INTRODUCTION

Plant galls are induced by physicochemical stimuli from a wide variety of organisms, including insects, mites, nematodes, fungi, viruses, and bacteria (e.g., Mani, 1964; Meyer, 1987). Galls provide gall-makers with nutritious tissues, a mild microclimate, and occasionally shelter from natural enemies (Price et al., 1987). Galls are therefore inhabited by various organisms such as predators, parasitoids, cecidophages (non-gall-making gall-feeders), and successori (secondary gall users), resulting in diverse communities on galls. These gall-centered arthropod communities have been examined from a community ecology perspective (e.g., Yukawa, 1983; Hawkins and Goeden, 1984; McGeoch and Chown, 1997); however, most studies of gall-centered arthropod communities have been restricted to parasitoids rather than examining all arthropods (Sanver and Hawkins, 2000), and arthropod communities on bacterium galls have rarely been reported.

Wisteria grows ubiquitously in Japan and is planted in parks and gardens worldwide due to its beautiful ornamental flowers (Fig. 1a). The bacterium Pantoea agglomerans pv. millettiiae (Ewing and Fife) Gavini et al. (Enterobacteriaceae), which was first described as ‘Bacillus millettiiae’ by Kawakami and Yoshida (1920), induces irregularly shaped knot galls (cankers) on the trunks and twigs of Wisteria floribunda (Fabaceae) in central Japan. We sampled bacterium galls from wisteria at six sites and report a diverse arthropod community, composed of 48 species, representing 33 families and 11 orders, associated with the galls. Dominant arthropods were the larvae of Matsumuraeses falcana (Lepidoptera: Tortricidae) and Synanthedon tenuis (Lepidoptera: Sesiidae) as facultative cecidophages, and Eudigraphis takakuwai takakuwai (Diplopoda: Polyxenidae) as a scavenger. The number of species, abundance of each feeding guild, and overall arthropod abundance were positively correlated with gall diameter.

Key words: Cecidophages; gall size; plant-bacterium-insect interactions; successori; Wisteria floribunda
galls facultatively. Thus, the entire arthropod community on wisteria galls needs to be examined.

In this paper, we examine and describe the arthropod community on bacterium galls in central Japan, and discuss the trophic groups of dominant species in the community and their effects on the gall and wisteria. Furthermore, to clarify factors affecting arthropod richness on galls, we analyze the relationship between gall size and the number of species or abundance of arthropods.

MATERIALS AND METHODS

Study sites. Bacterium galls were sampled at Kyoshi [34°17′N, 135°10′E; 110 m above sea level (a.s.l.)], Misaki-cho; Tannowa (34°20′N, 135°10′E; 20 m a.s.l.), Misaki-cho; Miyakojima Park (34°42′N, 135°32′E; 5 m a.s.l.), Osaka City; Sanadayama Park (34°40′N, 135°31′E; 10 m a.s.l.), Osaka City; Ishigatsuji Park (34°39′N, 135°31′E; 15 m a.s.l.), Osaka City; and Oizumi-ryokuchi Park (34°34′N, 135°32′E; 20 m a.s.l.), Sakai City. All study sites are located in Osaka Prefecture, central Japan. The number of galls sampled were 46 on 22 November 2004 in Kyoshi, 32 on 24 March 2005 in Tannowa, 4 on 12 February 2004 in Miyakojima Park, 14 on 29 November 2004 in Sanadayama Park, 9 on 29 November 2004 in Ishigatsuji Park and 7 on 13 February 2005 in Oizumi-ryokuchi Park. In Kyoshi, W. floribunda grew around an irrigation pond in a warm-temperate secondary forest dominated by Quercus serrata Thunb., Q. glauca Thunb., and Q. phillyraeoides A. Gray (Fagaceae). In Tannowa, W. floribunda occurred at the edge of a coastal forest composed mainly of bayberry Myrica rubra Sieb. et Zucc. (Myricaceae) and Ligustrum japonicum Thunb. (Oleaceae). Miyakojima, Sanadayama, Ishigatsuji and Oizumi-ryokuchi parks were located in urban areas, where W. floribunda was planted as an ornamental.

Sampling, rearing and analysis. Galls were removed from trunks and twigs using a cutter and pruning shears. The galls were individually placed in plastic bags, brought to the laboratory, and placed in 200-ml plastic cups under laboratory conditions. Several tiny holes were punctured in the cup lid for ventilation. A part of each fresh gall was dissected under a stereomicroscope to observe
the feeding activity of arthropods. When the galls in plastic cups became relatively dry, they were sprayed with tap water to prevent desiccation. Galls were checked daily for 9 months to detect emerged arthropods, which were removed and preserved for identification. In addition, the galls were finally dissected with a cutter to find dead specimens inside.

The diameter of each gall sampled in Kyoshi and Tannowa was measured in three different directions to the nearest 0.01 mm using a digital caliper. The product of the three diameters was used as an index of gall size. Each arthropod species was classified into the following five categories based on feeding habits, which were clarified by direct observations or inferred from the literature: predator, parasitoid, cecidophage, scavenger/detritivore, and unknown. The relationship between gall size and the number of species or individuals of each group (or all arthropods) was examined using Pearson correlation analysis. This analysis was performed only for samples from Kyoshi and Tannowa, because samples from other sites were too small to analyze.

RESULTS AND DISCUSSION

In total, 329 arthropods, representing 48 species, 33 families, and 11 orders were found in 112 wisteria bacterium galls (Table 1). The dominant arthropods were larvae of a tortricid, *Matsumuraeses falcana* (Walsingham) (Lepidoptera: Tortricidae) (Fig. 1c), and a clearwing moth, *Synanthedon tenuis* (Butler) (Lepidoptera: Sesiidae) (Fig. 1d), in Kyoshi, and a tiny millipede, *Eudigraphis takakuwai takakuwai* (Miyoshi) (Diplopoda: Polyxenidae), in Tannowa (Table 1). Although clearwing moth larvae and millipedes were not found in urban parks, tortricid larvae were observed in three of the four urban parks (Table 1). The tortricid and clearing moth larvae fed on live gall tissues, pupated in the galls, and eclosed as adults from pupae that protruded from the galls. Larvae of an adelid moth and *Mahasena aurea* (Butler) (Lepidoptera: Psychidae) walked and fed on the gall surface with their portable cases. Larvae of a psilid fly, *Chyliza splendida* Iwasa (Diptera: Psilidae), were relatively abundant in Oizumi Park (Table 1).

*M. falcana* is a major pest infesting soybean pods and other fabaceous crops (Hattori, 2003), and *S. tenuis* is also known to damage the wood of persimmon and chestnut trees (Arita and Ikeda, 2000); therefore, these moth larvae are considered facultative cecidophages (sensu Mani, 1964) that use gall tissues as well as normal plant tissues. To regulate these pests in agroecosystems, it may be recommended that wisteria galls be controlled because they may function as reservoirs of these pests. Since *M. falcana* was abundant and occurred in five of six sites (Table 1), the possibility that this moth functions as a vector of the bacterium should be examined in the future. Many tortricid species have been reported as facultative cecidophages (e.g., Clancy, 1993; Abe, 1995; Yamazaki and Sugiura, 2004; Sugiura et al., 2006), while relatively few clearwing moths have been documented to feed on galls. *Synanthedon scitula* (Harris) and *S. pictipes* (Grote and Robinson) (Lepidoptera: Sesiidae) attack galls formed by the gall wasp *Callicorixa cornigera* (Osten Sacken) and the fungi *Cytospora cincta* Sacc. and *C. leucostoma* (Pers.) Sacc., respectively (Swift, 1986; Eliason and Potter, 2000). Since plant galls generally have higher nutritional quality than normal plant tissues (Hartley and Lawton, 1992; Sugiura et al., 2006), these lepidopteran larvae appear to feed on gall tissues.

The psilid fly *C. splendida* larva is reported to feed on gall tissues induced by the cecidomyiid *Asphondylia baca* Monzen on *Weigela floribunda* (Sieb. and Zucc.) K. Koch (Caprifoliaceae) (Sugiura and Yamazaki, 2006). *P. agglomerans* pv. *millettiae* galls are the second host of this psilid, and *C. splendida* is the only psilid reported to be a cecidophage.

*E. takakuwai takakuwai* lives in leaf litter, under bark, and in arboreal ant nests (Shinohara and Tannabe, 1999). Since most galls sampled in Tannowa were heavily damaged by lepidopteran larvae that had already left, this millipede might enter the internal space of galls and feed on dead gall tissues, arthropod feces, and arthropod remains; therefore, this species can be classified as a successori. Eight ant species were found on the galls (Table 1), although ant colonies were not formed in the galls. The polyxenid millipede prevents ant assault using detachable bristles (Eisner et al., 1996); therefore, *E. takakuwai takakuwai* can coexist with ants in the galls.

Spiders and ants might feed on other arthropods or use the galls as shelters. Parasitoids of the families Ichneumonidae, Braconidae, and Encyrtidae...
Table 1. Arthropods associated with wisteria galls induced by the bacterium *Pantoea agglomerans* pv. *millettiae*. Total number of individuals and percentage of galls from which individuals emerged (in parentheses) for each arthropod species in each sample

<table>
<thead>
<tr>
<th>Class/Order</th>
<th>Family</th>
<th>Species</th>
<th>Feeding habits</th>
<th>Misaki-cho</th>
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<th>Osaka City</th>
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<td></td>
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<td></td>
<td>Kyoshi</td>
<td>Tannowa</td>
<td>Oizumi Park</td>
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<td>Theridiidae</td>
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<td>—</td>
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<tr>
<td></td>
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<td>Clubiona sp.</td>
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<td>1 (3.1)</td>
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<td>1 (3.1)</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Salticidae</td>
<td>Pseudicus vulpes (Grube)</td>
<td>pr</td>
<td>—</td>
<td>1 (3.1)</td>
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<td>Geophilidae</td>
<td>Anystis baccarum (Linnaeus)</td>
<td>pr</td>
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<td>1 (3.1)</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Clubiona sp.</td>
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<td>pr</td>
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<td>1 (3.1)</td>
<td>—</td>
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<td>Bassaniana</td>
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<td>Polyxenidae</td>
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<td>64 (40.6)</td>
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<td>Comodica contributa</td>
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<td>1 (3.1)</td>
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</tr>
<tr>
<td></td>
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<td>Unidentified</td>
<td>s</td>
<td>—</td>
<td>3 (6.3)</td>
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<td></td>
<td>Mahasena aurea (Butler)</td>
<td>Mahasena</td>
<td>ce</td>
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<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Buculatrix sp.</td>
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<td>un</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Scynthioides leucostola (Meyrick)</td>
<td>Scythioides</td>
<td>ce</td>
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<td>1 (3.1)</td>
<td>—</td>
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<tr>
<td>Cosmopterigidae</td>
<td>Lecitholaxa thiodora (Meyrick)</td>
<td>Lecitholaxa</td>
<td>s</td>
<td>1 (2.2)</td>
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<td>—</td>
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<tr>
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<td>Labdia bicolorella Snellen</td>
<td>Labdia</td>
<td>s</td>
<td>2 (2.2)</td>
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<td>Tortricidae</td>
<td>Matsumuraes falcana (Walshingham)</td>
<td>Matsumuraes</td>
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<td>46 (34.8)</td>
<td>4 (9.4)</td>
<td>2 (14.3)</td>
</tr>
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<td></td>
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<td>ce</td>
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<td>—</td>
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<td>1 (25.0)</td>
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<td>Unidentified</td>
<td>s</td>
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<td>ce</td>
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<td>16 (57.1)</td>
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<td></td>
<td>Ca. kehiitoi Forel</td>
<td>Ca. kehiitoi</td>
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<td>Technomyrmex</td>
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<tr>
<td></td>
<td>Ochetellus glaber (Mayr)</td>
<td>Ochetellus</td>
<td>pr</td>
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<td>—</td>
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<tr>
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<td>Cremaflator matsumurai Forel</td>
<td>Cremaflator</td>
<td>pr</td>
<td>—</td>
<td>3 (3.1)</td>
<td>—</td>
</tr>
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<td></td>
<td>Cr. navai Ito</td>
<td>Cr. navai</td>
<td>pr</td>
<td>—</td>
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<td>Unidentified</td>
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<td>Braconidae</td>
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<td>Iconella</td>
<td>pa</td>
<td>—</td>
<td>1 (14.3)</td>
<td>4 (25.0)</td>
</tr>
<tr>
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<td>Diachasmia</td>
<td>pa</td>
<td>2 (4.4)</td>
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<td>—</td>
</tr>
<tr>
<td></td>
<td>Apanteles sp.</td>
<td>Apanteles</td>
<td>pa</td>
<td>—</td>
<td>—</td>
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<tr>
<td></td>
<td>Echephys caudatus Ruschka</td>
<td>Echephys</td>
<td>pa</td>
<td>—</td>
<td>7 (6.3)</td>
<td>—</td>
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</table>
appeared to have emerged from other insects, such as lepidopteran and coleopteran larvae.

Gall size was positively correlated with the abundance of most feeding groups and with the abundance of all arthropods (Table 2). A positive relationship between gall size and arthropod abundance has been reported for several galls (e.g., Sota, 1988).

The positive relationship between gall size and arthropod richness in this study indicates that intense bacterial proliferation enhances arthropod richness via manipulation of plant tissues. The bacterium is an ecosystem engineer (sensu Jones et al., 1994), which modifies plant tissues physically and chemically and possibly provides a superior habitat for arthropods. Therefore, larger galls appear to provide more abundant food resources for cecidophages, subsequently attracting scavengers, predators, and parasitoids. However, gall damage by cecidophages may prevent gall development, while some cecidophages may act as bacterial vectors, although experiments such as cecidophage exclusion from galls or intact wisteria stems by net covering are needed to clarify these points. This is a previously unrecognized complex plant-bacterium-insect interaction.

### ACKNOWLEDGEMENTS

We thank the following taxonomic researchers for arthropod identification and valuable advice: H. Kuroko (Tineidae, Cosmopterigidae, Bucculatricidae), H. Yamanaka (Pyralidae), T. Saito (Lecithoceridae), Y. Nasu (Tortricidae), K. Kanmiya (Chloropidae), K. Maeto (Braconidae), and Y. Higashiura (Encyrtidae). Thanks are also due to Y. Takikawa and H. Kamiunten for taxonomic advice of the bacterium.

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**Table 1.** (Continued)

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<th>Family</th>
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<th>Feeding habits&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Misaki-cho</th>
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<th>Osaka City</th>
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<td></td>
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<td>Kyoshi Park</td>
<td>Tannowa</td>
<td>Oizumi Park</td>
<td>Sanada-ヤマ Park</td>
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<td></td>
<td></td>
<td>Cerchysiella togashii</td>
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<td>1 (7.1)</td>
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<sup>a</sup> pr: predator, pa: parasitoid, ce: cecidophage, s: scavenger/detritivore, un: unknown.

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**Table 2.** The relationship between gall size and (a) number of species or (b) number of individuals of each feeding group based on Pearson correlation analysis

<table>
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<tr>
<th>Feeding group</th>
<th>Kyoshi</th>
<th>Tannowa</th>
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<tbody>
<tr>
<td>(a) No. of species</td>
<td>r</td>
<td>p</td>
</tr>
<tr>
<td>Cecidophages</td>
<td>0.484</td>
<td>0.0005</td>
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<tr>
<td>Scavengers/Detritivores</td>
<td>0.377</td>
<td>0.0094</td>
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<tr>
<td>Predators/Parasitoids</td>
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<td>0.0235</td>
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<tr>
<td>Overall arthropods</td>
<td>0.613</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(b) No. of individuals</td>
<td>r</td>
<td>p</td>
</tr>
<tr>
<td>Cecidophages</td>
<td>0.456</td>
<td>0.0013</td>
</tr>
<tr>
<td>Scavengers/Detritivores</td>
<td>0.380</td>
<td>0.0087</td>
</tr>
<tr>
<td>Predators/Parasitoids</td>
<td>0.247</td>
<td>0.0984</td>
</tr>
<tr>
<td>Overall arthropods</td>
<td>0.603</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

No. of galls examined: 46, 32