

Establishment of *Acanthoscelides pallidipennis* (Coleoptera: Bruchidae) feeding in seeds of the introduced legume *Amorpha fruticosa*, with a new record of its *Eupelmus* parasitoid in Japan

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Abstract

A North American bruchid beetle *Acanthoscelides pallidipennis* (Motschulsky) was newly found on Kyushu Island, Japan, the larvae of which feed in seeds of introduced false indigo (or indigobush), *Amorpha fruticosa* L. (Fabaceae: Astragaleae). The morphological characters of the Japanese population were similar to those of introduced populations in Korea and China and of native populations in Texas. Plant quarantine records indicated that the introduction of *A. pallidipennis* was due to recent introductions of *A. fruticosa* seeds from China and/or Korea as soil cover on cut slopes. The proportions of seeds eaten by *A. pallidipennis* in three consecutive years (1997–1999) in Fukuoka, located in the northern part of Kyushu Island, were as high as 56.0% for the overwintered generation and 92.0% for the first generation feeding in the dry seeds of previous years. No parasitoid emergence was observed in the first two years. In 1999, however, *Eupelmus* sp. (Hymenoptera: Eupelmidae) had parasitized the overwintered generation at an extremely low level, which is the first record of a parasitoid of *A. pallidipennis* in Japan. Time lags required for parasitoids to use introduced phytophagous insects are reviewed. The ability of *Eupelmus* sp. and its host to overwinter and the short lag between our first observations of each of the two species in Japan may indicate a joint introduction of the parasitoid with its host.

Key words: *Acanthoscelides pallidipennis*, *Acanthoscelides collusus*, invasion, North America, Leguminosae

INTRODUCTION

The process of accumulation of natural enemies on introduced pests may provide us with information as to how a guild of natural enemies responds to introduced organisms. Although it is hard to detect when the invasions occur because initial population sizes are often very small, a few long-term studies indicate that investigation of the development of a host-parasitoid complex over decades is a worthwhile approach to uncovering the process of parasitoid accumulation (e.g., Claridge, 1962; Collins et al., 1983; Godfray et al., 1995; Schonrogge et al., 1998).

We report here a North American bruchid *Acanthoscelides pallidipennis* (Motschulsky) that was found feeding in seeds of an introduced legume *Amorpha fruticosa* L. The introduction route of *A. pallidipennis* is estimated by reviewing quarantine records and by comparing specimens of local pop-

ulations of China, Korea, and the United States with the Japanese population. We discuss possible application of the accidentally introduced seed predator as a natural enemy of the weedy legume that has been naturalized and is expanding its distribution in Japan.

MATERIALS AND METHODS

Plant. *Amorpha fruticosa* is a leguminous shrub native to the South-eastern and Mid-western United States (Allen and Allen, 1981). The plant was introduced to England and Europe in the 18th century (Szentesi, 1999) and to Korea (K. Morimoto, unpublished) and China approximately 50 years ago (Tan et al., 1980; Wang et al., 1999) from the United States. In China, the plant was used not only as soil cover for erosion control but also as green manure (Wang et al., 1999). In Japan, the first introduction for control of soil erosion dates

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Table 1. Records on *Acanthoscelides pallidipennis* infestation of *Amorpha fruticosa* seeds imported from Korea and China at plant quarantines in Japan. Only identified specimens are listed.

Imported date	Emergence date	Imported	
		from	to
Dec. 4, 1978	Mar. 5, 1979	Korea	Shimonoseki, Yamaguchi, Japan
—	Feb. 5, 1981	Korea	Shimonoseki, Yamaguchi, Japan
—	Mar. 9, 1981	Korea	Shimonoseki, Yamaguchi, Japan
—	May 21, 1981	Korea	Shimonoseki, Yamaguchi, Japan
Nov. 1997–Feb. 1998	—	China	Moji, Fukuoka, Japan ^a
—	Mar. 9, 1998	China	Yokohama, Kanagawa, Japan
1998	—	Korea	Yokohama, Kanagawa, Japan ^b
—	Apr. 21, 1998	China	Tokyo, Japan

^aTao et al. (1999).

^bKobayashi (1998).

back to the post-war period, i.e., late 1940's (Osada, 1986) from the United States and the establishment was as early as 1960 (<http://www.biology.tohoku.ac.jp/garden/plantlist/wild/wild2-1.html>). Additionally, since 1973, the seeds of *A. fruticosa* have been imported from Korea and later also from China, and have been planted on banks of rivers and lakes and cut slopes in forests to control soil erosion (Table 1, Tao et al., 1999). Seeds play a primary role in reproduction and dispersal of *A. fruticosa* (Szentesi, 1999). The pods yield amorphin, which is toxic to insects including pests such as aphids, cinch bugs and cucumber beetles (Wang et al., 1999). At maturity the fruits are one-seeded (rarely two-seeded), indehiscent, and continuously drop when ripe (Szentesi, 1999).

Insect. *Acanthoscelides pallidipennis* (Motschulsky), also known as *A. collusus* (Fall), is native to North America. The distribution in the United States is Northern California south to Arizona, east to Texas, and north to Minnesota. Geographical variation of the native populations appears in their integument color (see Morphology section in Results). It is widely distributed wherever *A. fruticosa* has been introduced: In Europe, the species was first recorded in Bulgaria as *A. tarnawskii* n. sp. (Borowiec, 1980) and synonymized with *A. pallidipennis* (Borowiec, 1983) (see also Wendt, 1981; Borowiec, 1988; Szentesi, 1999). In Asia, it was recorded in Korea (Borowiec, 1983 and 1987, p. 91) and in China (first misidentified as *A. plagiatus* by Tan et al. (1980), and corrected by Zhang and

Liu (1991)). The only study on the life history of *A. pallidipennis* has been done in Hungary (Szentesi, 1999, but see the following paragraph). In addition to *A. fruticosa*, it has been reared from seeds of *A. californica* Nutt. ex Torr. & A. Gray, *Errazurizia rotundata* (Wootton) Barneby (Johnson, 1970), *A. canescens* Pursh (Johnson, 1979) and *Parryella filifolia* Torrey & A. Gray ex A. Gray (Johnson, 1989). All belong to the tribe Amorpheae. None of the hosts other than *A. fruticosa* has been introduced to Japan.

The life history of *A. pallidipennis* in Japan is under investigation. Roughly, the population in Japan has a bivoltine life cycle, emerges in mid-July (overwintered generation) and mid-September (first generation), lays eggs on fresh pods of full size and also on dry mature pods, both of which larvae can develop upon. It overwinters at its final larval stage. There remains, however, the possibility of a second generation and consequent overwintering at the adult stage, depending on environmental conditions.

Damage on seeds of *A. fruticosa* by *A. pallidipennis* is as follows. Szentesi (1999) observed the larvae consume a large part of the seeds of *A. fruticosa*. Levels of pod infestation are as high as 61% of introduced populations in Hungary (Szentesi, 1999) and 87% of a native population in the United States (Rogers and Garrison, 1975).

The inspection records on *A. pallidipennis* infesting imported *A. fruticosa* seeds at plant quarantines of Japan are listed in Table 1 (see also

Table 2. Proportions of *Amorpha fruticosa* seeds eaten by *Acanthoscelides pallidipennis* larvae in Higashi-kubaru, Fukuoka, Japan. See text for the difference in rearing conditions among years.

Sampling date	Beginning of emergence	Number of racemes	Number of seeds	Proportion of seeds eaten (cumulative %)
Oct. 9, 1997	Nov. 17, 1997	60	6,219	
	Mar. 28, 1998			59.6 ^b
Oct. 29, 1998	Jan. 8, 1999 ^a	68	8,012	
	May 6, 1999			37.5 ^b
Oct. 29, 1999	May 12, 2000	24	977	56.0 ^c
	Aug., 2000			92.0 ^b

^a *A. pallidipennis* adults were found dead.

^b Data a year after sampling.

^c Data on the overwintered generation.

Kobayashi, 1996, 1997, 1998, and Kocha, 1999 for unidentified *Acanthoscelides* from *Amorpha*). All infested *A. fruticosa* seeds have been fumigated after inspection at quarantine (Tao et al., 1999).

Proportions of seeds eaten and percentage of parasitism. We collected racemes with mature pods from three plants of *A. fruticosa* on the banks of a pond in Higashi-kubaru, Fukuoka, Japan, in October, 1997, 1998 and 1999 (Table 2). About 10% of the racemes were collected. The racemes were kept in paper bags and placed in an air-conditioned room to check first adult emergence monthly. The emerged adults were left in the bag and a year later *A. pallidipennis* adults and *A. fruticosa* seeds were counted to determine the proportions of seeds eaten by the larvae of the beetle for the samples collected in 1997 and 1998. Since females were allowed to produce the next generation, the proportions for the two years are cumulative impacts of the overwintered and the first (and possibly the second) generations on the seeds.

The bag of pods from the 1999 sample was placed outdoors. First emergence was checked monthly and, once emergence had started, emerged adults were counted and removed every 1–2 weeks, which still allowed females to lay eggs on pods. Therefore, for the overwintered generation of the sample, to distinguish from the next generation (i.e., the first generation), the proportion of seeds eaten was estimated after seven months from the date of collection as follows: 100 pods were selected randomly and pods with emergence holes were counted. The pods without holes were dissected to count late-stadia larvae or pupae inside

seeds. They were added to the number with emergence holes and the sum was divided by the total number of pods examined. Final stadium larvae or pupae were returned to the bag for further development. Then, after a year from collection, we counted the number of newly emerged adults and added this value to the number of adults estimated from the previous generation for cumulative feeding by the two (or three) generations. Any other insect emergence was also recorded. Assuming solitary parasitism, percentage of parasitism was calculated as {(the number of emerged parasitoid adults)/(the number of emerged adult beetles+the number of emerged parasitoid adults)} × 100(%).

Morphology. We compared the specimens we collected to those collected from *A. fruticosa* imported from Korea and China and inspected at plant quarantines in Japan. Comparison was also made with specimens of native populations in the United States.

RESULTS

Proportions of seeds eaten and percentage of parasitism

The only phytophagous insect that emerged from the seeds was *A. pallidipennis*. Cumulative proportions of seeds eaten were as high as 56.0% for the overwintered generation and 92.0% for the two (the overwintered and the first) generations that fed in dry seeds of the previous year (Table 2). Small numbers of adults emerged in mid-November, 1997 and early January, 1998. However, the early emergence occurred only at room temperature and

light conditions.

No parasitoid emergence was observed in 1997 and 1998. In 1999, however, four adults (3 females and 1 male) of a parasitoid *Eupelmus* sp. (Hymenoptera: Eupelmidae) were found dead on April 28, 2000. This corresponds to a percentage of parasitism of 0.726% on the overwintered generation. No further parasitoid emergence was observed. The biology of the parasitoid was not determined.

Morphology of introduced population in Japan (Fig. 1)

Head black with sparse white hairs on frons and vertex, around eye and clypeus with denser white setae. Antennal segments 1 to 4 filiform brown, remainder black, 5 to 10 serrate, 11 acute apically (Fig. 2A). Frons width slightly less than eye width.

Prothorax: Disk conical to subcampanulate. Pronotum black, underpart covered with white

hairs, upperpart with pale brown and brown hairs, basal margin with white hairs. White hairs form a medial vertical line. Prosternum and procoxa black. Thoracic underparts with dense white hairs.

Elytron dark brown with a slight orange tint, with black basal, lateral and medial margins. Small individuals all black. Covered with white, pale brown, and brown hairs. Sterna and pygidium covered with dense white hairs.

Hind femur (Fig. 2B): Armed with acuminate spine followed by two smaller spines, which is a characteristic of the genus *Acanthoscelides*. Bases of femora black with apices brown, covered with pale brown hairs.

Genitalia (Fig. 2C): A large, elongate, acute spine disposed medially, which is a characteristic of *A. pallidipennis*.

Body size: 1.1–2.1 mm from pronotum to elytra.



Fig. 1. *Acanthoscelides pallidipennis* (Motschulsky).

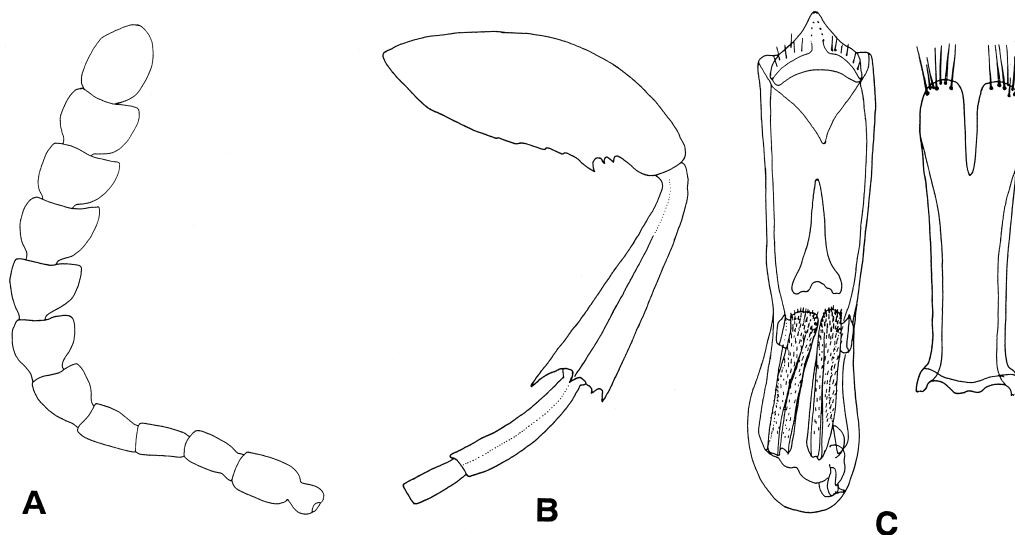


Fig. 2. A: Male antenna; B: hind leg; C: genitalia, median lobe (left), tegumen (right) of *Acanthoscelides pallidipennis*.

Morphology of native populations in the United States

Integument color: Head black; mouthparts sometimes brown; basal four (sometimes five) antennal segments red-orange, remainder dark brown to black. Pronotum, prosternum, and procoxa black. Elytron varies from all black to red-orange with narrow basal black margin, usually red-orange with basal, lateral and medial margins black; thoracic sterna black; legs usually red-orange, sometimes red-brown, sometimes bases of femora darker than apices. Abdominal sterna and pygidium usually black, sometimes apical sterna and pygidium red-orange.

Geographical variation in the United States: In California and Arizona approximately 95% of the individuals in populations have elytra that are mostly red-orange with their basal, lateral and medial margins black. The elytral coloration gradually becomes darker in populations toward the east until in central Texas and northward to Minnesota about 20–30% of individuals have all black or almost all black elytra.

The characteristics of specimens of *A. pallidipennis* in Japan resembled those found with *A. fruticosa* seeds from Korea (Morimoto, unpublished) and China (Tao et al., 1999). Among native populations in the United States, the Texas population showed close similarity with the Japanese population in darker integument color than those from California and Arizona (see also Johnson, 1970).

DISCUSSION

Origin and invasion route of *A. pallidipennis*

Based on the morphological similarity, consistent quarantine control since 1950 in Japan, and recent findings of *A. pallidipennis* specimens from *A. fruticosa* seeds imported from China and Korea, we hypothesize that *A. pallidipennis* was introduced from China and/or Korea. In 1997, when we started our observations, an individual of *A. pallidipennis* was also collected in Tochigi Prefecture in Honshu, the main island of Japan, but without records on the host (Sato et al., 1999). The coincidence of the two independent findings of the seed predator suggests that establishment of *A. pallidipennis* should have been shortly before 1997. If this hypothesis is correct, the introduction of the seed predator occurred approximately 20 years after the introduction of the host plant from the two Asian countries. Detailed quarantine records available for recent years show that *Acanthoscelides* sp. has been found every year from *Amorpha* seeds from China and Korea, which suggests that *A. pallidipennis* has been introduced from China and/or Korea. The origins of Korean and Chinese populations are estimated to be from the South-eastern and Mid-western United States, judging from the morphological similarity. Earlier records on *A. pallidipennis* in China (Tan et al., 1980) and Korea (Borowiec, 1983) than in Japan (present study, Sato et al., 1999) can be interpreted as the difference in times of introduction or establishment.

Recent innovation in planting methods could have enhanced the introduction of the seed predator *A. pallidipennis*. That is, instead of planting seeds directly, a mat consisting of packages of seeds with growth material has been applied to cut slopes since 1993. The high protection of seeds from rain and mechanical damage may have allowed the survival of larvae of *A. pallidipennis* that accidentally escaped fumigation at plant quarantines and remained in the seeds.

Origin and invasion route of *Eupelmus* sp.

The origin of *Eupelmus* sp. parasitizing *A. pallidipennis* cannot be determined at the present stage of identification of this group in Asia. By contrast, in North America and Europe, *Eupelmus* species are reported to attack *A. pallidipennis* or closely related species of the genus (Hetz and Johnson, 1988; Szentesi, 1999). These species have not been identified, either. Furthermore, the subgenus *Eupelmus* is cosmopolitan and has a wide host range attacking various holometabolous insects (Boucek, 1988; Gibson, 1995). At the species level, however, the same parasitoid species has been found in Taiwan from two bruchid species; one is of the genus *Acanthoscelides* feeding in seeds of an introduced legume from North America, and the other is a species of *Bruchidius* feeding in seeds of a native *Desmodium* (M. Tuda, L. Y. Chou, and Y. Tateishi, unpublished). Further studies are needed to identify these *Eupelmus* species found in different geographical regions.

In general, the time required for parasitoids to utilize invading insects appears to be longer when the invaders are more deeply concealed by host plant tissue. For example, 10 years was sufficient for parasitoids to utilize invading leaf-mining moths (Godfray et al., 1995) but more than 30 years was required to utilize introduced gall makers (Hoebeke and Wheeler, 1996; Schonrogge et al., 1998). The lag of *Eupelmus* sp. invading Japan following its host was short relative to such parasitoids of endophagous herbivores. Furthermore, the parasitoid has acquired the ability to overwinter. This evidence may indicate that the parasitoid was introduced with the host from China where populations of invading *Eupelmus* sp. may have already been established (M. Tuda et al., unpublished).

Control of weedy *A. fruticosa* in Japan

Similar to many exotic perennial shrubs, once established, the vegetation of *A. fruticosa* is predicted to be stable and no plant succession will take place for decades (Morimoto et al., 1996). *A. fruticosa* in Japan was observed to have escaped frequently from originally introduced sites, which seems to threaten native plant species (M. Ishihara, pers. comm.). The ongoing spread of *A. fruticosa* could be suspended by abandoning mass planting of its seeds as soil cover. Instead, annual plants may be applied, considering successional replacement with native plants.

Alternatively, specialist herbivores such as the accidentally introduced *A. pallidipennis* may be released to deter the reproduction and escape of *A. fruticosa*. Effectiveness of such seed predators as natural enemies of weedy plants is, however, still controversial. Two species of seed-feeding *Acanthoscelides* that have been introduced to control a leguminous weedy shrub *Mimosa pigra* are good examples: The seed predators have been introduced from Mexico to Australia and to Thailand as natural enemies of *M. pigra* (Kassulke et al., 1990; Waterhouse, 1994). They effectively destroyed up to 80% of the seeds in Thailand, whereas in Australia less than 1% of seeds was destroyed and the density of *M. pigra* has not been reduced (Wilson and Flanagan, 1991; Julien and Griffiths, 1999). In another control program, two seed-attacking weevils successfully arrested reproduction of a leguminous shrub *Sesbania punicea* (Hoffman and Moran, 1991, 1992). The variable effects could be due to variable persistence of seed banks, asexual reproduction of plants, seasonal reproduction of plants (or non-overlapping generations) and low or incomplete damage on seeds by the seed predators. Therefore, if these biological conditions of weeds and seed-predators are overcome, the probability of biological control of weedy plants by seed-predators will increase. In the case of *A. fruticosa* control by *A. pallidipennis*, the first condition has not been fully investigated (Szentesi, 1999) and must be subjected to close examination in the future.

Our hypothesis on an introduction route(s) of the Japanese population of *A. pallidipennis* should be tested using molecular techniques that we are now working on. In future papers, the detailed life history (including occurrence of the second generation) and distribution of *A. pallidipennis* as well as

the phenology of *A. fruticosa* and invasion status of the *Eupelmus* parasitoid in Japan will be reported.

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