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Review

Applied evolutionary ecology of insects of the subfamily Bruchinae (Coleoptera: Chrysomelidae)

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Abstract

Bean beetles of the subfamily Bruchinae (formerly, the family Bruchidae) include notorious pests of stored legumes, *Callosobruchus*, *Caryedon*, *Acanthoscelides* and *Zabrotes* that are able to feed and reproduce on dried beans and peas. Here, I review recent findings on the ecology, phylogeny, invasion and evolution in the bean beetles, based on field investigation of host plants and molecular studies. Possible future application of the new knowledge to weed and pest control is proposed, such as potential utility of the seed predators for modest control of beneficial yet invasive ('conflict') plants and new control methodology of pest bean beetles.

Key words: Bruchidae; seed predators; stored product pests; biological weed control; molecular phylogeny

INTRODUCTION

Beetles of the subfamily Bruchinae (Coleoptera: Chrysomelidae) are specialized internal feeders of bean family seeds (Fabaceae). They are frequently and erroneously referred to as the bean 'weevils' in spite of their affinity to the leaf beetles (Chrysomelidae). Here, I use the common name, the bean 'beetle' (or the seed 'beetle') to avoid taxonomic confusion. I also follow the recent taxonomic consideration that the bean beetle is not unique enough as a family but as a subfamily of Chrysomelidae (Lingafelter and Pakaluk, 1997).

The Bruchinae consist of about 1,700 species (Johnson et al., 2004). Although not very high in proportion of species, some of the bean beetles are notorious pests of stored beans with the highest intrinsic rate of increase among stored-products pests (Imura, 1990). They include several species of *Callosobruchus*, *Acanthoscelides* and *Zabrotes* that infest beans (Tribe Phaseoleae: *Vigna*, *Phaseolus*, *Glycine*, etc.) and *Caryedon* that feeds on peanuts or groundnuts (*Arachis hypogaea*) (Southgate, 1979; Johnson, 1981). *Bruchus* species that infest broad beans and peas (Fabeae: *Vicia* and *Pisum*) of economic importance may also be categorized as stored-bean pests. Strictly speaking, however, the genus *Bruchus* is different from other stored-bean pests in that it does not reproduce on dried hardened beans/peas and thus cannot cause further damage in storage.

PHYLOGENY

Recent molecular studies support that the Bruchinae are closely related to the frog-legged beetle subfamily, Sagrinae, within the family Chrysomelidae (Farrell and Sequeira, 2004). Within the Bruchinae, the tribes Amblycerini and Pachymerini are thought to be paraphyletic to a major tribe Bruchini (Farrell, 1998; Table 1). Although recent evidence supports the previously proposed phylogeny at the higher taxonomic levels, an intriguing new view of bean beetle phylogeny at the lower levels has been proposed. Kergoat et al. (2005a, b) supported the previously suggested view that *Acanthoscelides* and *Bruchidius* are polyphyletic groups (Johnson, 1981; Borowiec, 1987). However, some monophyletic groups of *Acanthoscelides* may be more closely related to those of *Bruchidius* than the other congeneric groups (Alvarez et al., 2006; Tuda, Kergoat, Kato, Ito, Bu-

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Table 1. Taxonomic position and composition of Bruchinae

Family Subfamily Tribe	
Chrysomelidae	
Bruchinae	
Amblicerini	3 genera (*Spermophagus*, ***Zabrotes***)
Bruchini	46 genera (***Acanthoscelides***, *Bruchidius*, ***Bruchus***, ***Callosobruchus***, *Mimosestes*)
Eubaptini	1 genus (*Eubaptus*)
Kytorhinini	1 genus (*Kytorhinus*)
Pachymerini	12 genera (***Caryedon***)
Rhaebini	1 genus (*Rhaebus*)

The genera in bold include pest species.

ranapanichpan, Szentesi and Jermy, unpublished). These molecular studies also indicate potential problems about relative phylogenetic positions among other recently described genera. For example, a recent molecular study found *Tuberculobruchus* to be polyphyletic (Kergoat, 2005b), indicating a plesiomorphic trait is used for the generic key and revision of the genus using genital morphology may be necessary. Data on recently described species, synonymies and host plants have been actively accumulated from different biogeographic regions of Asia and Africa that would contribute to the understanding of evolutionary diversity of the Old World (e.g., Arora, 1977, 1980; Egorov and Ter-Minassian, 1983; Morimoto, 1990; Anton et al., 1997; Anton, 1999, 2000; Kingsolver, 1999; Tuda, 2003; Johnson et al., 2004; Tuda and Morimoto, 2004; Tuda et al., 2005) and the New World (e.g., Johnson, 1970; Romero and Johnson, 2000) bean beetles (see also Zacher, 1952; Udayagiri and Wadhi, 1989 for overviews).

ECOLOGY

In most bean beetles, female adults deposit eggs on pods and/or seeds, hatched larvae burrow into seeds and emerge out as adults (Southgate, 1979). Adults lay eggs singly and larvae feed only single seeds (Center and Johnson, 1974). Exceptions to the typical life history are *Conicobruchus* (Prevett, 1967), *Merobruchus* (Johnson, 1967) and *Sennius* (Center and Johnson, 1972), which feed on several seeds in a single pod and *Bruchidius*, which feeds on multiple pods in single *Trifolium* inflorescences (Balachowsky, 1962; Tuda, pers. obs.). In both cases, the host seeds are too small to support bean beetle development into full adult. Finally, as an exception to the general pattern of pupating within seeds, the larvae of several species of *Caryedon* emerge out of seeds to form cocoons either on pods or on the ground for pupation (Center and Johnson, 1974; Southgate, 1979; Tuda, pers. obs.).

Batch egg laying is known only for a limited number of species such as *Pseudopachymerina spinipes* (Teran, 1962), *Caryedon fasciatus* (Prevett, 1966), *Caryoborus serripes* (Delobel et al., 1995a) and *Stator beali* (Nilsson and Johnson, 1993; Fox and Mousseau, 1995). The host pods and seeds of these beetles are hard and relatively large (Janzen, 1971; Moreno-Casasola et al., 1994; Delobel et al., 1995a; Delgado et al., 1997). In *Callosobruchus*, such egg clustering had previously not been observed but it was recently found in a non-pest species, which develops in a large, hard seeded legume (Tuda and Buranapanichpan, unpublished). These examples imply that egg laying pattern is not phylogenetically constrained but may respond to selection imposed by host plant characteristics (the size and/or hardness of pods and seeds), parasitoid pressure and abiotic factors (Janzen, 1971; Mitchell, 1977; Delobel et al., 1995a).

Typical hosts of bean beetles are legumes (Fabaceae) (84% of the known hosts; Johnson, 1970) but the palm (Arecaceae), morning glory (Convolvulaceae), mallow (Malvaceae) and about 30 other families are also used as hosts (Southgate, 1979; Johnson, 1981). Most bean beetles are either monophagous or oligophagous; their host range is limited to restricted plant taxa, usually subtribes and tribes at most (Jermy and Szentesi, 2003; Delobel and Delobel, 2003; Tuda et al., 2005; Kergoat et al., 2007a, b), although there are a few generalists that utilize different subfamilies of legumes.

Evolutionary relation between bean beetles and their host plants has been actively discussed as a model of plant-insect evolution. Proximate mechanisms for host-plant shifts are probably associated with chemical (Janzen, 1969), morphological (Janzen, 1969; Szentesi and Jermy, 1995) and geographical (Johnson and Siemens, 1991) proximity between the current and potential hosts. Delobel and Delobel (2006) suggest that the speciation in European bean beetles is sequential evolution

(sensu Jermy, 1984) or sequential radiation (sensu Abrahamson et al., 2003) that follows plant diversification, which contrasts to the reciprocal coevolution model that assumes plant evolution in response to insect evolution against plant defensive traits (sensu Ehrlich and Raven, 1964; Futuyma, 1983; Becerra, 2003).

EVOLUTION OF STORED PRODUCT PESTS

Evolution of stored bean pests is likely a two-step process. The first is preadaptation to utilize dried hard seeds (Watanabe, 1985) and the second is the evolution of dispersal, reproductive and competitive polymorphism to adapt to cultivated seeds and storage environments (Utida, 1954, 1981; Caswell, 1960; Nakamura, 1966; Sano, 1967; Ouedraogo and Huignard, 1981; Messina, 1984; Toquenaga, 1990; Tuda, 1997, 1998; Tuda and Iwasa, 1998; Takano et al., 2001). Hence, an ability to feed on dried mature host seeds is an inevitable prerequisite for bruchids to become pests. This requires first, female adults to deposit eggs on/near dried mature seeds and second, hatched larvae to burrow into the hard seeds to feed on.

What is it then that promotes evolution of utilization of dry, hard seeds? Using a comparative approach to study *Callosobruchus* pest and non-pest species, the potential effects of climate, host plants, phylogeny and endosymbiotic bacterium were examined (Tuda et al., 2006). Long dry season was shown to be the most important factor for evolution towards preadaptive stage to become stored bean pests (i.e., ability to use dry hard beans) when evolutionary history was accounted for (Tuda et al., 2006). Phylogenetic history of *Callosobruchus* and idiosyncrasy of their host plants also had significant effects on the evolution towards stored bean pests (Tuda et al., 2006). In future studies, hardness of dried seeds will be one of the foci of research because the hardness per se can serve as a deterrent against seed predators, including bean beetles (Janzen, 1977; Southgate, 1979; Kitch et al., 1991; Dongre et al., 1993). The loss of toxic chemicals during post-maturity drying processes may also increase survival of such granivores, which promotes host range expansion.

INVASION

With human aid, dispersal and invasion of living organisms in recent centuries are occurring at a speed that has been unattainable with plate tectonics and glacial dynamics. In Japan, examples of bean beetle invaders are *Bruchus rufimanus* and *Bruchus pisorum*, the pests of broad beans and peas, respectively (Table 2). *Bruchus loti* has also been considered to be an alien species but our recent finding indicates the current status as an introduced species may require reconsideration, as described later in this section. We found two additional bean beetle species have invaded Japan (Tuda et al., 2001; Tuda, Tateishi, Niyomdham, Morimoto, Chen, Zhu, Zhang, Murugan, Chou and Johnson, unpublished).

One recent invader is a bean beetle *Acanthoscelides pallidipennis* (=*A. collusus*) that feeds on a fast-growing, nitrogen-fixing legume, Indigobush (or False indigo; Itachi-hagi), *Amorpha fruticosa*. The legume had invaded from North America and established in England, Europe and East Asia except Japan by the mid 20th century (Szentesi, 1999; Tuda et al., 2001). In Japan, the bean beetle was first found at two locations in the central and southwestern parts of the country in 1997 (Tuda et al., 2001) and later in several areas in the southwestern Japan as well (Ishihara, unpublished). A molecular analysis of *A. pallidipennis*

Table 2. Bean beetle invasion to Japan

Bean beetle	Time of invasion	Source population
Bruchus pisorum[a]	1888	USA
Bruchus rufimanus[a]	1921	England/Europe
Callosobruchus maculatus[b]	1950	?
Acanthoscelides pallidipennis[c]	1970s–1997	Korea and China
Acanthoscelides macrophthalmus[d]	recent (–2000)	?

[a] Yoshida, 1990; [b] Morimoto and Kiritani, 1995; [c] Tuda et al., 2001; [d] Tuda, Tateishi, Niyomdham, Morimoto, Chen, Zhu, Zhang, Murugan, Chou and Johnson, unpublished.

from four States of the USA and from East Asia revealed that Japanese populations consist of several unrelated haplotypes that are shared by Chinese and Korean populations and individuals intercepted by import inspection at Japanese seaport quarantines (Tuda, Ishihara, Wasano, Morimoto, Paik, Houck and Johnson, unpublished). This molecular evidence supports our hypothesis (Tuda et al., 2001) that *A. pallidipennis* established in Japan was transported from the introduced populations in nearby East Asian countries. Indeed, from these regions, the host seeds (*A. fruticosa*) have been imported for erosion control since the 1970s (Tuda et al., 2001).

The other invader is *Acanthoscelides macrophthalmus* (Tuda, Tateishi, Niyomdham, Morimoto, Chen, Zhu, Zhang, Murugan, Chou and Johnson, unpublished). It is a Neotropical species that feeds on Wild tamarind, or Gin-nemu, *Leucaena leucocephala*. *Leucaena leucocephala* is a fast-growing nitrogen-fixing leguminous tree that is cultivated for fodder (Elharith et al., 1980), green manure (Chagas, 1981), reforestation, windbreak, fuel, pulp and erosion control (Kondo et al., 1987; Satake et al., 1989). Because *A. macrophthalmus* is specialized to *Leucaena* species (e.g., Johnson, 1979; Hughes and Johnson, 1996; Delobel and Johnson, 1998), *L. leucocephala* is the only *Leucaena* species that has been introduced to Japan, and airborne long-distance dispersal is highly unlikely for bean beetles (Tuda et al., 2001), there is little doubt that *A. macrophthalmus* has been introduced with the host seeds.

Accelerated long-range human transportation promotes unexpected dispersal of animals and plants that eventually become pests in the areas where they are introduced. As a consequence, it is sometimes difficult to determine geographic origins of widely distributed organisms. Whether local populations are native or of relatively recent introduction from foreign populations can be estimated by statistics based on population genetics theory if DNA sequence or restriction site data are available (e.g., Templeton et al., 1992; Templeton, 1998). Our recent findings regarding Japanese populations of *Bruchus loti* may be a good example. Palearctic fauna and flora share many species including *B. loti*. The Japanese populations of *B. loti* are currently listed as an alien species that would become a target of eradication. We found that haplotypes found in the Japanese populations are clearly different from those in European populations, which indicates that Japanese *B. loti* is not introduced from Europe and likely originated from the Far East including Japan (Tuda, Ichita and Kergoat, unpublished). The genetic uniqueness of the Japanese population indicates that *B. loti* should perhaps be conserved in this country. The status of Japanese *Callosobruchus chinensis* is also controversial. Our molecular study shows that populations of *C. chinensis* in agricultural habitats are genetically homogeneous, whereas those from natural habitats are heterogeneous, indicating a bottleneck event caused by human agricultural practice and transportation (Tuda et al., 2004).

APPLICATION TO BIOLOGICAL CONTROL

As natural enemy of conflict plants. A control agent should ideally be a specialist feeding only on targets of control and not harm beneficial organisms (Sweetman, 1936; Huffaker, 1964). Internal feeders ('endophages') tend to have narrower diet breadth than external feeders ('exophages') (Lewinsohn, 1991; Frenzel and Brandl, 1998) and are probably more suitable as biological control agents. Indeed, bean beetles have been used as biological control agents of weedy plants and proven to be effective, to some extent, once established in the release areas (Table 3; c.f., Julien, 1992).

I propose two bean beetle species that have been accidentally introduced and can be used for biological control of new leguminous weeds in Japan. The first is *A. pallidipennis*. The narrow diet range of *A. pallidipennis* and the absence of congeneric relatives of Indigobush and naturally associated parasitoids of the beetle are preferable features as a control agent, in contrast with the case of *Bruchidius villosus* that attacked not only the target but also non-target (but non-indigenous) congeners after its introduction to New Zealand (Paynter et al., 2004). In this respect, *A. pallidipennis* is suitable as an agent that controls escape of *Amorpha fruticosa* from cultivation by seed dispersal. The suitability of *A. pallidipennis* as a control agent has also been pointed out in the native distribution area of Indigobush (Rogers and Garrison, 1975). The bean beetle would be even more suitable if it would be applied for control in introduced areas where its naturally associated enemies (i.e., parasitoids,

Table 3. Bean beetles used as biological control agents of weeds (modified from Julien, 1992; ARC-PPRI, 2003)

Control agent	Target weed	Location of release
Acanthoscelides macrophthalmus	*Leucaena leucocephala*	South Africa
Acanthoscelides puniceus	*Mimosa pigra*	Australia, Thailand, Vietnam (Malaysia, Myanmar)
Acanthoscelides quadridentatus	*Mimosa pigra*	Australia, Thailand, Vietnam (Malaysia, Myanmar, USA)
Algarobius bottimeri	*Prosopis glandulosa*	South Africa
Algarobius prosopis	*Prosopis velutina*	South Africa
Bruchidius villosus	*Cytisus scoparius*	New Zealand
Bruchidius sahlbergi	*Acacia nilotica*	Australia
Sulcobruchus subsuturalis	*Caesalpinia decapetala*	South Africa

Locations in parentheses are due to natural spread of released agents.

predators, parasites, and pathogens) and competitors (e.g., *Acanthoscelides submuticus*) are rare or absent (Tuda et al., 2001). *Acanthoscelides pallidipennis* feeds only on *Amorpha* and related genera (Amorpheae: *Errazurizia* and *Parryella*) that distribute naturally only in North America (Center and Johnson, 1974).

The second is *A. macrophthalmus*. *Leucaena leucocephala*, initially introduced as a beneficial tree in the 19th century, escaped from cultivation by seed dispersal and has become weedy in tropical regions of Japan and other introduced areas (e.g., Smith, 1985; Henderson, 2001; Wu et al., 2003). Its seed predator, *A. macrophthalmus*, satisfies the above criteria as a control agent in Asia, i.e., narrow host range and scarcity of parasitoids. In fact, this bean beetle has already been deliberately introduced to South Africa for the control of *L. leucocephala* (ARC-PPRI, 2003; Olckers, 2004; Table 3). Nevertheless, there remains a risk that the control agent could easily accumulate local generalist parasitoids and in the long term the control effect could decrease as observed in West Africa (Delobel and Johnson, 1998).

Control of bean beetles. Fumigation has been widely applied to stored products as an effective method of control of stored products pests. However, methyl bromide, used for fumigation of grain legumes (Yoneda et al., 1990) has been recognized as one of the chemicals that deplete the stratospheric ozone layer and, hence, was called for its controlled use by the Montreal Protocol (UNEP, 2000).

Alternatively, parasitoids (e.g., a trichogrammatid egg parasitoid *Uscana*, larval-pupal parasitoids, pteromalid *Dinarmus*, *Anisopteromalus*, an eupelmid *Eupelmus*, and a braconid *Heterospilus*; e.g., Southgate, 1979; Steffan, 1981; Fujii and Wai, 1990; Mitsunaga and Fujii, 1999; Schmale et al., 2001; Tuda et al., 2001; Kobayashi et al., 2003; Jaloux et al., 2004; Tuda and Shimada, 2005; Wu et al., 2005; Vamosi, Hollander and Tuda, unpublished) and plant extracts (e.g., Lambert, 1985; Rahman, 1990) have been actively explored for biological control (see Fujii et al., 1990; Huis, 1991 for review). In addition to biological and botanical control, controlled temperature (e.g., Rahman, 1990), mechanical control (e.g., Quentin et al., 1991), controlled atmosphere (e.g., Oosthuzien and Schmidth, 1942) and radiation (e.g., Kiyoku and Tsukuda, 1968; Hossain et al., 1972; Reddy et al., 2006) have been proposed as effective control methodology (see also Highley et al., 1994). I suggest an endosymbiotic bacterium, *Wolbachia*, from bean beetle pests and its functional relation with the host (Kondo et al., 2002) may be applied to biological control of stored product pests. When the above-mentioned multiple methods are used in combination, the possibility of one agent negating the other must be taken into account (e.g., Boeke et al., 2003).

Identification of pest species. External and internal morphology of the adult stage is used for identification to species. Most recently male genital traits for *Callosobruchus* were compared and summarized by Tuda et al. (2006). Compared to adult morphology, egg and larval morphology is less well studied because they are not readily available (but see Pfaffenberger and Johnson, 1976; Arora, 1978; Delobel et al., 1995b), which makes identification based on pre-adult stages difficult. In contrast to the differential accessibility among developmental stages of morphological characters, molecular characters can be more stable and useful as

keys for identification. Using the PCR-RFLP technique, which is relatively easy and inexpensive, species of all developmental stages of important stored bean pests in the genus *Callosobruchus* have been successfully distinguished (Tuda et al., 1995).

CONCLUSION

Bean beetles, as other phytophagous insects, exhibit significant conservatism in host utilization. Feeding on dried seeds not only enables repeated generations but also broadens the diet of some bean beetle pests. Our study based on molecular phylogenetics indicates this preadaptation to use dry, hard beans that precedes human store of beans has been selected for by arid habitat climate (Tuda et al., 2006). Recent investigations of Asian bean beetle fauna have revealed diversity of the species and ecology of the seed predators. This also led to the finding of invasions of alien bean beetles (Tuda et al., 2001; Tuda et al., unpublished). Invasion routes estimated by our molecular approach indicated the invasion of the bean beetle was associated with imported alien host seeds. I propose the recent bean beetle invaders may be used for modest control of the seed dispersal of beneficial but invasive alien plants ('conflict plants' (Neser, 1994)).

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