1.5 m above groundline) and on opposite sides (downslope side and upslope side). Trees were assigned to one of three dieback classes: 1) apparently healthy, no or practically no wilted foliage, and no obvious platypodine frass near the base of the tree; 2) no or only partial wilting with obvious frass near the base of the tree; and 3) apparently recently killed by KOW with all foliage wilted and mostly retained with obvious frass near the base of the tree. As dieback class increased from 1 to 3, *P. koryoensis* entrance hole density increased at all four trunk locations. Attack density was highest on the downslope side of the trunk near groundline, and principal component analysis indicated that this trunk location was the best indicator of tree dieback. In addition, DBH tended to increase with dieback class suggesting that larger trees were infested first.

KEY WORDS *Platypus koryoensis*, Mongolian oak, Korean oak wilt, attack density, dieback

Adult ambrosia beetles and bark beetles (Coleoptera: Curculionidae, Platypodinae, and Scolytinae) construct galleries and lay eggs primarily in the phloem (i.e., the bark beetles) or in the wood (i.e., the ambrosia beetles) of their host plants. In general, all platypodines are ambrosia beetles, whereas some scolytines are ambrosia beetles while others are bark beetles (Wood 1982, Haack and Rabaglia 2011). Adult ambrosia beetles inoculate symbiotic fungi in their galleries and the fungi serve as the principal food of the developing larvae. Although bark beetle adults may introduce microorganisms into their host during gallery construction, bark beetle larvae primarily feed on host phloem tissue.

Mass attack is the basic strategy by which many tree-killing ambrosia and bark beetles overcome tree defenses and eventually kill their host. This occurs when a certain threshold number or density of colonizing beetles is reached in the trunk and major branches (Byers 1984). The parameter “attack density” often is measured in terms of the number of entrance holes or gallery systems per unit of bark surface area created by the adult beetles as they enter

the trunk and branches of trees to reproduce. Therefore, tree damage is dependent on the density of colonizing beetles and thus it may be possible to express the risk of tree mortality as a function of attack density.

Many species of ambrosia and bark beetles infest specific locations of a tree’s trunk and branches, which optimizes their colonization efficiency and allows for resource partitioning. These infestation patterns offer information on beetle behavior and the underlying attack strategy when beetles commence colonization of live host trees. For example, the bark beetle *Ips acuminatus* (Gyll.) (Scolytinae) generally infests branches (Lieutier 2002). By contrast, the platypodine ambrosia beetles *Platypus quercivorus* (Murayama) and *P. koryoensis* (Murayama) prefer to infest the lower trunk of their host trees, possibly in response to higher humidity levels near the forest floor, which would favor growth of their symbiotic fungi (Igeta et al. 2004, Choi et al. 2008, Esaki et al. 2009, Kim et al. 2010).

Platypus koryoensis is one of the ambrosia beetles that can attack and kill vigorous host trees. *P. koryoensis* primarily infests Mongolian oak, *Quercus mongolica* Fisch., in Korea. *P. koryoensis* is native to Korea (Park and Lyu 2007) and along with its symbiotic fungus, *Raffaelea quercus-mongolicae* K.H. Kim, Y.J. Choi, & H.D. Shin, has been involved in widespread oak mortality in Korea, which is commonly called Korean oak

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wilt (KOW) (Kim et al. 2009a). The first report of KOW in Korea was in 2004. The number of KOW-killed oak trees in Gyeonggi Province was estimated at 16,177 trees during 2006–2009 (KFRI 2009). *P. koryoensis* is univoltine in central Korea and overwinters in all life stage in its galleries (Park 2008). Adults emerge from late April to early October, peaking in late June and early July (Koo et al. 2008). Adult males initiate colonization along the trunk and release a pheromone that attracts females. A single female joins each male and together they construct the gallery (Kim et al. 2009b). Galleries are constructed mainly in the sapwood and occasionally in the heartwood (W. I. Choi, unpublished data). The spatial attack pattern of *P. koryoensis* entrance holes changes from contagious to uniform as attack density increases (Choi et al. 2008). Several hypotheses have been proposed to explain the recent outbreak of *P. koryoensis* and KOW-killed trees in Korea: 1) novel association between *P. koryoensis* and *R. quercus-mongolicae*, 2) warmer ambient temperatures are favoring *P. koryoensis* over the more cold-adapted Mongolian oak, and 3) increased age of the Mongolian oaks throughout Korea has made them more vulnerable to attack by *P. koryoensis* (Choi 2011). *P. koryoensis* has the potential to invade forests and contribute to oak decline outside of Korea. The aim of the current study was to characterize the within-tree attack pattern of *P. koryoensis* along the lower trunk of Mongolian oak trees and to relate *P. koryoensis* attack density to crown dieback conditions as well as other factors such as slope, elevation, and tree dbh (DBH).

Materials and Methods

Study Site. The study was carried out in oak-dominated forests located on Mt. Uam near Paju, Gyeonggi-Do Province, Korea (Fig. 1). The base of Mt. Uam is at an elevation of ≈ 100 m and the peak reaches to ≈ 400 m. Oak-dominated forests were found on Mt. Uam from 100 to 400 m. We located study plots along an altitudinal gradient on Mt. Uam where KOW-related oak mortality was highest based on a national survey conducted during 2008 (Korea Forest Research Institute, unpublished data). In the study area, which spanned elevations from 100 to 400 m, Mongolian oak was the dominant tree species followed by *Carpinus laxiflora* BL. and *Styrax obassia* S. et Z. The first collection of *P. koryoensis* in the Paju area was reported in 2008 (Choi et al. 2008); however, the first oak trees suspected of dying from KOW were observed in 2007 (W. I. Choi, unpublished data).

Experimental Procedures. Within the study area, six rectangular 5-ha plots (≈ 80 by 625 m) were randomly selected in June 2009. In each plot, a single oak tree was selected near one of the plot corners as the starting point. Oaks trees >20 cm DBH were selected at 10-m intervals while walking a zigzag path that covered the entire 5-ha study plot. At each stopping point, we selected the nearest oak tree that was growing within 5 m. If there were no oak trees within 5 m then we walked an additional 10 m, and so on. Because the density of oak trees varied in the plots, the final

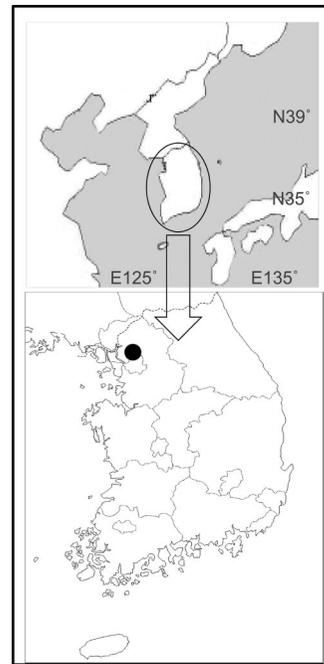


Fig. 1. Provincial outline map of Korea with location of field plots (solid circle) located on Mt. Uam near Paju, Gyeonggi-Do Province, Korea.

number of sampled trees per plot varied from 25 to 60 (Table 1). We excluded oak trees <20 cm DBH because *P. koryoensis* seldom colonizes such smaller trees (Choi et al. 2008). Each selected tree was assigned to one of three tree dieback classes based on the crown condition and presence of platypodine frass near the base of the tree trunk, indicating active tunneling by *P. koryoensis*. Trees assigned to Dieback class 1 were apparently healthy with no or practically no visible wilting of foliage and no obvious frass near the base of the tree trunk. Dieback class 2 trees had no or only partial wilting of the crown foliage with obvious frass around the base of the tree trunk. Dieback class 3 trees had foliage that had completely wilted within the past year and had obvious frass around the base of the tree trunk. In general, foliage on KOW-killed oaks wilts

Table 1. Summary data for the six plots on Mt. Uam near Paju, Korea

| Elevation (m) ¹ | No. trees surveyed | Slope (°) ^a | Mean (\pm SE) DBH ¹ (cm) ^b | Dominant direction of hillside slope faced ^a |
|----------------------------|--------------------|------------------------|---|---|
| 150 | 30 | 21.2 | 26.3 \pm 2.1 | Northwest |
| 200 | 60 | 22.8 | 22.8 \pm 0.7 | North |
| 230 | 65 | 26.3 | 24.4 \pm 0.8 | Northwest |
| 250 | 30 | 24.3 | 29.1 \pm 1.6 | North |
| 350 | 30 | 26.7 | 23.6 \pm 1.2 | West |
| 380 | 25 | 35.4 | 27.9 \pm 1.9 | Northwest |

^a Elevation, slope, and dominant direction of hillside slope were measured near the plot center.

^b DBH: Diameter at breast ht as measured at 1.5 m above ground-line.

completely during late July to September and is retained on the tree for about one year (W. I. Choi, unpublished data). We used this symptom (i.e., retained wilted foliage) to approximate the timing of tree death. For each surveyed tree, we recorded DBH (at 1.5 m above ground) and then the number of *P. koryoensis* entrance holes at four locations along the lower trunk: i.e., near groundline (i.e., the forest floor) and at 1.5 m above groundline on both the upslope and downslope sides of the trunk regardless of the age of the *P. koryoensis* entrance holes. We used a rectangular frame (21 by 15 cm) that enclosed an area of 315 cm². The number of entrance holes per 315 cm² later was transformed to the number of entrance holes per 1 m² of bark surface area so that the values could easily be compared with other studies of other ambrosia and bark beetles. We will refer to samples taken at 1.5 m as "at breast height" and those taken at groundline as "near groundline." In addition, based on an earlier survey in 2008 on Mt. Uam, *P. koryoensis* constituted 99.4% of all platypodines and scolytines landing on the lower trunks of Mongolian oak trees based on multiple-funnel-trap data (W. I. Choi, unpublished data). Therefore, all entrance holes found on the trunks of the sampled oak trees in the current study were considered to be made by *P. koryoensis*. In addition to the number of entrance holes on each tree, we recorded presence or absence of wilted canopy foliage, *P. koryoensis* entrance holes from 1.5 to 3 m along the trunk, and sap exudate near the *P. koryoensis* entrance holes along the lower 1.5 m of trunk.

Near the center of each plot, we recorded elevation; dominant cardinal direction that the plot faced (e.g., a north-facing slope); and slope. Geographical information was acquired by GPS (GEOXH, Trimble, Sunnyvale, CA) and analyzed by GPS Pathfinder software version 3.10 (Trimble Navigation Ltd. 2005).

Data Analyses. Mean attack density values (number of *P. koryoensis* entrance holes/m² of bark surface area) for the various tree factors (e.g., elevation, DBH, presence of sap exudates, etc.) were compared by using a *t*-test or Tukey's honestly significant difference (HSD) multiple comparison test after one-way analysis of variance (ANOVA) (ANOVA; Zar 1999). Similarly, mean attack density values were compared with respect to location along the trunk and tree dieback class by using Tukey's HSD multiple comparison test after two-way ANOVA (ANOVA; Zar 1999). The above statistical analyses were carried out with SAS, using PROC GLM and PROC TTEST (SAS Institute 2004) and an alpha level of 0.05. A possible linear relationship between elevation and mean attack density was analyzed with linear regression analysis, using PROC REG (SAS Institute 2004). Canonical discriminant analysis was conducted to evaluate the relative contribution of the various measured factors (elevation, slope, tree DBH, attack density at each of the four sampling locations, and presence or absence of the wilted canopy foliage, entrance holes above breast height, and sap exudates near entrance holes along the lower 1.5 m of trunk). Canonical discriminant analysis

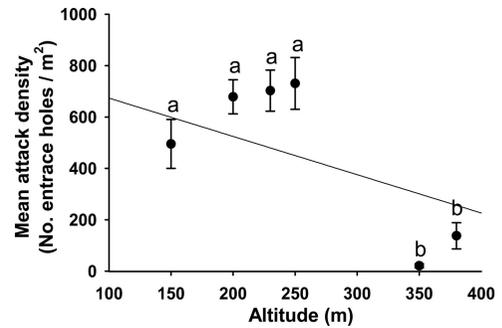


Fig. 2. Relationship between mean *P. koryoensis* attack density (mean \pm SE; number of entrance holes per m² of bark surface area) based on the average of all four trunk sampling locations per tree and elevation measured near the center of plots. Means with the same letter were not significantly different ($P < 0.05$; Tukey's multiple comparison test).

was conducted using STATISTICA (StatSoft Inc. 2004) with an alpha level of 0.05.

Results

The center of the six study plots ranged in elevation from 150 to 380 m above sea level, and in slope from 21.2 to 35.4° (Table 1). Mean DBH of the surveyed trees within a given plot ranged from 22.8 to 29.1 cm and the dominant direction that the hillside slopes faced generally within each plot ranged from north to northwest to west (Table 1).

Mean *P. koryoensis* attack density on Mongolian oaks was significantly higher for the four plots located between 150 and 250 m compared with the two plots located at 330–350 m ($F = 12.46$; $df = 5, 234$; $P < 0.001$; Fig. 2). The linear relationship between elevation (m) and mean attack density (no. entrance holes/m²), based on the average of all four trunk sampling locations on a per tree basis, was described by the following linear equation: Mean attack density = $822.39 - 1.49$ elevation ($F = 119.02$; $df = 1, 255$; $P < 0.05$, $r^2 = 0.32$).

Mean (\pm SE) DBH of the *P. koryoensis*-infested oak trees significantly increased with increasing dieback class from 23.8 ± 0.6 cm for trees in Dieback class 1– 29.3 ± 1.7 cm for trees in Dieback class 3 ($F = 8.29$; $df = 2, 237$; $P < 0.0013$; Fig. 3A). Similarly, mean *P. koryoensis* attack density, based on the average of all four trunk sampling locations per tree, significantly increased from 103.2 ± 9.7 – 1338.7 ± 99.9 entrance holes per m² with increasing tree dieback class ($F = 148.62$; $df = 2, 237$; $P < 0.001$; Fig. 3B). Attack density was generally highest near groundline as well as higher on the downslope side of the trees compared with the upslope side ($F = 76.07$; $df = 3, 956$; $P < 0.0001$; Fig. 4). Overall, 80.4% of the trees assigned to Dieback classes one had attack densities < 500 entrance holes/m² on the downslope side of the trunk near groundline, in contrast to 9.2 and 3.4% of the trees assigned to Dieback classes 2 and 3, respectively. The percentage of trees with over 2,000 entrance holes per

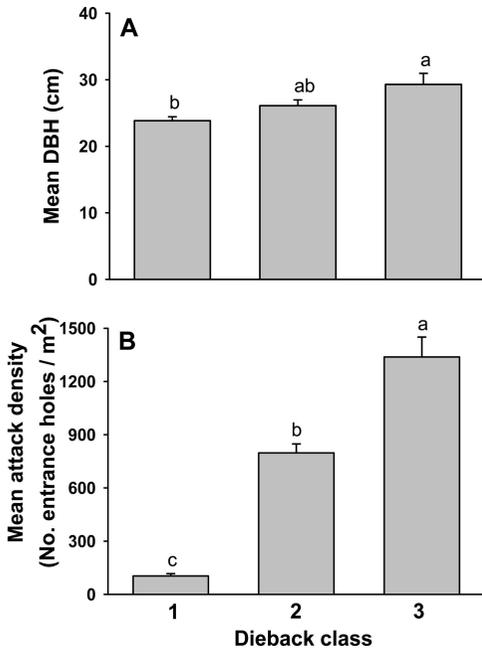


Fig. 3. Relationship between tree dieback class and mean tree DBH (A), and mean *P. koryoensis* attack density based on the average of all four trunk sampling locations per tree (B). Means with the same letter were not significantly different ($P < 0.05$; Tukey's multiple comparison test).

m² on the downslope side of the trunk near groundline were 1.1, 28.7, and 65.5% for the trees in Dieback classes 1, 2 and 3, respectively. Similarly, the percentage of trees with over 3,000 entrance holes per m² on the downslope side of the trunk near groundline were 34.5 and 62.1% for trees in Dieback classes 2 and 3,

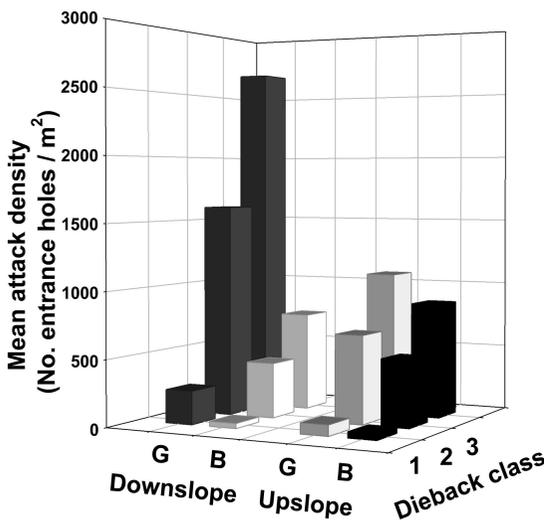


Fig. 4. Mean *P. koryoensis* attack density (No. per m²) on the trunks of Mongolian oak trees when measured near groundline (G) and at breast height (1.5 m; B) on both the downslope and upslope sides of each tree by tree dieback class.

respectively. The KOW-killed Mongolian oaks had from 2,324 to 2,993 (95% confidence interval) *P. koryoensis* entrance holes/m² on the downslope portion of the trunk near groundline. Surprisingly, one tree in Dieback class 1 had over 3,000 entrance holes per m² on the downslope side of the trunk near groundline. Given that no frass was present near this particular tree, the entrance holes were likely constructed at least 2 yr before our sampling.

Canonical discriminant analysis indicated that plot slope, mean attack density along the downslope side of the trunk near groundline, presence of wilted foliage, and presence of trunk sap exudates were significantly related to the observed differences in tree dieback classes (Table 2). Wilks' Lambda can range from 0 to 1, with one indicating no relationship between the descriptors (i.e., the recorded factors) and the responses (dieback classes); and 0 indicating a perfect relationship between predictors and responses (StatSoft Inc. 2004). Wilks lambda values for slope (0.33), attack density along the downslope portion of the trunk near groundline (0.40), presence of wilted foliage (0.33), and presence of sap exudates (0.34) all were significant (Table 2). Trees with partially wilted foliage or trunk sap exudates near entrance holes had higher *P. koryoensis* attack densities along the downslope portion of the trunk near groundline than trees without wilted foliage or trunk sap exudates ($t = -2.51$; $df = 238$; $P < 0.013$; $t = -5.99$; $df = 209$; $P < 0.001$). In addition, the percentage of trees with *P. koryoensis* entrance holes at trunk heights of 1.5–3 m above groundline increased with dieback class from 0.8% for trees in Dieback class 1–13.8% in Dieback class 3 (Table 3). The two-dimensional ordination solutions were statistically significant. The total variance explained by the final solution was 100%, with the coefficients of determination being 87% for axis 1 and 13% for axis 2 (Table 2). Considering that oak mortality increased along the X-axis from left to right (i.e., Dieback classes 1–3) and that the largest standardized coefficient was between attack density on the downslope side of the trunk near groundline and axis 1 (0.83), attack density on the downslope side of the trunk near groundline can be considered the principal component to explain oak mortality (Fig. 4 and 5). In addition, the largest standardized coefficient for axis 2 was for the presence of wilted foliage (0.65) (Table 2).

Discussion

Platypus koryoensis appears preferentially to attack the downslope portion of the trunk near groundline of Mongolian oaks in Korea. Preference for infesting the downslope portion of the trunk cannot be explained by flight behavior of *P. koryoensis*, given that Kim et al. (2010) noted that *P. koryoensis* adults were collected at significantly higher numbers in traps placed on the upslope side of trees. Our findings in combination with those of Kim et al. (2010) suggest that *P. koryoensis* adults tend to fly downslope, land primarily on the upslope portion of the tree trunks, and apparently then walk downward and around the trunk, congre-

Table 2. Discrimination parameters for physical and tree-condition factors analyzed with respect to Mongolian oak tree dieback class and *P. koryoensis* attack density, using canonical discriminant analysis. Wilks' Lambda can range from 0 to 1, with 1 indicating no relationship between the descriptors (i.e., the recorded factors) and the responses (dieback classes), and 0 indicating a perfect relationship between predictors and responses

| Factor | Wilks' Lambda | F _{2, 286} | P-level | Standardized coefficients | |
|---|---------------|---------------------|---------|---------------------------|--------|
| | | | | Axis 1 | Axis 2 |
| Elevation | 0.32 | 2.60 | 0.07 | -0.12 | -0.36 |
| Direction ^a | 0.32 | 2.13 | 0.12 | 0.13 | -0.30 |
| Slope | 0.33 | 4.69 | <0.01 | 0.23 | -0.32 |
| DBH at 1.5 m | 0.32 | 0.55 | 0.58 | 0.067 | 0.12 |
| Attack density | | | | | |
| On upslope portion at breast ht | 0.32 | 0.34 | 0.71 | -0.073 | 0.13 |
| On upslope portion near groundline | 0.32 | 0.78 | 0.46 | 0.15 | -0.085 |
| On downslope portion at breast ht | 0.32 | 1.95 | 0.14 | 0.21 | 0.28 |
| On downslope portion near groundline | 0.40 | 31.15 | <0.001 | 0.83 | -0.44 |
| Presence of wilted foliage | 0.33 | 4.24 | 0.016 | -0.11 | 0.42 |
| Presence of <i>P. koryoensis</i> entrance holes above 1.5 m along trunk | 0.32 | 0.91 | 0.40 | 0.028 | -0.22 |
| Presence of sap exudates | 0.34 | 7.19 | <0.001 | 0.013 | 0.65 |

^a Plot direction was calculated from the dominant cardinal direction that the plot faced (e.g., a north-facing slope).

gating on the downslope side. Similarly, Esaki et al. (2009) reported that *P. quercivorus* also attacked the downslope portion of the trunk at higher densities. However, Esaki et al. (2004) reported that *P. quercivorus* adults tended to fly upslope in Japan. We do not know why attack density generally is higher on the downslope portion of the tree trunk, but it may be related to heavy furrowing of the bark on the downslope side because of the eccentric growth patterns of oaks growing on steep slopes (Clark and Hallgren 2004), which could provide more cracks and crevices where beetles can initiate tunneling as well as more areas where pheromone-laden frass can be trapped and thereby attract more colonizing adults. Alternatively, given that wood density is often lower in the downslope portion of the lower trunk of oaks with eccentric growth patterns (Lehringer et al. 2009), it should be easier for adults to excavate their galleries.

Preference for initial colonization along the lower trunk (<1.5 m above groundline) also has been reported for the platypodine *P. quercivorus* in Japan (Igeta et al. 2004), and several scolytines such as *Corthylus columbianus* Hopkins (Nord 1972), *Dendroctonus valens* LeConte (Gao et al. 2005), *Dendroctonus ponderosae* Hopkins (McCambridge 1967), *Scolytus quadrispinosus* Say (Goeden and Norris 1965), and

Xylosandrus germanus (Blandford) (Weber and McPherson 1983). Although constructing galleries in the lower trunk of trees may require more energy, given the relatively thick outer bark, it also may benefit the beetles and their progeny by offering more nutritious host tissues (e.g., higher moisture content and thicker phloem) that can result in higher brood survival and thus faster population buildup (Haack and Slansky 1987; Haack et al. 1987a,b; Kolb et al. 2006; Choi et al. 2008). In addition, as beetle populations increase they may be able to more easily overcome tree defenses present in live trees. It is likely that many of the primary ambrosia beetle species that attack and kill live trees have this type of attack strategy, e.g., *P. koryoensis* and *P. quercivorus* (Igeta et al. 2004, Choi et al. 2008). Wood moisture content can be limiting for

Table 3. Percentage of Mongolian oak trees in each tree dieback class that had wilted foliage, entrance holes between heights of 1.5 and 3 m along the trunk, and trunk sap exudates on the lower 1.5 m of trunk

| Parameter | Percent of trees with attribute by dieback class (%) | | |
|--|--|---------|---------|
| | Class 1 | Class 2 | Class 3 |
| Wilted foliage present | 2.4% | 10.3% | 100% |
| Entrance holes present between 1.5-3 m | 0.8% | 4.6% | 13.8% |
| Trunk sap exudates on lower 1.5 m of trunk | 12.1% | 41.4% | 13.8% |
| Number of trees | 124 | 87 | 29 |

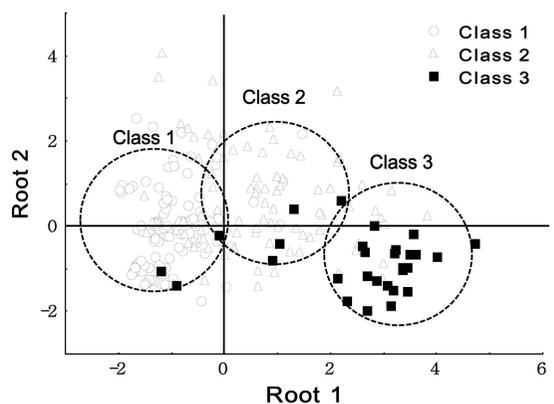


Fig. 5. Discriminant analysis of tree dieback class on the basis of physical factors, condition of trees based on presence of wilted foliage and sap exudate, and the number of entrance holes on the upslope- and downslope portion of the trunk near groundline and breast height trunk of each sampled Mongolian oak tree. Attack density on the downslope side of the trunk near groundline and the presence of wilted foliage were the highest standardized coefficient for axis 1 (0.83) and axis 2 (0.65), respectively.

ambrosia beetles considering that adequate moisture is needed for growth of their symbiotic ambrosia fungi. When oak trees are killed by *P. quercivorus* and its associated fungi, it is likely that wood moisture levels remain relatively high at the base of the tree, compared with the upper trunk or canopy branches, given that the lower trunk has greater diameter and is in closer proximity to the soil (Igeta et al. 2004). Moreover, the fact that the percentage of trees with entrance holes along the trunk between 1.5 and 3 m increased with increasing dieback class provides further evidence that *P. koryoensis* first infests the lower trunk (<1.5 m) (Table 3). The preference for *P. koryoensis* to initiate colonization along the lower trunk would be advantageous for the growth and survival of their symbiotic fungus and brood.

Mortality of Mongolian oak trees increased with increasing *P. koryoensis* attack density, especially when measured along the downslope side of the trunk near groundline (Fig. 5), suggesting that *P. koryoensis* and its fungal symbiont are the principal causal factors of tree mortality. Similarly, a positive relationship was reported between the density of *P. quercivorus* galleries that succeeded in producing offspring and the degree of discoloration in the sapwood by its ambrosial fungus *Raffaelea quercivora* Kubono & Shin, suggesting that the degree of oak dieback and mortality in Japan increased with increasing *P. quercivorus* attack density (Kinuura and Kobayashi 2006). These results suggest that oak mortality occurs when platypodine attack density is sufficiently high enough that water translocation in the sapwood is effectively blocked by the associated fungi.

The colonization behavior exhibited by *P. koryoensis* could be useful in predicting future tree mortality caused by this ambrosia beetle, considering that the principal component analysis indicated that attack density on the downslope side of the trunk near groundline was a good predictor of tree mortality (Fig. 5). Similarly, Fierke et al. (2005) used crown condition and the number of red oak borer, *Enaphalodes rufulus* (Haldeman) (Cerambycidae), emergence holes along the lower 2 m of trunk to predict future population trends.

The relationship between *P. koryoensis* mean attack density and tree dieback class was affected by factors such as stand elevation and slope (Fig. 2 and 3, Table 2). These findings suggest that physical and environmental conditions can influence *P. koryoensis* population dynamics and subsequent tree mortality. Overall, oak dieback at our study site was most severe at elevations of 150–250 m, and dramatically dropped at elevations over 330 m. Mongolian oak trees occur naturally up to elevations of 1,100 m in Korea, and *P. koryoensis* has been observed up to 500 m, although attack densities were very low (W. I. Choi, unpublished data). The above findings suggest that local air temperatures have a strong influence on *P. koryoensis* altitudinal distribution Williams et al. (2008) for various scolytine bark beetles. Slope also can affect attack density of *P. koryoensis* given that the beetles' flight activity (Kim et al. 2010) can be influenced by slope,

and trees growing on steep slopes also may be prone to more water stress. In fact, many of the Mongolian oak trees killed by KOW in Korea are growing on steep slopes (W. I. Choi, unpublished data). The influence of local air temperature and slope on *P. koryoensis* population dynamics need further study. In addition, our finding that larger-diameter oaks were among the first to die from KOW suggests that *P. koryoensis* preferentially colonizes larger diameter trees or that larger, and presumably older trees, are more susceptible to infestation (Fig. 3). This relationship that older trees are more vulnerable to attack is well known for many other ambrosia and bark beetles (Shore et al. 2000), including *D. ponderosae* (Mitchell and Preisler 1991), *Ips pini* (Say) (Kolb et al. 2006), and *P. quercivorus* (Yamasaki and Futai 2008). For example, lodgepole pine (*Pinus contorta* Douglas) tree resistance to *D. ponderosae* attack decreases as trees age beyond 60 yr (Safranyik et al. 1974).

Partial wilting of Mongolian oaks and sap exudates near *P. koryoensis* entrance holes were probable symptoms of heavy current-year *P. koryoensis* infestation, which was especially common in the Dieback class 2 trees. Apparently, many trees in Dieback class 2 can survive for one or more years after initial *P. koryoensis* infestation, given that only minor wilting was observed on many of these trees. It is likely that in succeeding years, many trees in Dieback class 2 will be attacked again by *P. koryoensis*, which will often result in total tree mortality. The trunk sap exudates observed on many infested trees may indicate a defensive reaction by the tree (Table 3); however, this relationship needs further study.

Conclusions and Management Implications. In conclusion, *P. koryoensis* preferentially attacks the lower trunk of Mongolian oak trees in Korea. The risk of Mongolian oak mortality increased with increasing attack density as measured by the density of *P. koryoensis* entrance holes, especially along the downslope side of the trunk near groundline, which indicates that attack density along the downslope portion of the lower trunk can serve as a good indicator of future oak dieback. Because the 95% confidence interval for the *P. koryoensis* attack density on the downslope portion of the trunk near groundline of KOW-killed Mongolian oaks was from 2,324 to 2,993 entrance holes/m², this level of attack density may be close to the threshold for complete wilting of most Mongolian oak trees.

References Cited

- Byers, J. A. 1984. Nearest neighbor analysis and simulation of distribution pattern indicates an attack spacing mechanism in the bark beetle, *Ips typographus* (Coleoptera: Scolytidae). *Environ. Entomol.* 13: 1191–1200.
- Choi, W. I. 2011. Influence of global warming on forest coleopteran communities with special reference to ambrosia and bark beetles. *J. Asia Pac. Entomol.* 14: 227–231.
- Choi, W. I., J.-S. Lee, K.-S. Choi, J.-K. Kim, and S.-C. Shin. 2008. Tree trunk level distribution of entry hole by *Platypus koryoensis* (Coleoptera: Platypodidae) and its implication to tree damage. *Korean J. Appl. Entomol.* 47: 127–131.

- Clark, S. L., and S. W. Hallgren. 2004. Age estimation of *Quercus marilandica* and *Quercus stellata*: applications for interpreting stand dynamics. *Can. J. For. Res.* 34: 1353–1358.
- Esaki, K., K. Kato, and N. Kamata. 2004. Stand-level distribution and movement of *Platypus quercivorus* adults and patterns of incidence of new infestation. *Agric. For. Entomol.* 6: 71–82.
- Esaki, K., K. Kato, and N. Kamata. 2009. Early attack distribution of the oak borer *Platypus quercivorus* (Coleoptera: Platypodidae) on the trunk surface of newly infested trees. *J. Jpn. For. Soc.* 91: 208–211.
- Fierke, M. K., D. L. Kinney, V. B. Salisbury, D. J. Crook, and F. M. Stephen. 2005. A rapid estimation procedure for within-tree populations of red oak borer (Coleoptera: Cerambycidae). *For. Ecol. Manage.* 215: 163–168.
- Gao, B., X. Wen, H. Guan, M. Knizek, and J. Zdarek. 2005. Distribution and attack behavior of the red turpentine beetle, *Dendroctonus valens*, recently introduced to China. *J. For. Sci.* 51: 155–160.
- Goeden, R. D., and D. M. Norris. 1965. Some biological and ecological aspects of ovipositional attack in *Carya* spp. by *Scolytus quadrispinosus* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.* 58: 771–777.
- Haack, R. A., and R. J. Rabaglia. 2011. Exotic bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in the United States: potential and current invaders. In J. E. Peña (ed.), *Potential invasive pests of agricultural crop species*. CABI International, Wallingford, United Kingdom (in press).
- Haack, R. A., and F. Slansky. 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera, and Hymenoptera, pp. 449–486. In F. Jr. Slansky and J. G. Rodriguez (eds.), *Nutritional ecology of insects, mites, spiders and related invertebrates*. John Wiley, New York.
- Haack, R. A., R. C. Wilkinson, and J. L. Foltz. 1987a. Plasticity in life-history traits of the bark beetle *Ips calligraphus* as influenced by phloem thickness. *Oecologia (Berl.)* 72: 32–38.
- Haack, R. A., R. C. Wilkinson, J. L. Foltz, and J. A. Corneil. 1987b. Spatial attack pattern, reproduction, and brood development of *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine phloem thickness: a field study. *Environ. Entomol.* 16: 428–436.
- Igeta, Y., K. Esaki, K. Kato, and N. Kamata. 2004. Spatial distribution of a flying ambrosia beetle *Platypus quercivorus* (Coleoptera: Platypodidae) at the stand level. *Appl. Entomol. Zool.* 39: 583–589.
- [KFRI] Korea Forest Research Institute. 2009. Annual report of monitoring for forest insect pests and diseases in Korea. SeongMunSa, Seoul.
- Kim, K.-H., Y.-J. Choi, S.-T. Seo, and H.-D. Shin. 2009a. *Raf-faelea quercus-mongolicae* sp. nov. associated with *Platypus koryoensis* on oak in Korea. *Mycotaxon* 110: 189–197.
- Kim, J., S.-G. Lee, S.-C. Shin, Y.-D. Kwon, and I.-K. Park. 2009b. Male-produced aggregation pheromone blend in *Platypus koryoensis*. *J. Agric. Food Chem.* 57: 1406–1412.
- Kim, J., J.-S. Lee, I.-K. Park, and W. I. Choi. 2010. Influence of trap types and locations in trunk on trapping efficiency against *Platypus koryoensis* (Coleoptera: Platypodidae). *Korean J. Appl. Entomol.* 49: 145–149.
- Kinuura, H., and M. Kobayashi. 2006. Death of *Quercus crispula* by inoculation with adult *Platypus quercivorus* (Coleoptera: Platypodidae). *Appl. Entomol. Zool.* 41: 123–128.
- Kolb, T. E., N. Guerard, R. W. Hofstetter, and M. R. Wagner. 2006. Attack preference of *Ips pini* on *Pinus ponderosa* in northern Arizona: tree size and bole position. *Agric. For. Entomol.* 8: 295–303.
- Koo, C. D., J. K. Kim, J. K. Kim, J. J. Kim, G. S. Park, S. C. Park, S.-C. Shin, S. Y. Lee, S. Y. Lee, W. S. Lee, et al. 2008. New forest protection. Hyangmoon, Seoul, Korea.
- Lehringer, C., G. Daniel, and U. Schmitt. 2009. TEM/FE-SEM studies on tension wood fibres of *Acer spp.*, *Fagus sylvatica* L. and *Quercus robur* L. *Wood Sci. Technol.* 43: 691–702.
- Lieutier, F. 2002. Mechanisms of resistance in conifers and bark beetle attack strategies, pp. 31–77. In M. R. Wagner, K. M. Clancy, F. Lieutiers, and T. D. Paine (eds.), *Mechanism and deployment of resistance in trees to insects*. Kluwer Academic Publishers, Boston, MA.
- McCambridge, W. F. 1967. Nature of induced attacks by the black hills beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.* 60: 920–928.
- Mitchell, R. G., and H. K. Preisler. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *For. Sci.* 37: 1390–1408.
- Nord, J. C. 1972. Biology of the Columbian timber beetle, *Corthylus columbianus* (Coleoptera: Scolytidae) in Georgia. *Ann. Entomol. Soc. Am.* 65: 350–358.
- Park, K.-H. 2008. Ecological characteristics and chemical control of *Platypus koryoensis* (Coleoptera: Platypodidae). M.S. thesis, Chungbuk National University, Cheongju, Korea.
- Park, S., and D. Lyu. 2007. Checklist of the family Platypodidae (Coleoptera) in Korea. *J. Asia-Pacific Entomol.* 10: 275–280.
- SAS Institute. 2004. SAS user's guide. SAS Institute, Cary, NC.
- Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service Technical Reports 1: 1–24.
- Shore, T. L., L. Safranyik, and J. P. Lemieux. 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. *Can. J. For. Res.* 30: 44–49.
- StatSoft Inc. 2004. Statistica (data analysis software system), version 7.0. (www.statsoft.com).
- Trimble Navigation Ltd. 2005. GPS Pathfinder office version 3.10. Trimble Navigation Ltd. Sunnyvale, CA.
- Weber, B. C., and J. E. McPherson. 1983. Life history of the ambrosia beetle *Xylosandrus germanus* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.* 76: 455–462.
- Williams, K. K., J. D. McMillin, T. E. DeGomez, K. M. Clancy, and A. Miller. 2008. Influence of elevation on bark beetle (Coleoptera: Curculionidae, Scolytinae) community structure and flight periodicity in Ponderosa pine forests of Arizona. *Environ. Entomol.* 37: 94–109.
- Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Nat. Mem.* 6: 1–1359.
- Yamasaki, M., and K. Futai. 2008. Host selection by *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae) before and after flying to trees. *Appl. Entomol. Zool.* 43: 249–257.
- Zar, J. H. 1999. *Biostatistical analysis*, 4th ed. Prentice Hall, Upper Saddle River, NJ.

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