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Sex Pheromones and Reproductive Isolation of Three Species in Genus *Adoxophyes*

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Abstract We tested differences in female pheromone production and male response in three species of the genus *Adoxophyes* in Korea. Females of all three species produced mixtures of (*Z*)-9-tetradecenyl acetate (*Z*9–14:OAc) and (*Z*)-11-tetradecenyl acetate (*Z*11–14:OAc) as major components but in quite different ratios. The ratio of *Z*9–14:OAc and *Z*11–14:OAc in pheromone gland extracts was estimated to be ca. 100:200 for *Adoxophyes honmai*, 100:25 for *Adoxophyes orana*, and 100:4,000 for *Adoxophyes* sp. Field tests showed that males of each species were preferentially attracted to the two-component blends of *Z*9–14:OAc and *Z*11–14:OAc mimicking the blends found in pheromone gland extracts of conspecific females. The effects of minor components identified in gland extracts on trap catches varied with species. Addition of 10-methyldodecyl acetate (10me-12:OAc) or (*E*)-11-tetradecenyl acetate (*E*11–14:OAc) to the binary blend of *Z*9–14:OAc and *Z*11–14:OAc significantly increased captures of *A. honmai* males, whereas *E*11–14:OAc exhibited a strongly antagonistic effect on catches of *Adoxophyes* sp. males. Moreover, (*Z*)-9-tetradecen-1-ol (*Z*9–14:OH) or (*Z*)-11-tetradecen-1-ol (*Z*11–14:OH) added to the binary blends increased attraction of male *A. orana* but not *A. honmai* and *Adoxophyes* sp. males, suggesting that these minor components, in addition to the relative ratios of the two major components, play an important role in reproductive isolation between *Adoxophyes* species in the southern and midwestern Korea where these species occur sympatrically.

Keywords *Adoxophyes* · (*Z*)-9-tetradecenyl acetate · (*Z*)-11-tetradecenyl acetate · Lepidoptera · Tortricidae · Reproductive isolation

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Introduction

Several species in the genus *Adoxophyes* (Lepidoptera: Tortricidae) are economically important pests of fruit and tea trees in Asia and Europe (Tamaki et al. 1971a; Meijer et al. 1971; Kou et al. 1990). In the past, it was believed that *Adoxophyes orana* is the only species found in Korea (Shin et al. 1994), but field trapping revealed that there is considerable variability in male response to pheromone blends among different geographical populations of *Adoxophyes* spp. (Han 2002; Yang et al. 2005). These findings prompted us to study the taxonomic status of Korean *Adoxophyes* populations by using mitochondrial gene sequences, and we found three distinct species, *Adoxophyes honmai*, *A. orana*, and *Adoxophyes* sp. (Park et al. 2008). Larvae are difficult to differentiate, but adults of the different species are distinguishable by wing patterns and male genitalia (Han 2002; Byun, personal communication).

Adoxophyes species often share host plants (Han 2002; Yang et al. 2005) and have some seasonal overlap in Korea (Choi 2002; Yang 2002). Furthermore, the diel periodicity of pheromonal emission also overlaps, with females of all

three species calling at the end of the scotophase and beginning of the photophase (Sato and Tamaki 1977; Den Otter and Klijnstra 1983; Han 2002). Therefore, differences in these parameters appear insufficient to maintain reproductive isolation among these species. Males of *Adoxophyes* species, however, are rarely attracted to heterospecific females in fields (Yang, unpublished), suggesting that species-specific blends of pheromone components may be responsible for reproductive isolation between sympatric species (Roelofs and Brown 1982; Löfstedt et al. 1991). Thus, the principal objectives of this study were to identify the sex pheromones of three *Adoxophyes* species and to determine the role of the pheromones as prezygotic reproductive isolating mechanisms between sympatric congeners in Korea.

Methods and Materials

Insects

Larvae of *Adoxophyes* spp. were collected from pear orchards in Naju, Cheonan, and Namyangju, Korea during June and July of 2006. The larvae were reared individually on artificial diet (Bio-serv, Frenchtown, NJ, USA) in transparent plastic Petri dishes (1.5 cm high and 5.5 cm diameter) and maintained at 23°C under a 16:8-h ratio of light to dark photoperiod. Pupae were separated by sex and kept individually in plastic bottles (7 cm high and 2.5 cm diameter). After eclosion, moths were identified based on forewing color patterns (Han 2002) and then provided with a cotton pad soaked with a 5% (*w*/*v*) sucrose solution as food.

Chemicals

Synthetic dodecenyl acetate (12:OAc), tridecyl acetate (13:OAc), (*Z*)-9-dodecenyl acetate (*Z*9–12:OAc), 10-methyldodecyl acetate (10me-12:OAc), tetradecyl acetate (14:OAc), *Z*9–14:OAc, *E*11–14:OAc, *Z*11–14:OAc, (*Z*)-11-hexadecenyl acetate (*Z*11–16:OAc), (*Z*)-9-tetradecen-1-ol (*Z*9–14:OH), (*Z*)-11-tetradecen-1-ol (*Z*11–14:OH), and octadecanal (18:Ald) were purchased from Pherobank (Wageningen, The Netherlands). Isomeric purity of these compounds exceeded 99%.

Gland Extraction

Pheromone gland extracts were taken from 2- to 3-day-old females at the end of the scotophase, during their calling periods (Den Otter and Klijnstra 1983; Han 2002). The pheromone gland of each female was extruded by applying gentle pressure to the abdomen, excised with fine forceps, and individually extracted in 10 μl hexane containing 10 ng of 13:OAc as an internal standard in a 0.3-ml conical vial (Wheaton, Millville, NJ, USA) for 30 min at room temperature. The supernatant was transferred into another vial and stored at −80°C until analysis.

Chemical Analysis

Pheromone gland extracts were analyzed on an Agilent 6890N GC equipped with a split/splitless injector and a flame ionization detector. Samples were run on DB-5 and DB-Wax columns (30 m×0.25 mm ID, 0.25 μm film thickness, J&W Scientific, Folsom, CA, USA) in the splitless mode. Injector and detector temperature were 250°C. Helium was used as carrier gas (1 ml/min). The gas chromatograph (GC) oven temperature was programmed from 80°C (1 min hold) to 220°C at 5°C/min and held for 10 min. Components in pheromone gland extracts were identified by comparison of retention times with those of authentic standards on two different columns. The quantity of each component was estimated by comparing its GC peak area with that of the internal standard.

Gas chromatography–mass spectrometry (MS) analyses of the crude extract of pheromone glands were performed on an Agilent 6890N GC interfaced to an Agilent 5973 mass-selective detector. Samples were analyzed on the DB-Wax column (30 m×0.25 mm ID, 0.25 μm film thickness) with the temperature program described above. The ionization voltage was 70 eV. The ion source temperature was 230°C. Components in gland extracts were tentatively identified by comparison of their mass spectra with the mass spectra library (Wiley-NIST, Hoboken, NJ, USA), and identifications were confirmed by comparison of retention times and mass spectra with those of authentic standards.

Field Experiments

Field experiments were conducted in pear orchards at Naju, Cheonan, and Namyangju, respectively, during May–July of 2007. Sticky Delta traps (Green Agro Tech, Korea) baited with rubber septa (Aldrich Chemical Co., Milwaukee, WI, USA) impregnated with test chemicals in hexane were hung on branches 1–1.5 m above ground level. All field tests employed a complete randomized block design with five replicate blocks. The distance between traps within a block was at least 15 m. Twice a week, moths were counted, removed, and identified to species by using wing venation and then verified by examination of the genitalia.

Experiment 1 investigated the attraction of *A. honmai*, *A. orana*, and *Adoxophyes* sp. males to the two major components *Z*9–14:OAc and *Z*11–14:OAc singly and in binary blends. Experiment 2 was conducted to test the individual effects of the nine minor components identified

in female gland extracts; 12:OAc, *Z*9–12:OAc, 10me-12:OAc, 14:OAc, *E*11–14:OAc, *Z*9–14:OH, *Z*11–14:OH, *Z*11–16:OAc, and 18:Ald as possible synergists or antagonists, by using standard baits of the two major components. The standard baits used for *A. honmai*, *A. orana*, and *Adoxophyes* sp. were 1 mg of 35:65, 80:20, and 3:97 mixtures of *Z*9–14:OAc and *Z*11–14:OAc, respectively. Trap catch data (x) were transformed to log (x+1) and submitted to one-way analysis of variance. Means were compared by Tukey's test at α=0.05 (SAS Institute Inc. 2004).

Distribution of *Adoxophyes* Species

We sampled larvae of *Adoxophyes* spp. from pear orchards at eight different sites in Korea during June–August of 2007 and 2008 and reared them on artificial diet. After eclosion, female moths were assigned to three species according to their wing characters and subsequently verified by examination of the sex pheromones. Individuals were classified as *A. honmai*, *A. orana*, and *Adoxophyes* sp. when *Z*9–14:OAc and *Z*11–14:OAc in pheromone gland extracts were present in a ca. 100:200, 100:25, and 100:4,000 ratios, respectively. In all cases, the pheromone blend of individual glands supported the initial species identification based on adult morphological characters.

Results

Chemical Analysis

GC and GC–MS analyses of pheromone gland extracts showed that *Z*11–14:OAc is the major component of *A. honmai* and *Adoxophyes* sp., whereas *Z*9–14:OAc is the most abundant component in the pheromone blend of *A. orana* (Fig. 1). The ratios of *Z*9–14:OAc and *Z*11–14:OAc in pheromone blends were 100:209, 100:25, and 100:3,810 for *A. honmai*, *A. orana*, and *Adoxophyes* sp., respectively. In addition to these two major components, three acetate esters (12:OAc, 14:OAc, and *E*11–14:OAc), *Z*11–14:OH, and 18:Ald, as well as nonadecane, heneicosane, and tricosane, were detected in gland extracts of all species (Table 1). Small amounts of *Z*9–14:OH and *Z*11–16:OAc were detected in *A. honmai* and *A. orana*, while *Z*9–12:OAc and 10me-12:OAc were present only in *A. honmai*.

Field Experiments

Traps baited with *Z*9–14:OAc or *Z*11–14:OAc alone caught no *Adoxophyes* males. Responses of males to various blends of *Z*9–14:OAc and *Z*11–14:OAc differed markedly among species. Male *A. honmai* were equally attracted

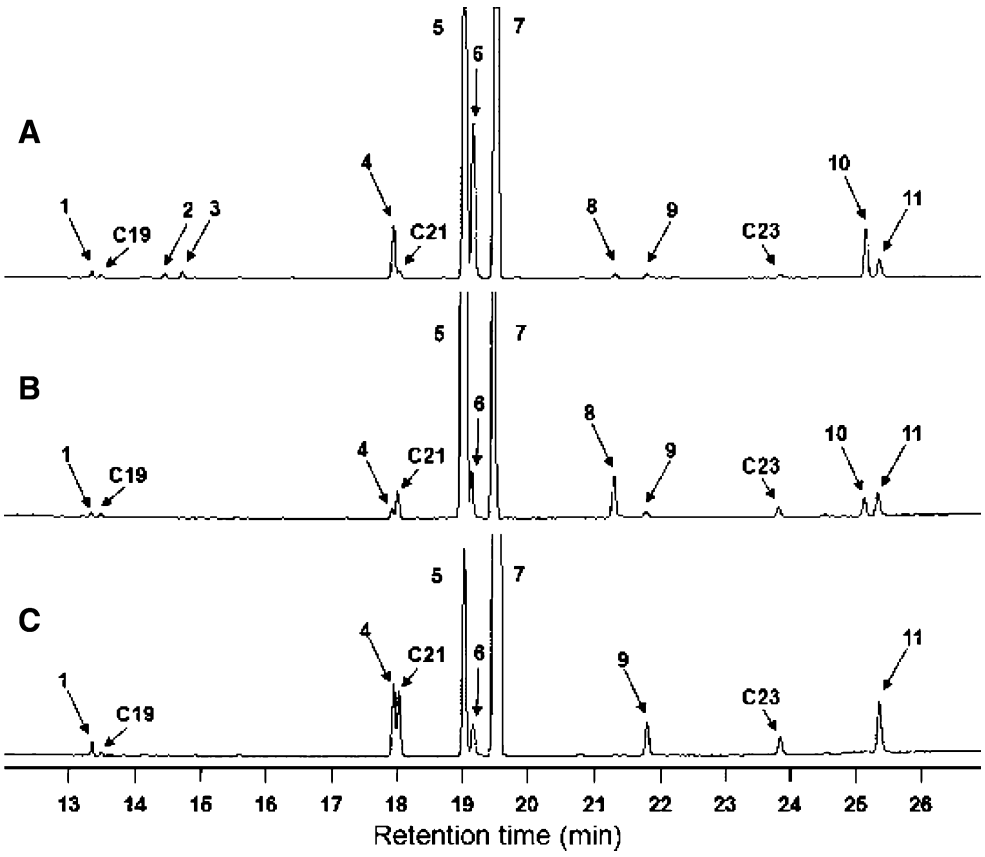

Fig. 1 Comparison of gas chromatograms of pheromone gland extracts of *Adoxophyes honmai* (*A*), *A. orana* (*B*), and *Adoxophyes* sp. (*C*) collected in Korea. *1* Dodecyl acetate, *2* (*Z*)-9-dodecenyl acetate, *3* 10-methyldodecyl acetate, *4* tetradecyl acetate, *5* (*Z*)-9-tetradecenyl acetate, *6* (*E*)-11-tetradecenyl acetate, *7* (*Z*)-11-tetradecenyl acetate, *8* (*Z*)-9-tetradecen-1-ol, *9* (*Z*)-11-tetradecen-1-ol, *10* (*Z*)-11-hexadecenyl acetate, *11* octadecanal, *C19* nonadecane, *C21* heneicosane, *C23* tricosane

Table 1 The amount (ng) and relative ratios (mean ± SE) of pheromone components in female extracts of three Korean *Adoxophyes* species (N=25)

Compound	*A. honmai*		*A. orana*		*Adoxophyes* sp.	
	Amount	Ratio	Amount	Ratio	Amount	Ratio
Dodecyl acetate	0.29±0.05	0.8±0.1	0.23±0.04	0.8±0.2	0.16±0.02	7.1±0.7
(*Z*)-9-dodecenyl acetate	0.25±0.04	0.7±0.1	–	–	–	–
10-Methyldodecyl acetate	0.32±0.06	0.9±0.2	–	–	–	–
Tetradecyl acetate	2.44±0.30	6.9±0.6	0.60±0.13	1.7±0.4	0.80±0.09	31.9±2.6
(*Z*)-9-tetradecenyl acetate	35.88±4.18	100	38.38±3.15	100	2.65±0.27	100
(*E*)-11-tetradecenyl acetate	5.02±0.58	14.7±1.6	0.54±0.07	1.6±0.2	0.40±0.04	16.9±1.3
(*Z*)-11-tetradecenyl acetate	73.77±8.19	209±6.3	10.05±1.26	25.4±1.4	98.44±9.62	3,810±245
(*Z*)-9-tetradecen-1-ol	0.25±0.02	0.8±0.1	0.32±0.05	0.9±0.1	–	–
(*Z*)-11-tetradecen-1-ol	0.41±0.03	1.3±0.1	0.11±0.01	0.3±0.1	0.31±0.06	11.6±1.8
(*Z*)-11-hexadecenyl acetate	1.65±0.27	4.6±0.7	0.68±0.13	2.0±0.6	–	–
Octadecanal	1.28±0.12	4.3±0.4	0.82±0.14	2.5±0.5	0.90±0.11	39.7±4.9

30:70 to 80:20 ratios of *Z*9–14:OAc and *Z*11–14:OAc (Fig. 2a), while *A. orana* males were preferentially attracted to ratios from 50:50 to 90:10 (Fig. 2b). In contrast, *Adoxophyes* sp. males were most attracted to traps baited with *Z*11–14:OAc as a major component (Fig. 2c). Regression analysis indicated a positive linear relationship between trap catch of male *A. orana* and *Z*9–14:OAc concentration for binary blends (r^2=0.75, P<0.05), while a negative relationship was observed with *Adoxophyes* sp. (r^2=0.86, P<0.01).

The effects of minor component of gland extracts on field trap catches varied significantly among species. Specifically 10me-12:OAc and *E*11–14:OAc showed a strong synergistic effect with the 35:65 mixture of *Z*9–14:OAc and *Z*11–14:OAc for *A. honmai* (Fig. 3a), while the capture of male *A. orana* increased when the two alcohols,

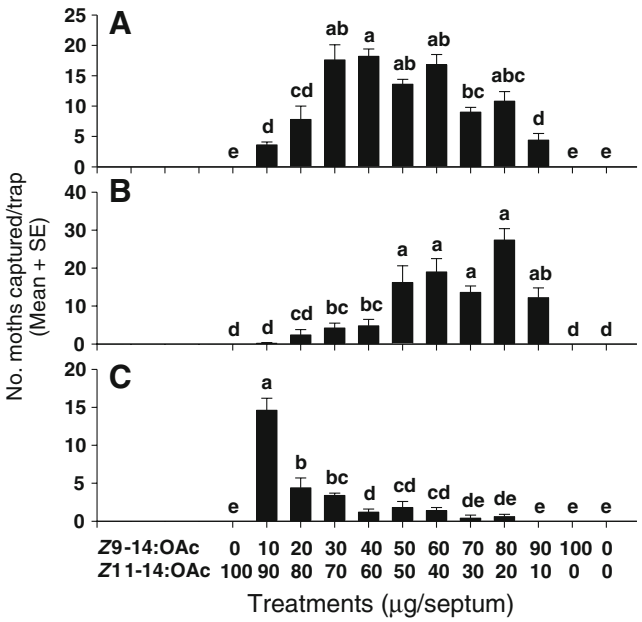

Fig. 2 Number of *A. honmai* (**a**; Naju, May 11–18, 2007), *A. orana* (**b**; Cheonan, May 17–24, 2007), and *Adoxophyes* sp. (**c**; Namyangju, May 18–25, 2007) males captured in traps baited with lures containing different ratios of *Z*9–14:OAc and *Z*11–14:OAc at pear orchards in Korea. *Bars with the same letter* are not significantly different (Tukey's test: P>0.05)

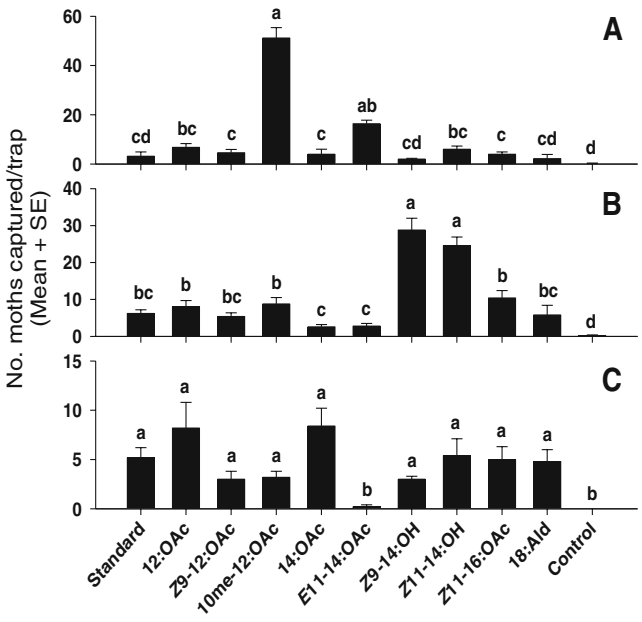

Fig. 3 The effect of adding 5% of different minor components to standard baits with 1 mg/septum of *Z*9–14:OAc and *Z*11–14:OAc on captures of male *A. honmai* (**a**; Naju, June 22–29, 2007), *A. orana* (**b**; Cheonan, July 12–19, 2007), and *Adoxophyes* sp. (**c**; Namyangju, July 13–20, 2007) at pear orchards in Korea. *Bars with the same letter* are not significantly different (Tukey's test: P>0.05)

*Z*9–14:OH and *Z*11–14:OH, were added to the 80:20 mixture of *Z*9–14:OAc and *Z*11–14:OAc (Fig. 3b). In the case of *Adoxophyes* sp., the only significant effect of minor components was the strong inhibitory effect of adding *E*11–14:OAc to a 3:97 ratio of the primary binary blend (Fig. 3c).

Distribution of *Adoxophyes* Species

It is evident from the pheromone gland analyses of females collected as larvae from different sites that there is considerable difference in the geographic distribution of the three species (Table 2).

Discussion

The analyses of glands extracts indicate that all three *Adoxophyes* species have *Z*9–14:OAc and *Z*11–14:OAc as major components, but in markedly different ratios. Males were preferentially attracted to the blend found in pheromone gland extracts of their conspecific females, but males of *A. honmai* and *A. orana* both responded to a broad range of ratios of *Z*9–14:OAc and *Z*11–14:OAc. These findings suggest that while difference in the relative composition of two major pheromone components is a component in the reproductive isolation of the sympatric *Adoxophyes* species, this is not sufficient to provide species-specific communication channels. However, our data suggest that two minor components, 10me-12:OAc and *E*11–14:OAc, play a role in isolating *A. honmai* and *Adoxophyes* sp. where they occur sympatrically in the southern part (Ulju, Jinju) of Korea.

A. orana also produces *Z*9–14:OH and *Z*11–14:OH. Their presence in the lure increases trap catch and our results support the idea that these two alcohols, as well as the relative ratios of the two major components, contribute to the maintenance of premating reproductive isolation between sympatric populations of *A. orana* and *Adoxophyes* sp. in the midwestern part (Ansung, Cheonan) of Korea. In our study, we found no evidence that *A. honmai* and *A. orana* occur sympatrically in Korea, but if they do, the differences in the ratios of major components and synergistic pheromone compounds, such as 10me-12:OAc and *Z*9–14:OH, may prevent cross-attraction between them.

Even though *E*11–14:OAc is present at low levels in the pheromone glands of *A. orana* and *Adoxophyes* sp., the addition of this compound to standard baits significantly decreased attraction for conspecific males. The antagonistic effect of minor compounds found in gland extracts of conspecific females has been reported for other moths (McElfresh and Millar 1999; Wu et al. 1999). However, it is not known whether *E*11–14:OAc is actually released from the female glands during calling. Further research is required to compare the attractiveness of pheromone blends actually emitted with those found in female gland extracts of these two species. Similarly, the roles of *Z*9–12:OAc and *Z*11–16:OAc, present in small amounts in gland extracts of some *Adoxophyes* species, need to be elucidated. Do they function as antagonists to sympatric moth species, or are they just by-products of the pheromone biosynthesis? Additionally, the influence of several components present simultaneously within blends on male trap catch also needs to be investigated.

Female pheromone glands from Japanese females of *A. honmai* contain *Z*9–14:OAc and *Z*11–14:OAc as major components at 67:33 (Tamaki et al. 1971a) or 73:27 (Noguchi et al. 1985) ratios, with two behaviorally important minor components, 10me-12:OAc and *E*11–14:OAc, at 4–5% and 2–3% of the two major components, respectively (Tamaki et al. 1979; Noguchi et al. 1985). These ratios are markedly different from those observed in this study (see Table 1), providing evidence of pheromonal variation in geographic populations of *A. honmai*. Interestingly, the observed ratio of the two major pheromone components in Korean *A. honmai* feeding on tea tree as well as on fruit trees (Han 2002) is similar to that reported

Table 2 The relative proportion of three *Adoxophyes* species collected from pear orchards at eight different sites in Korea

Site	Geographic location	*A. honmai*		*A. orana*		*Adoxophyes* sp.	
		2007	2008	2007	2008	2007	2008
Namyangju	37.4° N, 127.1° E	0	0	0	0	37	15
Ansung	37.0° N, 127.1° E	0	0	2	5	7	17
Cheonan	36.5° N, 127.1° E	0	0	42	25	11	8
Yeongi	36.4° N, 127.2° E	0	0	0	0	5	9
Sangju	36.2° N, 128.1° E	0	0	0	0	22	16
Ulju	35.2° N, 129.2° E	10	17	0	0	4	8
Jinju	35.1° N, 128.1° E	21	14	0	0	5	2
Naju	35.0° N, 126.4° E	45	22	0	0	0	0

from an *Adoxophyes* sp. from tea gardens in Taiwan (Kou et al. 1990), again supporting the idea of geographic variability in the pheromones within the genus.

The pheromone glands of *A. orana* females in Switzerland (Guerin et al. 1986) and females from different populations of *A. orana fasciata* in Japan (Tamaki et al. 1971b; Sugie et al. 1984; Noguchi et al. 1985) have similar ratios (77:23 to 88:12) of the two major components. Furthermore, pheromone traps baited with lures with similar ratios are effective in capturing males at all sites (Tamaki et al. 1971b; Meijer et al. 1971; Sugie et al. 1984; Guerin et al. 1986), thus supporting the idea that populations of *A. orana* and/or *A. orana fasciata* in Asia and Europe use similar blends of the major pheromone components. The addition of *Z*9–14:OH or *Z*11–14:OH to the binary blend of *Z*9–14:OAc and *Z*11–14:OAc significantly increased captures of *A. orana* males in Europe (Guerin et al. 1986), and a similar pattern was noted in our field trials in Korea (Fig. 3). However, while these minor components are present in pheromone gland extracts of *A. orana fasciata* (Noguchi et al. 1985), their addition to lures does not enhance trap efficiency in Japan (Sugie et al. 1984). Thus, the pheromone characteristics of Korean population of *A. orana* are identical to those of European population of *A. orana*, but different from those reported for Japanese *A. orana fasciata*.

Our field results show that *Adoxophyes* sp. is the dominant species of *Adoxophyes* in Korea. This species has a 3:97 blend of *Z*9–14:OAc and *Z*11–14:OAc, a ratio that has not been reported from any *Adoxophyes* species in Japan, Taiwan, or Europe. A 1:9 ratio of *Z*9–14:OAc and *Z*11–14:OAc captured *Adoxophyes privatana* males in Vietnam (Hai et al. 2002), so the Korean *Adoxophyes* sp. may be *A. privatana*, although nothing is known about the pheromone gland content of this species. Additional research that examines different *Adoxophyes* species around the world is necessary to clarify the composition of sex pheromones of different species within this genus. Parallel morphological and molecular studies should also be carried out to clarify the phylogenetic relationships and to understand the evolution of pheromone communication in this genus.

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