INTRODUCTION

In forest ecosystems, outbreaks of herbivorous insects sometimes cause serious damage and tree death (e.g. Gerardi and Grimm, 1979; Kamata, 2002). In 1998, many trees of Abies firma Siebold and Zuccarini (Pinaceae) were found to be seriously defoliated and dead in a natural stand on Mount Unzen in the Unzen-Amakusa National Park, Nagasaki Prefecture, northern Kyushu, Japan. Many herbivorous insects were collected and identified from damaged and dead trees (Tokuda et al., 2000; Tokuda and Yukawa, 2003). Major herbivores were Paradiplosis manii (Inouye) (Diptera: Cecidomyiidae), Parendaeus abietinus Kojima and Morimoto (Coleoptera: Curculionidae), and Polygraphus proximus Blandford (Coleoptera: Scolytidae). Paradiplosis manii is a needle galler and Tokuda and Yukawa (2003) have recorded that current galled needles of A. firma fell to the ground in autumn, significantly earlier than ungalled needles; however, the effects of other insects on A. firma have not been intensively studied.

In order to gather further information on the effects of these insects on A. firma trees, field surveys were performed on Mount Unzen from October 1998 to September 2001. This paper focuses on: 1) seasonal occurrence of P. abietinus; 2) effects of infestation by P. abietinus on the fall of A. firma needles; 3) seasonal occurrence of P. proximus; and 4) effects of bark infestation by P. proximus on the survival of A. firma trees. Based on these data, the possible dieback process of A. firma by these insects is discussed.
MATERIALS AND METHODS

Abies firma and associated insects. Abies firma is a coniferous tree endemic to Japan and is distributed in the uplands of Honshu, Shikoku, and Kyushu at elevations between 50 and 1,900 m (commonly 300–1,000 m) and is the only Abies species growing naturally in Kyushu (Farjon, 1990). On Mount Unzen, budburst of A. firma occurs once a year during the period from late April to mid-May (Tokuda and Yukawa, 2003).

Parendaeus abietinus is a small weevil that is widely distributed in Honshu, Shikoku, and Kyushu, Japan (Kojima and Morimoto, 1996; Tokuda et al., 2000). The adults feed on needles of A. firma (Fig. 1) and Abies homolepis Siebold and Zuccarini, and the larvae mine the apical portions of current needles (Fig. 2) (Kojima and Morimoto, 1996; Tokuda et al., 2000). Based on field observation, one adult fed on plural needles by making many holes (Fig. 1) and one larva mined a single needle. The life history of this species has not been studied before.

Polygraphus proximus is widely distributed in Hokkaido, Honshu, Shikoku, and Kyushu, Japan as well as in the Korean Peninsula, the Russian Far East, and the Siberian Region (Nobuchi, 1966; Koizumi, 1994). This species is a bivoltine, phloem-feeding bark beetle and is known to produce double-armed horizontal mother-galleries in the bark of conifers such as A. firma, Abies mariesii Masters, Abies sachalinensis (Fr. Schmidt) Masters, and Pinus koraiensis Siebold and Zuccarini (Nobuchi, 1966; Koizumi, 1994). The male is considered to make an entry hole and tunnel into the host bark, a few females enter the tunnel through the entrance hole for mating, probably attracted by the sex pheromone of the male, and the offspring individually make an exit hole in the bark (Kabe, 1959; Nobuchi, 1980).

Census fields and census trees. Field surveys were conducted chiefly at a natural stand of A. firma on Mount Unzen (32°44’N, 130°16’E; ca. 1,000 m a.s.l.). An additional A. firma stand was surveyed on Mount Hiko (33°29’N, 130°55’E; ca. 700 m a.s.l.), Fukuoka Prefecture, northern Kyushu, Japan. In both census fields, the tree height of A. firma was mostly about 10 m or more.

On 15 October 1998, 100 trees (tree nos. U1–U100) were selected randomly as census trees in a highly damaged area and its neighbouring areas on Mount Unzen. Diameter at breast height (DBH) of the census trees ranged from 30 to 730 mm (mean±SD=193.2±95.4 mm). Three A. firma trees (H1–H3) with DBH (mean±SD=203.3±40.4 mm) similar to that of U1–U100 were selected as census trees on Mount Hiko.

Seasonal occurrence of P. abietinus on Mount Unzen. When the field survey on Mount Unzen commenced in 1998, most A. firma trees had been injured to some extent by the aforementioned three herbivorous insects. Because these trees were too tall to observe needle damage directly and continuously, two healthy A. firma saplings (1.5 m tall; tree nos. S1 and S2) were transplanted to the census field on Mount Unzen from Mount Hiko on 4 March 1999. Three one-year-old shoots (budburst
in 1998) were randomly selected on each sapling, and all current shoots (budburst in 1999) extended from old shoots were surveyed. Needles attached to the current shoots were numbered from the proximal to distal ends to identify individual needles. The remaining current needles, mines caused by *P. abietinus* larvae, and injury holes made by *P. abietinus* adults (Fig. 1) were surveyed at two-week intervals from 4 March to 9 December 1999. The numbers of mines and injury holes that appeared freshly during each census interval were regarded as indicators of the seasonal occurrence of *P. abietinus* larvae and adults, respectively. In addition, one- to four-year-old shoots were also observed on each census date to confirm whether old needles were mined or injured.

In this study, the actual number of *P. abietinus* was not used to evaluate its density and seasonal occurrence for the following reasons: (1) the actual number of *P. abietinus* could not evaluate annual changes in *P. abietinus* density before we started this study (i.e. 1995–1998); (2) the number of *P. abietinus* adults appearing in 1999 was too small to evaluate clear seasonal trends by the direct counting of larvae and adults on census shoots.

**Effect of *P. abietinus* infestation on the fall of *A. firma* needles.** On Mount Unzen, the effects of infestation by *P. abietinus* on the fall of *A. firma* needles were surveyed by periodical shoot sampling from *A. firma* trees. On 15 October 1998, 25 current, 25 one-year-, 25 two-year-, and 12 three-year-old shoots were collected randomly from 3–5 m high branches of five selected census trees (U1–U3, U77, and U78; each shoot included approximately 60 needles) with moderate DBH (mean±SD=176.0±29.7 mm). Needles attached to and fallen from each shoot, as well as needles mined by *P. abietinus* larvae and injured by *P. abietinus* adults were counted. The number of fallen needles was easily recognized by the ring scars of fallen needle bases remaining on each shoot. The percentages of needles mined and injured among the surviving needles were calculated for respective shoots as indicators of the degree of larval and adult infestation. When a needle was both mined by a larva and injured by adult(s), it was included both in mined and injured needles in the calculation of percentages. Similar surveys were performed on 9 December 1999, 28 September 2000, and 7 September 2001, respectively, for current, one-year-, two-year-, and three-year-old shoots of the five census trees. When some of the sampling trees died, they were replaced in the survey by trees that had similar DBH and were growing close to the dead trees. As a result, U47, U49, U76, U77, and U80 were surveyed on 9 December 1999, U76, U81, U82, U89, and U91 on 28 September 2000, and U76, U81, U82, U84, and U91 on 7 September 2001.

The population density of *P. abietinus* on Mount Unzen was expressed as the percentage of current needles that had been infested by adults every year from 1998 to 2001. The percentages of current needles in 1997, 1996, and 1995 were assessed on 15 October 1998 by surveying one-year-, two-year-, and three-year-old needles, respectively, because *P. abietinus* was observed in this survey to have fed on current needles alone (see Results). In order to clarify the effect of needle infestation by *P. abietinus* adults on needle fall of *A. firma*, needle data for respective trees and year classes were also used for linear regression analysis between the ratio of remaining needles to all needles, and the ratio of needles infested by *P. abietinus* adults to remaining needles. The percentages might not correlate with the actual density of *P. abietinus*, especially when the density was extremely high. Nevertheless, we used this value for evaluation because it was the only possible indicator to assess the density of *P. abietinus* before 1999.

On Mount Hiko, where these insects were rarely found (M. Tokuda and J. Yukawa, personal observation), a similar survey was conducted for H1–H3 on 26 January 1999.

During the survey on Mount Unzen and Mount Hiko, galled needles caused by *P. manii* were found infrequently, because current galled needles mostly fell to the ground soon after gall midge larvae had left the galled needles in autumn (Tokuda and Yukawa, 2003). Needle damage by other herbivores was rare throughout the survey.

**Seasonal occurrence of *P. proximus* on Mount Unzen.** In order to clarify the seasonal occurrence of *P. proximus*, the number of holes produced by *P. proximus* on *A. firma* bark at a trunk height of 1.0–1.5 m was surveyed for 14 census trees (U1–7 and U9–15) with various values of DBH (140 to 350 mm in range; mean±SD=199.3±51.1 mm) at two-week intervals from 12 March to 9 September 1999. Fresh holes produced on the bark of each
tree during the census intervals were marked with a black felt pen, except on rainy census days (25 March, 3 and 18 June, 29 July, and 26 August, 1999) when the holes could not be marked due to wet conditions. Because entry holes by *P. proximus* males and exit holes by the offspring were not distinguishable based on the diameter of each hole, these two types of holes were grouped together to express the seasonal occurrence of *P. proximus*.

Scolytids other than *P. proximus* were not found in the bark of *A. firma* on Mount Unzen throughout the survey.

**Bark infestation of *A. firma* by *P. proximus*.** Bark infestation of *A. firma* by *P. proximus* was surveyed on 9 February 1999 for all 100 census trees. In this survey, living census trees were distinguished from dead ones by having green needles and fresh terminal buds. The percentages of needles remaining were estimated visually on 30 shoots randomly selected on all living census trees for the respective year classes: current, one-year-, two-year- and three-year-old shoots. The mean percentage of needles remaining on the 120 shoots examined was calculated for all census trees to indicate the degree of needle fall from each tree.

At the same time, the presence or absence of bark holes caused by *P. proximus* at a trunk height of 0–2.0 m was examined on the census trees. When a census tree had holes in the trunk, the presence or absence of exuded oleoresin from the holes was also recorded. Preliminary surveys indicated that no living *P. proximus* individuals colonized the bark when oleoresin exuded from all holes (=entry holes, in this case), while living adults and larvae of *P. proximus* were found in the bark when oleoresin was not exuded from any holes (oleoresin exudation was categorized into ‘all or nothing’, because its effect was clearly distinguishable between the two categories in this case). By examining oleoresin production as an indicator of success or failure in the colonization of *A. firma* barks by *P. proximus*, living census trees were divided into the following three ordinal categories: 1) trees not yet attacked by *P. proximus*; 2) trees attacked but not colonized by *P. proximus* (=trees with active oleoresin production from bark holes); and 3) trees attacked and colonized by *P. proximus* (=trees without any oleoresin production from bark holes).

The presence or absence of bark holes and oleoresin production as well as dead or alive respective trees were also surveyed for all 100 census trees on 9 December 1999, 22 April and 28 September 2000, and 25 April and 7 September 2001. Changes in the ratio of trees freshly attacked and colonized by *P. proximus* during the census intervals to trees freshly attacked but not colonized were assessed on each census date.

**Statistics.** Statistical analyses were performed using the JMP 5.1.1 statistical package (SAS Institute Inc., 2003). The degree of needle infestation by *P. abietinus* adults (=the percentages of needles injured by *P. abietinus* adults) was analyzed among different years using ANOVA, and treatment means were compared using the Tukey-Kramer HSD test. Infestation by *P. abietinus* and various factors other than infestation were analyzed by ANCOVA to determine the degree of the effect on the fall of needles (=percentages of fallen needles from each shoot). In the analysis, the census date was treated as continuous scale numeric data expressed by the calendar date, shoot length was represented by the length from the base of the shoot to the base of the terminal bud or that of the subsequent year’s shoot, the age of needles was expressed as the number of months elapsed from budburst in June to the respective census dates, and adult infestation and mine formation were determined respectively as the percentages of needles injured by *P. abietinus* adults and mined by larvae on the remaining needles of each shoot. The ratio of the remaining needles to all needles for each tree and each year class was linearly regressed on the ratio of needles infested by *P. abietinus* adults to those remaining on the census shoots. Ordinal logistic regression analysis was employed to determine the effects of the degree of needle fall (=the mean percentage of remaining needles) and tree size (=DBH) on the attack and colonization by *P. proximus*, because success or failure of colonization was divided into three ordinal categories, as mentioned earlier. Changes in the ratio of *A. firma* trees that were freshly attacked and colonized by *P. proximus* to the trees that were freshly attacked but not colonized were analyzed by logistic regression analysis. The relationship between *P. proximus* attack and the degree of needle fall (=the mean percentage of remaining needles) as well as DBH of *A. firma* trees were analyzed by ANOVA, and treatment means were compared using the Tukey-Kramer
HSD test. All percentile data used for ANOVA and ANCOVA were arcsine transformed prior to the respective analyses.

RESULTS

Seasonal occurrence of *P. abietinus*

Bud burst of trees S1 and S2 on Mount Unzen occurred between 3 and 18 June 1999, and no mines or injury holes made by *P. abietinus* were found during this period. The number of holes on the census shoots increased rapidly between 15 and 29 July on S1 and between 29 July and 11 August on S2, respectively (Fig. 3), indicating that adult *P. abietinus* actively infested needles in these periods. In correlation with the infestation of needles by *P. abietinus* adults, current needles on the census shoots fell to the ground (Fig. 3). On S1, no needles were mined throughout the survey, while on S2, four, five, and one needle were newly mined on 1, 15, 29 July, respectively. Among the ten mined needles on S2, three fell within two weeks and four within four weeks after the first finding of infested needles, but the rest of the needles remained on the shoots until 9 December 1999.

On S1 and S2, no mines or injured holes by *P. abietinus* occurred on one- to four-year-old needles throughout the survey.

Effect of *P. abietinus* infestation and various other factors on needle falling of *A. firma*

There were significantly greater percentages of infestation by *P. abietinus* adults on the surviving needles that appeared in 1995, 1996, and 1997 as well as in 1998 than those that appeared in 1999 and in 2001 (Fig. 4). More than 50% of the remaining needles were infested in 1998 or earlier, but
only 6% in 2001. The mean percentage of needles mined by \textit{P. abietinus} larvae on surviving needles was also significantly different among years (Fig. 5). The mean percentages were more than 7.5% from 1995 to 1998, while less than 1.2% from 1999 to 2001.

On Mount Unzen, the needle age and needle infestation by \textit{P. abietinus} adults strongly affected the fall of needles (Table 1). In addition, the census date, tree, shoot length, and mining by \textit{P. abietinus} larvae had significant effects on the fall of needles (Table 1), as did the interaction effect of the census date and adult infestation (Table 1). The ratio of the remaining needles to all needles was significantly and negatively correlated with the ratio of needles infested by \textit{P. abietinus} adults to those remaining (Fig. 6), indicating that shoots heavily infested by adults suffered severe needle fall.

On Mount Hiko, the needle age of \textit{A. firma} had the most significant effect on the fall of needles (Table 2). Tree and needle infestation by \textit{P. abietinus} adults also had significant effects on the fall of needles. The mean percentages of fallen needles were less than 10% on current to three-year-old shoots on Mount Hiko (data not shown; 22–94 shoots were examined for respective year classes). Needles infested by \textit{P. abietinus} adults on the remaining shoots were 0.8% \((n=4,652\) remaining needles), 0.9% \((n=2,993)\), 1.9% \((n=2,248)\), and 1.0% \((n=999)\) for current (budburst in 1998), one-year-, two-year-, and three-year-old needles, respectively. Only one needle mined by \textit{P. abietinus} larva was found in three-year-old needles. Needles galled by \textit{P. manii} were not found in the survey on Mount Hiko.

![Fig. 5. Percentage of Abies firma needles mined by Parendaecus abietinus larvae in different years. The percentage in each year was calculated from the mean percentages of infested needles on 12 shoots in 1995 and 25 shoots in 1996–2001, respectively, on five census trees on Mount Unzen. The total number of needles remaining on the shoots was 1,051 in 1995, 1,328 in 1996, 1,427 in 1997, 2,004 in 1998, 3,923 in 1999, 3,145 in 2000, and 6,889 in 2001. Values are the means±standard deviations. Different letters above bars indicate significant differences between years of budburst (ANOVA followed by Tukey-Kramer HSD test; \(p<0.05\)).](image1)

![Fig. 6. Linear regression between the ratio of remaining needles to all needles and the ratio of needles infested by Parendaecus abietinus adults to remaining needles on Mount Unzen.](image2)

![Table 1. ANCOVA to detect effects of census date, Abies firma tree, shoot length, needle age, and the adult infestation and larval mining of Parendaecus abietinus on the needle fall of A. firma on Mount Unzen on 15 October 1998, 9 December 1999, 28 September 2000, and 7 September 2001.](table1)

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>(F)</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Census date</td>
<td>1</td>
<td>6.09</td>
<td>61.96</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Tree</td>
<td>13</td>
<td>31.76</td>
<td>24.86</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Shoot length</td>
<td>1</td>
<td>3.49</td>
<td>30.10</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Needle age (months)</td>
<td>1</td>
<td>51.77</td>
<td>57.71</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Adult infestation</td>
<td>1</td>
<td>16.40</td>
<td>166.90</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mine formation</td>
<td>1</td>
<td>0.73</td>
<td>7.50</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Date\times adult infestation</td>
<td>1</td>
<td>0.45</td>
<td>4.56</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Date\times mine formation</td>
<td>1</td>
<td>0.23</td>
<td>2.36</td>
<td>0.12</td>
</tr>
</tbody>
</table>

![Table 2. ANCOVA to detect effects of Abies firma tree, shoot length, needle age, and the adult infestation and larval mining of Parendaecus abietinus on the needle falling of A. firma on Mount Hiko on 26 January 1999.](table2)

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>(F)</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree</td>
<td>2</td>
<td>0.49</td>
<td>4.47</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Shoot length</td>
<td>1</td>
<td>0.06</td>
<td>1.05</td>
<td>0.31</td>
</tr>
<tr>
<td>Needle age (months)</td>
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<td>1.68</td>
<td>30.73</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Adult infestation</td>
<td>1</td>
<td>0.27</td>
<td>4.91</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Mine formation</td>
<td>1</td>
<td>0.00</td>
<td>0.06</td>
<td>0.81</td>
</tr>
</tbody>
</table>
Seasonal occurrence and bark infestation of *P. proximus* on Mount Unzen

Seasonal changes in the number of newly produced bark holes by *P. proximus* exhibited two peaks (Fig. 7). The first peak appeared in spring and the second one in summer.

Both tree size and the degree of needle fall correlated significantly with bark infestation by *P. proximus* (Table 3). The relationship between bark infestation and needle fall is shown in Fig. 8. Significantly more needles remained on trees that were not yet attacked by *P. proximus* than those attacked (Fig. 8). The trees attacked and colonized tended to have fewer needles than those attacked but not colonized. There were no significant differences in DBH among trees not yet attacked, attacked but not colonized, and attacked and colonized (Fig. 9). The ratio of trees freshly colonized by *P. proximus* to those freshly attacked but not colonized decreased significantly from February 1999 to April 2001 (Table 4).

The number of dead trees among the 100 census trees increased markedly before November 1999, while few trees died after December 1999 (Fig. 10). During the survey, all 68 census trees that had been colonized by *P. proximus* died without exception (Fig. 10). In contrast, none of the census trees died unless they had been colonized by *P. proximus*.

In addition, few trees seemed to have died in 1997 or earlier, based on our observation, for the

### Table 3. Ordinal logistic regression to detect effects of the tree size (DBH) and degree of needle fall of *Abies firma* on the attack and colonization by *Polygraphus proximus* on Mount Unzen on 9 February 1999

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>Wald Chi-square</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree size (DBH)</td>
<td>1</td>
<td>8.13</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Needle falling</td>
<td>1</td>
<td>7.51</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Tree size×needle falling</td>
<td>1</td>
<td>5.48</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

Fig. 7. Seasonal changes in the number of new holes produced on *Abies firma* bark by *Polygraphus proximus* on Mount Unzen.

Fig. 8. Relationship between *Polygraphus proximus* attack and the mean percentage of needles remaining on *Abies firma* shoots on 9 February 1999. Different letters above bars indicate significant differences between *P. proximus* attack (ANOVA followed by Tukey-Kramer HSD test; *p*<0.05).
following reason: When we started the field survey in October 1998, dead trees were distributed only in a restricted area and they were still inhabited by *P. proximus* in the bark, suggesting that the trees had been colonized in spring and/or summer of 1998.

**DISCUSSION**

*P. abietinus* and needle fall of *A. firma*

The field survey indicates that *P. abietinus* is a univoltine species (Fig. 3), infesting only current needles. Adult infestation and larval mining affected the needle fall of *A. firma* significantly (Table 1), and shoots heavily infested by adults suffered severe needle fall (Fig. 6). This means that needles infested by *P. abietinus* adults and mined by larvae fall to the ground earlier and more frequently than normal needles. In Fig. 4, data for 1995, 1996, and 1997 needles were obtained from old needles remaining on the census trees; therefore, the percentages of infested needles in these years were possibly underestimated due to more frequent losses of infested needles than normal needles. The higher percentages of needles infested by *P. abietinus* adults and mined in 1998 or earlier years (Figs. 4 and 5) suggest that the population density of *P. abietinus* was higher in earlier years and then decreased after 1998. On Mount Hiko, where *P. abietinus* was rarely found, the effects of adult infestation and larval mine formation on needle fall were not so striking in comparison with the effect on Mount Unzen (Tables 1 and 2).

Gall formation by the cecidomyiid, *P. manii*, also caused needle fall of *A. firma* on Mount Unzen (Tokuda and Yukawa, 2003). The relative intensity of damage causing needle fall could not be quantified between *P. abietinus* and *P. manii* for the following reasons: infestation by *P. abietinus* lasted three months (Fig. 3) and needle fall occurred gradually during this period, so the actual number of needles infested by the weevil could not be evaluated. Current galled needles by *P. manii* fell in the autumn, thus gall midge density before 1998 could not be examined at the beginning of the field survey ( Tokuda and Yukawa, 2003); however, we consider that *P. abietinus* had the primary role in *A. firma* needle fall, compared with *P. manii*, because the mean percentage of current needles galled by *P. manii* was only 3.6% in 1999 (0–9.9% in range; 9 census trees were examined) (Tokuda and Yukawa, 2003), which was distinctly lower than the percent-

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**Table 4.** The number of *Abies firma* trees whose bark was attacked by *Polygraphus proximus* and that of trees freshly colonized by *P. proximus* among those freshly attacked on Mount Unzen

<table>
<thead>
<tr>
<th>Date</th>
<th>Attacked</th>
<th>Colonized (%)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>9 February 1999</td>
<td>23</td>
<td>12 (52.2)</td>
</tr>
<tr>
<td>9 December 1999</td>
<td>7</td>
<td>2 (28.6)</td>
</tr>
<tr>
<td>22 April 2000</td>
<td>8</td>
<td>1 (12.5)</td>
</tr>
<tr>
<td>28 September 2000</td>
<td>6</td>
<td>1 (16.6)</td>
</tr>
<tr>
<td>25 April 2001</td>
<td>4</td>
<td>0 (0)</td>
</tr>
<tr>
<td>7 September 2001</td>
<td>0</td>
<td>0 (—)</td>
</tr>
</tbody>
</table>

*Significantly reduced from 9 February 1999 to 25 April 2001 (logistic regression; d.f. = 1, Chi-square = 17.83, $R^2 = 0.278, p<0.0001$).
age of needles infested by *P. abietinus* adults (Fig. 4). Moreover, galls of *P. manii* were not induced on trees whose budburst had occurred later than the emergence of *P. manii* adults (e.g. U43, U44, U59) (Tokuda and Yukawa, 2003). Even so, some (U43, U44) were heavily defoliated in 1998 or earlier and died in 1999.

**P. proximus** and dieback of *A. firma*

Entry holes made by *P. proximus* males and exit holes by the offspring were not distinguishable in this study, so the detailed life history of *P. proximus* could not be clarified. In the survey, however, two peaks were detected in bark hole production by *P. proximus* (Fig. 7). Because the peaks possibly indicate the appearance of offspring from exit holes and further colonization of the bark by newly emerged adults, *P. proximus* seems to be bivoltine, as has been noted by Koizumi (1994), also on Mount Unzen.

As shown in Fig. 8, *P. proximus* preferably attacked and successfully colonized trees with fewer needles. Although DBH of *A. firma* significantly affected the attack and colonization by *P. proximus* when it was analyzed together with the degree of needle fall in ordinal logistic regression analysis (Table 3), there was no clear tendency between DBH alone and the attack and colonization by *P. proximus* (Fig. 9). The observation that the number of *A. firma* trees attacked and colonized by *P. proximus* decreased significantly from 1999 to 2001 on Mount Unzen (Table 4) suggests that *P. proximus* could not colonize *A. firma* trees after they had survived heavy needle fall by *P. abietinus*. Only a few census trees died after December 1999 (Fig. 10), when needle damage by *P. abietinus* had become low (Fig. 4); therefore, on Mount Unzen, *P. proximus* was considered to act as a secondary pest, attacking weakened trees.

The threshold density of *P. proximus* attacks per unit area of bark surface to kill *A. firma* could not be examined in this study, because, as mentioned earlier, we could not distinguish entrance and exit holes of *P. proximus*. Based on field observation, a census tree with severe needle fall died only due to 5.6 holes/m² on the trunk height of 0–2.0 m, but another tree survived, by oleoresin exudation, even with 29.6 holes/m² on the trunk, so the threshold density of *P. proximus* attacks seems to vary according to the degree of needle damage.

Some recent studies have referred to fungi associated with *Polygraphus* species other than *P. proximus* (e.g. Ohsawa et al., 2000; Rollins et al., 2001), but no sign of associated fungi was found with *P. proximus* during the field survey on Mount Unzen (personal observation).

In Europe and North America, many trees have died due to severe infestation by defoliators (e.g. Gerardi and Grimm, 1979; Bejer, 1988). In Japan, however, tree mortality following insect defoliation is generally low, probably because the intensity of water stress is low under the oceanic climate conditions (Kamata, 2002). The mortality of *A. firma* trees following severe defoliation by *P. abietinus* was also low if there was no attack by the bark beetle, *P. proximus*. A similar example was reported for other *Polygraphus* species: in Newfoundland, *Polygraphus rufipennis* successfully colonized the bark of *Picea mariana* that had been weakened by the eastern spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae) (e.g. Bowers et al., 1996).

A possible dieback process of *A. firma* on Mount Unzen is considered as follows: (1) Around 1995, *P. abietinus* increased its population density and caused serious needle fall of *A. firma*; (2) In 1998 and 1999, *P. proximus* successfully colonized the bark of heavily defoliated trees and played an important role in the dieback of *A. firma* trees; (3) After 1998, the population density of *P. abietinus* decreased; (4) thereafter, *P. proximus* could not colonize the bark of *A. firma* trees that survived serious defoliation and actively produced oleoresin.

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