

Trail-following Disruption in the Invasive Argentine Ant with a Synthetic Trail Pheromone Component (*Z*)-9-hexadecenal

by

Yasutoshi Tanaka¹, Koji Nishisue¹, Eiriki Sunamura^{1†}, Shun Suzuki¹, Hironori Sakamoto², Takehiko Fukumoto³, Mamoru Terayama¹ & Sadahiro Tatsuki¹

ABSTRACT

We newly conceived the idea of trail-following disruption of a highly invasive ant species, the Argentine ant *Linepithema humile*, using a synthetic trail pheromone component (*Z*)-9-hexadecenal. Along with this concept, attempts have been made to develop novel methodologies to control this cosmopolitan pest. In this report, polyethylene tube dispensers containing synthetic (*Z*)-9-hexadecenal were prepared, and effects on Argentine ant trail-following behavior and recruitment to baits were investigated. Treatment with a dispenser near a natural Argentine ant trail dramatically disrupted the trail-following behavior, and the ants wandered around an area near the trail and dispenser. Furthermore, treatment with dispensers of a 100 m² field largely suppressed Argentine ant recruitment to baits. These results demonstrated the usefulness of the long-life dispensers for further long-term field experiments to develop practical control methodologies for pest ants with synthetic trail pheromones. However, despite the above clear effects, the data also suggested an incomplete effect of the disruption using (*Z*)-9-hexadecenal alone. Further improvement of the trail-disruption effects and realizing practical control with synthetic trail pheromone are discussed.

Key words: invasive species, *Linepithema humile*, pest management, pheromone, trail pheromone, (*Z*)-9-hexadecenal

¹Graduate School of Agricultural and Life Sciences, The University of Tokyo, Bunkyo-ku, Tokyo 113-8657, Japan.

²National Institute for Agro-Environmental Sciences, Kannondai, Tsukuba 305-8604, Japan.

³Shin-Etsu Chemical Co., Ltd., Chiyoda-ku, Tokyo 100-0004, Japan.

[†]These authors contributed equally to this work.

[†]Corresponding author. E-mail: aa087004@mail.ecc.u-tokyo.ac.jp

INTRODUCTION

Conservation of biodiversity is one of the most important subjects for sustainable human development and resource use. With the expansion of international trade, invasive alien species have become a major cause of biodiversity loss on the global scale (Sala *et al.* 2000). In particular, invasive ants are among the most harmful groups, causing serious problems to ecosystems, agriculture, and human life (Holway *et al.* 2002). However, eradication or effective management of invasive ants is extremely difficult with existing strategies (i.e. application of toxic baits and insecticides) (Soeprono & Rust 2004; Silverman & Brightwell 2008).

Inadequate or mass treatment with pesticides and toxic baits can cause serious damage to the local biodiversity. Therefore, in pest management, control methodologies less harmful to non-target organisms, including humans, are required. Pheromones are excellent materials because of their species-specific effects and lack of toxicity. However, their use in pest management has been restricted mainly to mating disruption and mass-trapping of insects, primarily moths, using their sex pheromones (Bjostad *et al.* 1993), and more attention should be paid to the utility value of various pheromones from various taxa.

The social behavior of ants depends heavily on chemical communications among nestmates via various pheromones (Hölldobler & Wilson 1990; Vander Meer *et al.* 1998). In particular, trail pheromones are key pheromones that contribute greatly to the ecological success of ants, by enabling their efficient foraging. Here, trials were conducted towards developing a new methodology to control invasive pest ants using synthetic trail pheromone.

The Argentine ant *Linepithema humile* is native to South America, but it has been introduced to many parts of the world and has become one of the most notorious invasive ants (Holway *et al.* 2002; Suarez *et al.* 2001). The major component of its trail pheromone is (*Z*)-9-hexadecenal (Z9-16:Ald) (Cavill *et al.* 1979, 1980). Previously, one of the authors, S. Tatsuki, identified Z9-16:Ald as the third component of the sex pheromone of a distantly related species, the rice stem borer moth *Chilo suppressalis*, and thereby developed a mating disruption technique for this major pest of rice (Tatsuki *et al.* 1983; Tatsuki 1990). Based on this experience, the idea of a novel potential strategy

was conceived to control Argentine ants with synthetic trail pheromone: high concentration synthetic Z9-16:Ald dispersed above the foraging area might disrupt Argentine ant trail-following behavior and reduce foraging efficiency (Tatsuki *et al.* 2005).

Until recently, the response of ants to over-dose trail pheromones was scarcely reported (Van Vorhis Key *et al.* 1981). However, recent studies demonstrated that the above trail disruption concept is feasible. Tanaka *et al.* (2008) observed that Argentine ants following their natural trail showed unusual behaviors, such as zigzagging and breaking away from the trail, when a paper treated with a high concentration of synthetic Z9-16:Ald was placed above the trail. Suckling *et al.* (2008) showed that a high concentration of synthetic Z9-16:Ald completely disrupted Argentine ant trail integrity and reduced foraging success, using short-life formulations. We have been pursuing the same line of research with polyethylene-tube dispensers containing synthetic Z9-16:Ald, and effects on Argentine ant trail-following behavior and recruitment to baits are reported here.

The present approach was similar to those of Suckling *et al.* (2008), but this study was different in several aspects. First, the pheromone carrier and the life-span were different from the previous study. Second, the present experiment was conducted in an urban district of Japan, whereas the experiment in the previous study was conducted in a natural ecosystem of Hawaii. Although Argentine ants and other invasive ants sometimes invade natural environments, particularly in remote islands (e.g. O'Dowd *et al.* 2003; Krushelnycky & Gillespie 2008), most of the places invaded by these ants are disturbed urban areas (Holway *et al.* 2002). Third, field treatment of synthetic Z9-16:Ald was carried out over a larger scale (100 m²) than the previous study (4 m²). Large scale treatment may be essential for the successful control of invasive ants (Silverman & Brightwell 2008).

MATERIALS AND METHODS

Pheromone dispensers

'Rope' type pheromone dispensers, which are used worldwide for moth mating disruption, were used (Shin-Etsu Chemical Co., Ltd. Tokyo: Tatsuki *et al.* 2005) (Fig. 1). Each dispenser was a closed polyethylene tube (high density polyethylene including red-ocher rouge for shading; 1.5 mm OD × 20 cm long)

supported by an aluminum line for handling, and each tube contained 75-80 mg synthetic Z9-16:Ald (Shin-Etsu Chemical Co., Ltd. Tokyo; total purity > 98%, isomeric purity >99% by GLC analysis using a fused silica capillary column; DB-Wax, 30 m × 0.25 mm ID, J & W Scientific, USA), lipid-soluble antioxidant (2%) and UV absorbent (2%). A dispenser released 56.3-74.2% of Z9-16:Ald during a month (i.e., 42.2-59.4 mg/month) in the environment we used for the present study (sunny house garden, see below).

Effect of a dispenser on Argentine ant trail-following behavior

1) Number of ants passing natural trails

The experiment was conducted in September and November 2007 using five separate natural trails of introduced Argentine ants in Japan. Two trails were in Iwakuni City, Yamaguchi Prefecture, one was in Yokohama City, Kanagawa Pref., and the remaining two were in Kobe City, Hyogo Pref. These trails were formed either on soil or concrete ground. Three kinds of treatment were given to each trail in the following order: 1) no treatment; 2) treatment with a dispenser wrapped in polyvinylidene chloride wrapping film (the wrapped dispenser should not evaporate Z9-16:Ald into the air); and 3) treatment with a bare dispenser. The number of Argentine ants passing a fixed measuring point on each trail (irrespective of direction) was counted for 40 sec in every min during a 10 min observation for each of the above three treatments. In

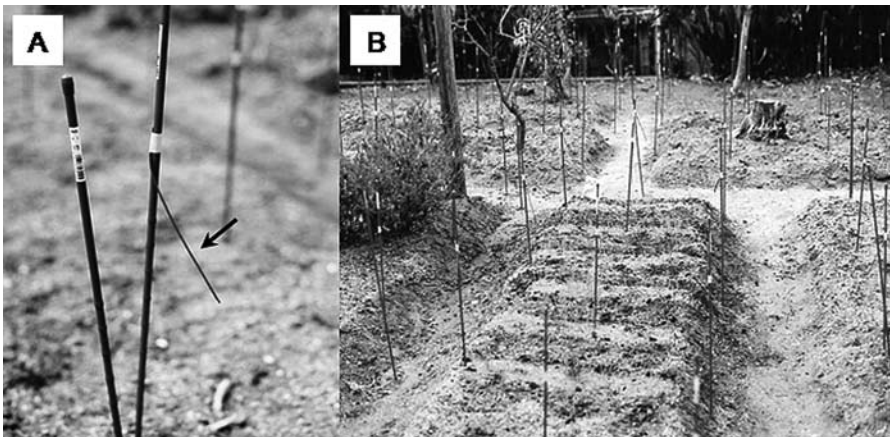


Fig. 1. Pheromone dispensers containing synthetic Z9-16:Ald. In field treatment experiments, the dispensers were tied to plastic poles at ca. 40 cm above ground level (indicated by an arrowhead in A), and deployed every 1 m in 100 m² plots of kitchen gardens of private houses (B).

treatments 2 and 3, no treatment was conducted for the first five min, but after five min passed from the start of the observation, a wrapped or bare Z9-16:Ald dispenser was placed on the ground 10 cm away from the measuring point (irrespective of wind direction). The three treatment trials were conducted at five-minute intervals.

The mean number of Argentine ants passing the fixed point during the former or latter five min of the observation was calculated for each trail and each treatment. The value for the latter five min was divided by the value for the former five min, to calculate the rate of change in the traffic density on the trail. To test statistically whether this rate for treatments 2 or 3 differed from that of the treatment 1, Steel's test was conducted.

2) Radius of trail-following disruption

The experiment was conducted between April and October 2005, using four Argentine ant natural trails in Iwakuni City, Yamaguchi Pref. The trails were formed on either soil or building floor. A dispenser was placed 10 cm away from each trail. The radius of the trail-following disruption caused by the dispenser treatment was evaluated by measuring the length of the disrupted part in the trail (length of disruption) and the maximum distance between wandering ants and the trail (width of disruption). The measurements were conducted at 1, 3, 6, and 12 min after the start of dispenser treatment. Dispenser treatment was conducted after confirming the absence of disturbance on the trail for 12 min (i.e. a radius of disruption of 0 cm in both length and width).

Effect of field application of dispensers on Argentine ant foraging

The experiment was conducted using well-kept kitchen gardens of four private houses in Iwakuni City, Yamaguchi Pref., Japan, during 20-25 April 2007. Around this area, Argentine ants had become well established by the time of first detection in 2002, and indigenous ants had been almost completely displaced. In the kitchen gardens, various vegetables and flowers were planted regularly. In P2 (see below), crops were planted rather densely compared with the other three gardens. For each garden, a 10 m × 10 m plot was set. The study plots were separated by at least 20 m. Dispensers were applied to two of the four plots (P1 and P2) between 20 and 23 April, and no treatment was conducted on the other two plots (C1 and C2) throughout the course of the experiment. The dispensers were tied to plastic poles at ca. 40 cm above ground level, and

deployed every 1 m (121 dispensers/100 m², pheromone release rate 71-100 g/h/m²) (Fig. 1).

Argentine ant recruitment to baits in the study plots was investigated in three phases: 1) before application of the dispensers; 2) during application of the dispensers; 3) after removal of the dispensers. In the center of each plot, nine bait monitoring stations were fixed with 2 m spacing. Sugar water was smeared on a 15 cm diameter paper dish, and the dish was set on each bait station. After 40 min, the number of Argentine ants on each dish was counted. During the above phases 1, 2, and 3, count trials were conducted three, six, and three times, respectively, with at least 40 min intervals. Count trials were not conducted on rainy days. The experimental period was one day for phase 1, three days for phase 2, and two days for phase 3. The first count trial for phase 2 or 3 was conducted at least after 12 h from the placement or removal of the dispensers.

To test if Argentine ant recruitment to baits was affected by dispenser treatment, a generalized linear mixed model (GLMM) was used, and a likelihood ratio test was performed. A model was constructed with dispenser treatment and plot as fixed effects, and bait station and trial as random effects (errors: Poisson; approximation: Laplace; link: log).

RESULTS

Effect of a dispenser on Argentine ant trail-following behavior

When a bare dispenser was placed 10 cm away from a natural trail, the nearby Argentine ants scattered in a panic (46-465 cm part of the trail: Table 1). These ants wandered around the trail or dispenser (within 16-117 cm from the trail: Table 1), not running far away from the trail. Outside of the disrupted area, ants normally followed the trail, but most of them no longer did so once they entered the area. The radius of disruption differed among trails and changed over time, probably depending on factors such as original traffic density of trails, wind speed, and wind direction, but the disturbance persisted through the treatment period (Table 1). Consequently, the number of ants passing the fixed point on the trail dropped to 0.13-0.34-fold (median 0.27-fold) of the values observed before the treatment (Fig. 2). In contrast, a dramatic change in the value was not observed in the no-treatment trials (0.95-1.13-fold: median 1.02-fold) or wrapped dispenser treatment trials

(0.85-1.10-fold: median 0.99-fold). The rate of change in the value did not differ significantly between no-treatment trials and wrapped dispenser treatment trials (Steel's test, $P = 0.54$), but significantly differed between no-treatment trials and bare dispenser treatment trials ($P < 0.05$).

Note that a certain number of ants passed the fixed points on the natural trails, even in the presence of the dispensers (Fig. 2). Some of these individuals appeared to pass the point by mere chance, but some appeared to manage to distinguish and follow the natural trails.

Table 1. Radius of trail-following disruption caused by a Z9-16:Ald dispenser. A dispenser was placed 10 cm away from a natural Argentine ant trail. The length and width (cm) of disruption caused by the treatment were measured four times during a 12 min observation period and for each of four trails (a-d).

Trail		Time (minutes)				Mean \pm SD
		1	3	6	12	
a	Length	230	170	190	180	193 \pm 26
	Width	36	55	50	41	46 \pm 9
b	Length	95	220	390	240	236 \pm 121
	Width	16	22	20	30	22 \pm 6
c	Length	260	370	344	465	360 \pm 84
	Width	35	31	40	36	36 \pm 4
d	Length	46	67	87	115	79 \pm 29
	Width	61	56	110	117	86 \pm 32

Effect of field application of dispensers on Argentine ant foraging

In dispenser treatment plots, Argentine ant recruitment to baits was severely reduced during dispenser treatment (phase 2) compared with the recruitment level before treatment (phase 1), but the recruitment recovered strongly after removal of the dispensers (phase 3) (Fig. 3). Recruitment to baits, when represented by the mean number of Argentine ants that came to baits across all bait stations and all trials, dropped by 89% from phase 1 to phase 2 in plot P1 and by 60% in plot P2. On the other hand, the value for phase 3 was 5.85-fold (for P1) and 3.83-fold (for P2) of the value for phase 2. In contrast to the treatment plots, the change in ant recruitment was low to moderate in the no-treatment plots (from phase 1 to 2: 28% increase in plot C1, and 16% decrease in plot C2; from phase 2 to 3: 56% and 10% increases in plots C1 and C2, respectively). Dispenser treatment significantly suppressed recruitment (GLMM, Estimate = -1.24 , $Z = -52.4$, $P < 0.001$), but the plot was not related to recruitment (Estimate = -0.036 , $Z = -0.23$, $P = 0.82$). Interaction between dispenser treatment and plot

was significant (Estimate = 4.55, $Z = 10.8$, $P < 0.001$), suggesting that the trail disruption effect of the dispensers was different between treatment plots.

By visual observation, obvious trails were confirmed in no-treatment plots throughout the course of the experiment. Conspicuous trails were also observed in treatment plots during phase 1 and 3. During phase 2, trails were not obvious in the treatment plots. However, in some instances, Argentine ants appeared to form vague trails and advanced awkwardly toward the baits. Detailed mapping of these trails was difficult because weeds and crops made some or most of the ground invisible.

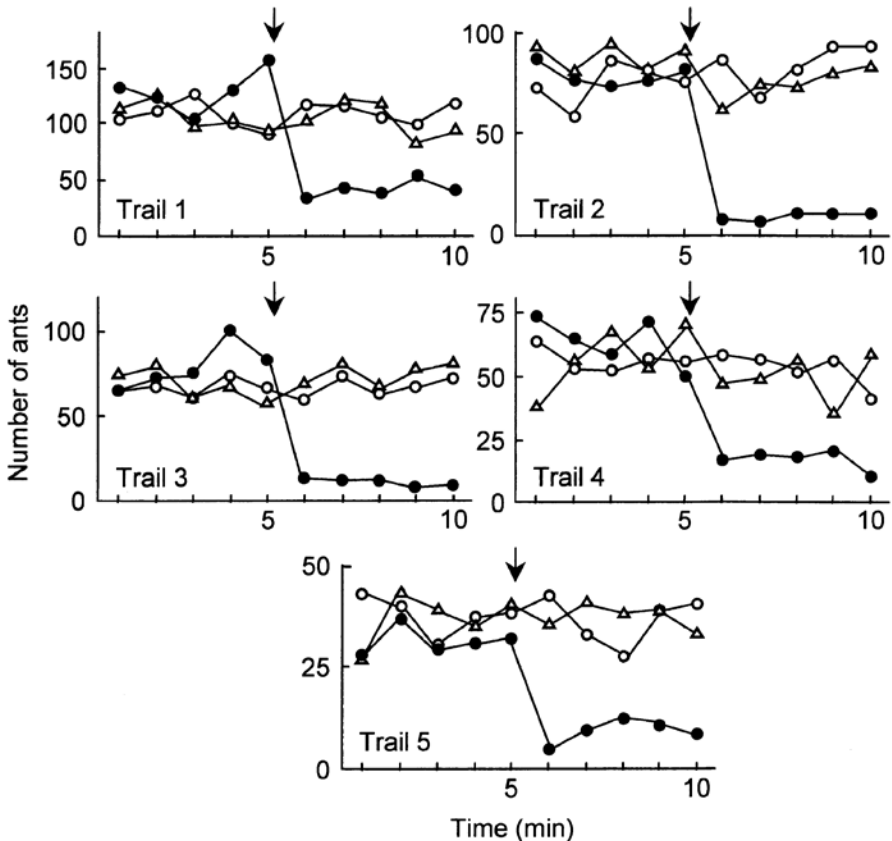


Fig. 2. Effect of a Z9-16:Ald dispenser on Argentine ant trail-following behavior. Three treatments were performed on each of five natural Argentine ant trails: no treatment (open circles), wrapped dispenser treatment (triangles), and bare dispenser treatment (closed circles). The number of ants passing a fixed point on the trail was counted for 10 min. Treatment was performed five min after initiation of each trial (shown by an arrowhead).

DISCUSSION

When a Z9-16:Ald dispenser was placed near a natural Argentine ant trail, the majority of the trail-following ants near the dispenser scattered in a panic, leading to a dramatic decrease in the number of ants passing the correct path (Fig. 2, Table 1). The observed trail disruption was not caused by physical disturbance, because polyvinylidene-wrapped dispensers did not affect Argentine ant trails. Thus, the present data suggest that Argentine ants could not easily distinguish their natural trail from a synthetic trail pheromone component that pervaded the air, just like synthetic sex pheromone prohibits male moths from finding female moths in mating disruption methodology.

The disruption of trail integrity was similar to that reported in previous studies (Tanaka *et al.* 2008; Suckling *et al.* 2008). The methods for these studies were similar in the point that they used single point sources of Z9-16:Ald.

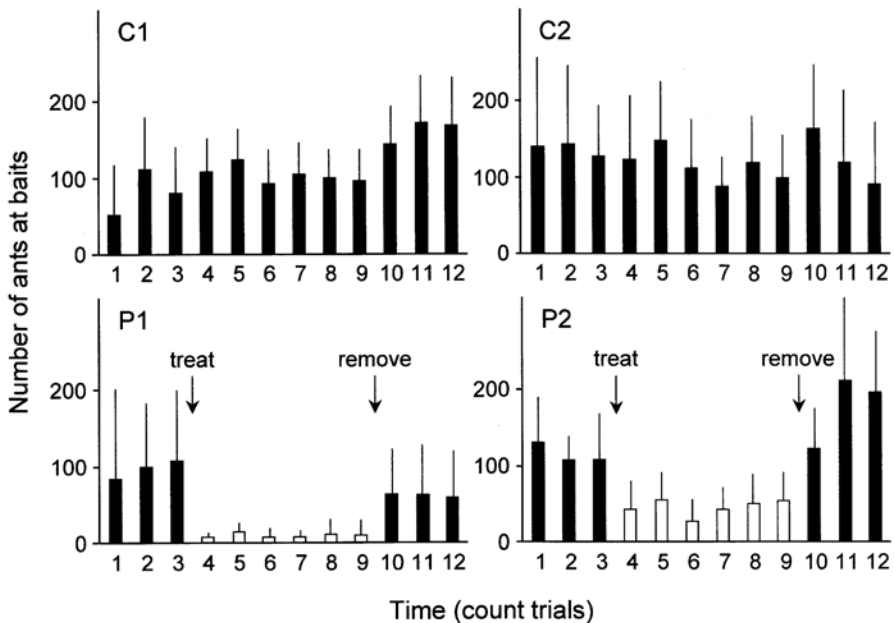


Fig. 3. Effect of field treatment with Z9-16:Ald dispensers on Argentine ant recruitment to baits. Mean + SD number of Argentine ants that came to the baits ($n = 9$) in each of 12 count trials are shown for each of four study plots. In plots C1 and C2, no treatment was conducted throughout the course of the experiment. In plots P1 and P2, Z9-16:Ald dispensers were applied after the third count trial, and the dispensers were removed after the ninth count trial. Results for the dispenser treatment plots during the treatment period are shown with blank columns.

However, the previous studies did not count ants that followed natural trails. The present results showed that a certain number of ants apparently managed to follow the natural trail despite the presence of synthetic Z9-16:Ald. These individuals might have distinguished their true trail from synthetic Z9-16:Ald. Although not yet identified, previous work suggested the presence of minor components in Argentine ant trail pheromone complex (Van Vorhis Key & Baker 1982). In other ant species, differences in the ability to detect trail pheromone components among subcastes (Jackson *et al.* 2006) and the involvement of footprint hydrocarbons in colony-specific trail-following (Akino & Yamaoka 2005; Akino *et al.* 2005) have been reported. Further studies on trail pheromones and other related chemicals, as well as trail-following behavior, are required, to maximize the trail-following disruption effect produced by synthetic chemicals.

Argentine ant recruitment to baits decreased after field treatment with Z9-16:Ald dispensers, but these effects dissipated after removal of the dispensers (Fig. 3). This suggests that high concentrations of synthetic Z9-16:Ald in the field atmosphere interfered with efficient foraging via trail formation by Argentine ants. If the physical disturbance associated with the handling of dispensers was responsible for the decrease in recruitment to baits during the treatment phase, ant recruitment to baits would have further decreased after the physical disturbance concomitant with the removal of the dispensers.

Low to moderate numbers of Argentine ants came to the baits, even during the dispenser treatment period (Fig. 3). In some cases, Argentine ants appeared to form vague trails. Because Z9-16:Ald (pheromone release rate: 20-260 g/h/m²) dispensers were placed ca. 40 cm above the ground level, their trail disruption effect on the ground foraging ants may have been weakened. Environmental factors such as wind and vegetation may have also affected the efficacy of the dispensers. In plot P2, suppression of ant recruitment to baits by dispensers was not as evident as observed in plot P1 (Fig. 3). In P2, the undergrowth was rather dense, and this may have interfered with the diffusion of synthetic Z9-16:Ald over the ground.

Similar to the present study, Suckling *et al.* (2008) demonstrated a dramatic reduction in Argentine ant recruitment to baits in 1 or 4 m² plots using synthetic Z9-16:Ald. They used quartz sand as the pheromone carrier, which was quite different from the present tube dispenser. Depression of ant recruitment

to baits by quartz sand appeared to be greater than that by the tube dispensers (compare Fig. 4 and 6 of Suckling *et al.* (2008) with Fig. 3 of the present study). However, it cannot be readily concluded that this difference stemmed from the difference of formulation. The environment and probably ant density also differed between these studies. Furthermore, in Suckling *et al.* (2008), ant recruitment to the baits in control plots increased greatly several hours after initiation of the experiment, probably because of an increase in recruitment activity or the formation of new trails to the constant food sources or because of diurnal variation in ant activity. A similar increase was also seen in their Z9-16:Ald treatment plots. It is unclear whether this increase was due to the short life of their formulation or some other factor.

An array of recent studies, including the present study, points to a new field of pheromone use in pest management, showing that high concentration of a synthetic trail pheromone component disrupts the trail-following behavior and decreases the foraging activity of an invasive ant species (Tanaka *et al.* 2008; Suckling *et al.* 2008). The trail disruption technique can be tested for other pest ant species. The disruption effect may depend on the chemical structure and number of trail pheromone components. It is predicted that long-term, as well as area-wide treatment of synthetic Z9-16:Ald may make Argentine ants short of foods, and therefore decrease their densities. Because synthetic trail pheromone may not have a direct effect on the mortality of ants, eradication of ants would not be achieved by treatment with synthetic trail pheromone alone. However, the trail-following disruption may be a novel and useful technique that can be incorporated in IPM (integrated pest management) systems for ants. The presumably species-specific, non-toxic, and long-term effect of synthetic trail pheromone is suitable for IPM and can become important in control programs in both natural ecosystems, where negative impacts of toxic chemicals on vulnerable species are of concern, and in urban areas, where public concerns over the negative effect of these chemicals on human health are strong.

To evaluate if synthetic trail pheromone can be applied for the practical control of ants, long-term effects of synthetic Z9-16:Ald on Argentine ants at nest and larger colony levels should be investigated. Large-scale treatment may be especially important for the control of invasive ants, because the difficulties with controlling them can be attributed to their large colony size (Silverman & Brightwell 2008, but see Heller *et al.* 2008). Argentine ants are renowned

for forming expansive supercolonies, sometimes extending over thousands of kilometers, in the introduced range (Suarez *et al.* 1999; Giraud *et al.* 2002; Corin *et al.* 2007; Sunamura *et al.* 2007, 2009a; Suhr *et al.* 2009). Recent studies even provided evidence for a gigantic global-scale supercolony (Wetterer & Wetterer 2006; Brandt *et al.* 2009; Sunamura *et al.* 2009b). Neither the short-life formulations in Suckling *et al.* (2008) nor the present tube dispensers can be used for landscape-scale treatment. However, the long-life (> 1 month) dispensers in the present study can be used for further control experiments for longer-term and household-scale areas (< several hundred square meters).

ACKNOWLEDGMENTS

We would like to express our sincere gratitude to the townspeople of Kuroiso, Iwakuni City for generously providing experimental field sites and various support for this study, and to Ryo Nakano and Wataru Kojima for analytical advice.

REFERENCES

- Akino, T., M. Morimoto & R. Yamaoka. 2005. The chemical basis for trail discrimination in *Lasius nipponensis* (Hymenoptera: Formicidae). *Chemoecology* 15: 13-20.
- Akino, T. & R. Yamaoka. 2005. Trail discrimination signal of *Lasius japonicus* (Hymenoptera: Formicidae). *Chemoecology* 15: 21-30.
- Bjostad, L.B., B.E. Hibbard & W.S. Cranshaw. 1993. Application of semiochemicals in integrated pest-management programs. *ACS Symposium Series* 524: 199-218.
- Brandt, M., E. van Wilgenburg & N.D. Tsutsui. 2009. Global-scale analyses of chemical ecology and population genetics in the invasive Argentine ant. *Mol. Ecol.* 18: 997-1005.
- Cavill, G.W.K., P.L. Robertson & N.W. Davies. 1979. An Argentine ant aggregation factor. *Experientia* 35: 989-990.
- Cavill, G.W.K., N.W. Davies & F.J. McDonald. 1980. Characterization of aggregation factors and associated compounds from the Argentine ant, *Iridomyrmex humilis*. *J. Chem. Ecol.* 6: 371-384.
- Corin, S.E., K.A. Abbott, P.A. Ritchie & P.J. Lester. 2007. Large scale unicoloniality: the population and colony structure of the invasive Argentine ant (*Linepithema humile*) in New Zealand. *Insect. Soc.* 54: 275-282.
- Giraud, T., J.S. Pedersen & L. Keller. 2002. Evolution of supercolonies: the Argentine ants of southern Europe. *Proc. Natl. Acad. Sci.* 99: 6075-6079.
- Heller, N.E., K.K. Ingram & D.M. Gordon. 2008. Nest connectivity and colony structure in unicolonial Argentine ants. *Insect. Soc.* 55: 397-403.
- Hölldobler, B. & E.O. Wilson. 1990. *The Ants*. Belknap Press of Harvard University Press. pp 732.

- Holway, D.A., L. Lach, A.V. Suarez, N.D. Tsutsui & T.J. Case. 2002. Causes and consequences of ant invasions. *Ann. Rev. Ecol. Syst.* 33: 181-233.
- Jackson, D.E., S.J. Martin, M. Holcombe & F.L.W. Ratnieks. 2006. Longevity and detection of persistent foraging trails in Pharaoh's ants, *Monomorium pharaonis*. *Anim. Behav.* 71: 351-359.
- Krushelnycky, P.D. & R.G. Gillespie. 2008. Compositional and functional stability of arthropod communities in the face of ant invasions. *Ecol. Appl.* 18: 1547-1562.
- O'Dowd D.J., P.T. Green & P.S. Lake. 2003. Invasional 'meltdown' on an oceanic island. *Ecol. Lett.* 6: 812-817.
- Sala, O.E., F.S. Chapin III, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker & D.H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.
- Silverman, J. & R.J. Brightwell. 2008. The Argentine ant: challenges in managing an invasive unicolonial pest. *Annu. Rev. Entomol.* 53: 231-252.
- Soeprono, M. & M.K. Rust. 2004. Strategies for controlling Argentine ants (Hymenoptera: Formicidae). *Sociobiology* 44: 669-682.
- Suarez, A.V., N.D. Tsutsui, D.A. Holway & T.J. Case. 1999. Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. *Biol. Invasions* 1: 43-53.
- Suarez, A.V., D.A. Holway & T.J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proc. Natl. Acad. Sci.* 98: 1095-1100.
- Suckling, D.M., R.W. Peck, L.M. Manning, L.D. Stringer, J. Cappadonna & A.M. El-Sayed. 2008. Pheromone disruption of Argentine ant trail integrity. *J. Chem. Ecol.* 34: 1602-1609.
- Suhr, E.L., S.W. McKechnie & D.J. O'Dowd. 2009. Genetic and behavioural evidence for a city-wide supercolony of the invasive Argentine ant *Linepithema humile* (Mayr) (Hymenoptera: Formicidae) in southeastern Australia. *Aus. J. Entomol.* 48: 79-83.
- Sunamura, E., K. Nishisue, M. Terayama & S. Tatsuki. 2007. Invasion of four Argentine ant supercolonies into Kobe Port, Japan: their distributions and effects on indigenous ants (Hymenoptera: Formicidae). *Sociobiology* 50: 659-674.
- Sunamura, E., S. Hatsumi, S. Karino, K. Nishisue, M. Terayama, O. Kitade & S. Tatsuki. 2009a. Four mutually incompatible Argentine ant supercolonies in Japan: inferring invasion history of introduced Argentine ants from their social structure. *Biol. Invasions*, in press (doi: 10.1007/s10530-008-9419-7).
- Sunamura, E., X. Espadaler, H. Sakamoto, S. Suzuki, M. Terayama & S. Tatsuki. 2009b. Intercontinental union of Argentine ants: behavioral relationships among introduced populations in Europe, North America, and Asia. *Insect. Soc.*, in press (doi: 10.1007/s00040-009-0001-9).

- Tanaka, Y., E. Sunamura, K. Nishisue, M. Terayama, H. Sakamoto, S. Suzuki, T. Fukumoto & S. Tatsuki. 2008. Response of the invasive Argentine ant to high concentration of a synthetic trail pheromone component suggests a potential control strategy of pest ants. *Ari* 31: 43-50.
- Tatsuki, S., M. Kurihara, K. Usui, Y. Ohguchi, K. Uchiumi, J. Fukami, K. Arai, S. Yabuki & F. Tanaka. 1983. Sex pheromone of the rice stem borer, *Chilo suppressalis* (Walker) (Lepidoptera: Pyralidae): the third component, Z-9-hexadecenal. *Appl. Entomol. Zool.* 18: 443-446.
- Tatsuki, S. 1990. Application of the sex pheromone of the rice stem borer moth, *Chilo suppressalis*. In: "Behavior-Modifying Chemicals for Insect Management: Application of Pheromones and Other Attractants", Ridgway, R.L., R.M. Silverstein & M.N. Inscoc, eds., Marcel Dekker, Inc., New York and Basel, pp 387-406.
- Tatsuki, S., M. Terayama, Y. Tanaka & T. Fukumoto. 2005. Behavior-disrupting agent and behavior disrupting method of Argentine ant. Patent pub. No. US2005/0209344A1.
- Vander Meer, R.K., M.D. Breed, M.L. Winston & K.E. Espelie, eds. 1998. Pheromone communication in social insects. Westview Press. pp 368.
- Van Vorhis Key, S.E., L.K. Gaston & T.C. Baker. 1981. Effects of gaster extract concentration on the trail following behaviour of the Argentine ant, *Iridomyrmex humilis* (Mayr). *J. Insect Physiol.* 27: 363-370.
- Van Vorhis Key, S.E. & T.C. Baker. 1982. Trail-following responses of the Argentine ant, *Iridomyrmex humilis* (Mayr), to a synthetic trail pheromone component and analogs. *J. Chem. Ecol.* 8: 3-14.
- Wetterer, J.K. & A.L. Wetterer. 2006. A disjunct Argentine ant metacolony in Macaronesia and southwestern Europe. *Biol. Invasions* 8: 1123-1129.

