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ORIGINAL ARTICLE

A novel host shift and invaded range of a seed predator, *Acanthoscelides macrophthalmus* (Coleoptera: Chrysomelidae: Bruchinae), of an invasive weed, *Leucaena leucocephala*

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Abstract

An endophagous seed predator, *Acanthoscelides macrophthalmus* (Coleoptera: Chrysomelidae: Bruchinae), utilizes Neotropical *Leucaena* (Fabaceae: Mimosoideae). One of its hosts, *Leucaena leucocephala*, is a fast-growing nitrogen-fixing tree that serves as a multipurpose beneficial plant but eventually becomes an aggressive invader where it was introduced. Herein, we report *A. macrophthalmus* invasion of the Far East, South Asian tropics and subtropics (Japanese Pacific Islands, Taiwan, Southern China, Northern Thailand and Southern India). Of other field-collected mimosoid legumes, an introduced tree, *Falcataria moluccana*, in Taiwan was found to be used by the seed predator. Conversely, our published work review revealed that the seed predator had retained high host specificity to *Leucaena* species in its native and introduced regions. *Acanthoscelides macrophthalmus* was able to utilize aphagously postharvest mature seeds for oviposition and larval development, which is a trait of post-dispersal seed predators. We confirmed that *A. macrophthalmus* that was reared on *L. leucocephala* was able to utilize *F. moluccana* as well. Although the relatively high host specificity of the oligophagous beetle is suitable for controlling the weedy *L. leucocephala*, the potential host range expansion confirmed by this study must be cautioned.

Key words: Bruchidae, host specificity, invasion, Leguminosae, pre-dispersal and post-dispersal seed predator, weed control.

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INTRODUCTION

Host range of control agents is a critical factor in biological control programs because the risk of host shift to non-target organisms should be minimized. In this respect, narrower host range of endophagous (i.e. internal feeding) insects (Lewinsohn 1991; Gaston *et al.* 1992; Frenzel & Brandl 1998; for host ranges of

endophagous seed predators, Johnson 1981; Tuda *et al.* 2005; Delobel & Delobel 2006; Kergoat *et al.* 2007a,b) may be preferable as weed control agents. Seed predators have been used as control agents in weed control programs before but with mixed results (e.g. Louda 1982, 1983; Sheppard *et al.* 1994; Norambuena & Piper 2000; review in Crawley 1992). Plants that produce abundant seeds and rich seed banks are not seed-limited and predator satiation (inverse density dependence) allows weed population to explode (Janzen 1971; Crawley 1989).

In recent centuries, human activity has accelerated the speed of range expansion of living organisms that has been unattainable with plate tectonics and glacial dynamics (Carlton 1999). Furthermore, transportation of economic plants can be accompanied by and expand distribution of associated insect herbivores. In particular, internal seed predators that are protected and concealed inside hard host seeds are more likely to be transported successfully than external feeders through commercial trading, as in the bruchine *Acanthoscelides pallidipennis* infesting the seeds of the North American legume, *Amorpha fruticosa* introduced to Eurasia (Szentesi 1999; Tuda *et al.* 2001). Once introduced, novel enemy-free environments could promote their establishment as in most non-indigenous organisms (Torchin *et al.* 2003).

Leucaena leucocephala (Lam.) de Wit (Fabaceae) is a fast-growing nitrogen-fixing tree/shrub that is cultivated for fodder (Elharith *et al.* 1980), green manure (Chagas 1981), reforestation, windbreak, fuel, pulp, erosion control (Kondo *et al.* 1987; Satake *et al.* 1989) and vegetable crop (Barrett 1990). This multipurpose beneficial tree is, however, a "conflict plant" (Neser 1994). *Leucaena leucocephala* excludes plants growing nearby, by allelopathic effect caused by the chemical, mimosine, produced and stored especially in young leaves and mature seeds (Chou & Kuo 1986; Adeneye 1991; Xuan *et al.* 2006; Williams & Hoagland 2007). The extract of *L. leucocephala* also has insecticidal effect (Cavalcante *et al.* 2006). Seed production of *L. leucocephala* is heavy and prolific (up to 1700 pods/tree, Janzen 1969; Raghu *et al.* 2005), each pod containing approximately 20 seeds (Stone 1970), 2–4 podding cycles a year (Raghu *et al.* 2005) and seed dispersal by rodents and birds or through cattle manure, following seed release as pods dehiscing, promotes its spread throughout adjacent areas (Smith 1985). *Leucaena leucocephala* has eventually become an aggressive invader in tropical and subtropical disturbed areas in more than 20 of the more than 105 countries where it was introduced (Walton 2003) and is cautioned as one of the 100 worst invasive alien species in the world (Lowe *et al.* 2000). *Leucaena leucocephala* also endorses the invasion by more aggressive alien plants (Yoshida & Oka 2004). In Asia, the times of introductions date back to as early as 1645 in Taiwan (Wu *et al.* 2003), approximately 1920 in continental China (Guangdong Province) (Li & Xie 2002), prior to 1815 in the Philippines (Merrill 1921–1926), prior to 1867 in Japan (Iinuma 1977) and during the Sukhothai Period (1238–1378) in Thailand (the Royal Institute, pers. comm.). Transportations within Asia are also known, such as when in 1939 a botanist brought *L. leucocephala* to Thailand from India (Sophanodora 1995). *Leucaena leucocephala* was introduced to Yunnan Province from Hainan Province after 1961 (Yang 2000).

Acanthoscelides macrophthalmus (Schaeffer) (Coleoptera: Chrysomelidae: Bruchinae) is a Neotropical seed predator that feeds on *L. leucocephala* and congeneric plants. The bruchine is considered to have potential to limit the invasiveness of *L. leucocephala* in dry areas where leucaena psyllids are not abundant (Raghu *et al.* 2005). In Eurasia, the species was recorded in Vietnam and Cyprus (Kergoat *et al.* 2005; Vassiliou & Papadoulis, unpubl. data).

Herein, we report the invasion of the Far East through the South Asian tropics and subtropics by the bruchine beetle, presumably along with the introduction of its host. Host specificity of *A. macrophthalmus* in the field is studied by collecting mature seeds of mimosoid plants that are phylogenetically related to its original host, *L. leucocephala*, at the subfamily level, and this allows evaluation of its suitability as a control agent of invasive *L. leucocephala*. We examine the potential of *A. macrophthalmus* playing a role of not only a pre-dispersal but also post-dispersal seed predator and the capability to host shift.

MATERIALS AND METHODS

Since 1995, mature pods of *L. leucocephala* (Lam.) de Wit (Fabaceae: Mimosoideae: Mimoseae) were collected in Asian countries (i.e. Japan, Taiwan, China, Thailand and India). Likewise, mature pods and/or seeds of legumes of the subfamily Mimosoideae were collected for possible host shifts in the bruchine seed predator, *A. macrophthalmus*. These plants belong to the genera *Adenanthera*, *Entada*, *Mimosa* (tribe Mimoseae), *Acacia* (tribe Acacieae), *Albizia* and *Falcataria* (tribe Ingeae) of the subfamily Mimosoideae (see Table 1 for species names). Approximately 2–5% of available mature pods were collected for each population. Resultant ranges of the number of collected seeds were approximately 130–5900 seeds for *L. leucocephala* and ten (*Entada tonkin-*

Table 1 Mimosoid legume species sampled

Plant species	Tribe	Country	Status	No. of sampled populations
Adenanthera microsperma Teijsm. & Binn.	Mimoseae	Taiwan	N	1
Entada phaseoloides (L.) Merr.	Mimoseae	Ryukyu, Japan	N	>10
		Taiwan	N	
Entada tonkinensis Gagnep.	Mimoseae	Hong Kong, China	N	3
		Vietnam	N	
Leucaena leucocephala (Lam.) de Wit	Mimoseae	Ogasawara and Ryukyu, Japan	I	51
		Taiwan	I	
		Thailand	I	
		India	I	
Mimosa invisa Colla	Mimoseae	Thailand	I	2
Mimosa pigra L.	Mimoseae	Thailand	I	2
Mimosa pudica L.	Mimoseae	Taiwan	I	14
		Thailand	I	
Albizia chinensis (Osb.) Merr.	Ingeae	Thailand	N	>4
Albizia julibrissin Durazz.	Ingeae	Kyushu, Japan	N	4
		Southern China	N	
Albizia lebbeck (L.) Benth.	Ingeae	Ryukyu, Japan	I	11
		Taiwan	I	
		Thailand	I	
		India	N	
Albizia lebbekoides (DC.) Benth.	Ingeae	Thailand	N	1
Albizia lucidior (Steud.) I.C. Nielsen	Ingeae	Thailand	N	1
Calliandra surinamensis Benth.	Ingeae	Taiwan	I	1
Falcataria moluccana (Miq.) Barneby & J.W. Grimes	Ingeae	Taiwan	I	1
Acacia confusa Merrill	Acacieae	Taiwan	N	4
Acacia farnesiana (L.) Willd.	Acacieae	Taiwan	I	1
Acacia pruinescens Kurz	Acacieae	Southern China	N	1

Status: N, native, I, introduced.

ensis) to 3100 seeds (*Albizia chinensis*) for the other mimosoid legumes (Tuda *et al.*, unpubl. data).

Each sampled population of pods and/or seeds was put in a bag connected to a clear bottle, following Fursov (2004), and kept under semi-natural room conditions in the regions where collections were made. Emerging bruchine beetles trapped in the bottles were collected daily for a month and weekly later on until no more adults emerged. Bruchine adults were identified by external and internal (genital) morphological traits. The insect specimens and part of plant specimens were deposited at the Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka, Japan (KUF) and the National Taiwan University, Taipei, Taiwan (NTUT) and the rest of the plant specimens at the University of the Ryukyus, Nishihara, Okinawa, Japan (URO). We extensively reviewed the published work for bruchine beetles associated with *L. leucocephala* and their geographical distribution to study host ranges of the beetles.

To study the potential of *A. macrophthalmus* as a post-dispersal seed predator, we did the following experiments. Five newly emerged, mated *A. macrophthalmus* females were separated into a Petri dish with 200 un-infested seeds of host plants that had been put in a freezer (at approximately –20°C) for a week (i.e. either *L. leucocephala* or, if any, other host(s)); and were allowed for oviposition and larval development into adults for populations collected in Taiwan and Thailand. The experiments were done under semi-natural room conditions in the regions where seeds were collected. Likewise, we performed a host shift experiment from *L. leucocephala* to an alternative host(s).

RESULTS

Acanthoscelides macrophthalmus was the only bruchine beetle to emerge from the seeds of *L. leucocephala* (Table 2, Fig. 1). This seed predator has emerged also from an introduced *Falcataria moluccana* (Fabaceae) in Taiwan (Table 2) that is native to Moluccas and New Guinea (Polhill 1990; Du Puy *et al.* 2001).

We confirmed that the females can reproduce aphagously (i.e. without any food, such as water, sugar and protein resource). *Acanthoscelides macrophthalmus* emerged from *L. leucocephala* (tribe Mimoseae) was

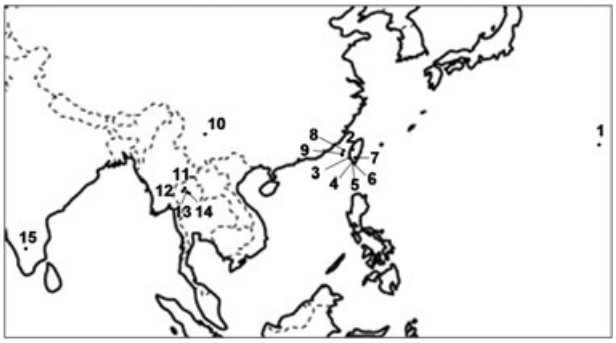

Figure 1 A map of collection sites of *Leucaena leucocephala*, from which *Acanthoscelides macrophthalmus* adults emerged. Numbers correspond to locations listed in Table 2.

able to deposit eggs on and hatching larvae were able to consume the seeds of *L. leucocephala*. We confirmed that adults emerged from these seeds. Likewise, *A. macrophthalmus* females reared on *F. moluccana* (tribe Ingeae) were able to deposit eggs on and hatching larvae were able to consume *F. moluccana* seeds. Furthermore, *A. macrophthalmus* females emerged from *L. leucocephala* seeds were able to deposit eggs and develop into adults on *F. moluccana*.

Conversely, *A. macrophthalmus* emerged neither from species of the same tribe as its host *Leucaena* nor from the species of other tribes (Ingeae and Acacieae) of the same subfamily as *Leucaena* (Table 1). Our review of the published work indicated that *A. macrophthalmus* had high host fidelity to the Neotropical mimosoid genus *Leucaena* not only in native regions but also in introduced regions (Table 3).

Table 2 *Acanthoscelides macrophthalmus* emerged from the seeds of introduced *Leucaena leucocephala* (except the record shown in italic) in South Asia through the Far East Asia

	Location	Country	Collector, date (voucher number, herbarium)
1	Minamitori-shima (Marcus Is.), Ogasawara	Japan†	Morimoto, 16 Jun. 2000 (KUF)
2	Shinyi, Nantou Co.	Taiwan	L.-H. Wu *et al.*, 19 Nov. 2007 (NTUT)
2′	*Shueili, Nantou Co.*	*Taiwan*	*L.-H. Wu et al., 19 Nov. 2007 (NTUT)*
3	Chungshan, Kaohsiung City, Kaohsiung Co.	Taiwan†	Tuda and Chou, 18 Oct. 1995
3	Chungshan, Kaohsiung City, Kaohsiung Co.	Taiwan	Tuda and Chou, 18 Nov. 1999 (9946, KUF)
4	Maopitou, Pingtung Co.	Taiwan	Tuda and Chou, 9 Nov. 1997 (9710, KUF)
5	Kending 1, Pingtung Co.	Taiwan	L.-H. Wu, 10 Jul. 2007 (Dy2007, NTUT)
5	Kending 2, Pingtung Co.	Taiwan	L.-H. Wu, 10 Jul. 2007 (Nw2007, NTUT)
5	Kending 3, Pingtung Co.	Taiwan	L.-H. Wu, 10 Jul. 2007 (Kdf2007, NTUT)
6	Eluuanbi, Pingtung Co.	Taiwan	Tuda and Chou, 17 Nov. 1999 (9933, KUF)
7	Taimali 1, Taitung Co.	Taiwan	L.-H. Wu, 10 Aug. 2007 (NTUT)
7	Taimali 2, Taitung Co.	Taiwan	L.-H. Wu, 10 Aug. 2007 (NTUT)
8	Baisha, Penghu Co.	Taiwan	H.-S. Fang, 10 Sep. 2007 (NTUT)
9	Wangan, Penghu Co.	Taiwan	H.-S. Fang, 10 Sep. 2007 (NTUT)
10	Yuanmou, Yunnan	China†	Zhu, Zhang, Chen and Tuda, 31 Oct. 2004
11	Mt. Doi Suthep, Chiang Mai Prov.	Thailand†	Tuda, Tateishi and Niyomdham, 10 Nov. 1998 (9806, KUF)
11	Mt. Doi Suthep, Chiang Mai Prov.	Thailand	Tuda, Tateishi and Niyomdham, 10 Nov. 1998 (9807, KUF)
12	Mt. Doi Inthanon, Chiang Mai Prov.	Thailand	Tuda, Tateishi and Niyomdham, 11 Nov. 1998 (9818, KUF)
13	Mae Tha, Lamphun Prov.	Thailand	Tateishi, Tuda and Niyomdham, 13 Dec. 1999 (52111, URO)
14	Hang Chat, Lampang Prov.	Thailand	Tuda and Buranapanichpan, 16 Dec. 2003 (0315, KUF)
14	Hang Chat, Lampang Prov.	Thailand	Tuda and Buranapanichpan, 16 Dec. 2004 (0451, KUF)
15	Coimbatore, Tamil Nadu	India†	Murugan, 14 Mar. 2005

†New country records. Italics indicate the host is *Falcataria moluccana* instead of *L. leucocephala*. KUF, Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka, Japan; NTUT, National Taiwan University, Taipei, Taiwan (NTUT); URO: University of the Ryukyus, Nishihara, Okinawa, Japan.

Table 3 Review of host plants and geographical distribution of *Acanthoscelides macrophthalmus*

Host plant	Distribution	Status
Falcataria moluccana (Miq.) Barneby & J.W. Grimes **I**†	Taiwan (present study)†	I
Leucaena collinsii Britton & Rose **M**	Guatemala (HJ88, Johns89)	N
L. confertiflora Zárate **M**	Mexico (HJ)	N
L. esculenta (DC.) Benth. **M**	Mexico (Johns79)	N
L. greggii S. Watson **M**	Mexico (HJ)	N
L. lanceolata S. Watson **M**	Mexico (Johns79)	N
L. leucocephala (Lam.) de Wit **M**	Taiwan (present study)	I
	Yunnan, China (present study)†	I
	Thailand (present study)†	I
	India (present study)†	I
	Ogasawara, Japan (present study)†	I
	Vietnam (K)	I
	Senegal (DJ)	I
	South Africa (ARC)	I
	Australia (J)	I
	Mexico (HJ88)	N
(as *L. glauca* Benth.)	Mexico (PJ)	N
L. macrophylla Benth. **M**	Mexico (Johns79)	N
L. magnifica (C.E. Hughes) C.E. Hughes **M**	Guatemala (HJ)	N
L. multicapitula Schery **M**	Costa Rica (HJ)	N
L. pallida Britton & Rose **M**	Mexico (HJ)	N
L. pulverulenta (Schltdl.) Benth. **M**	USA (Johns79)	N
L. retusa Benth. **M**	USA (Johns79)	N
L. salvadorensis Britton & Rose **M**	El Salvador (Johns79)	N
L. shannonii Donn.Sm. **M**	Mexico (HJ88)	N
	Guatemala (HJ88)	N
L. trichandra (Zucc.) Urban **M**	Guatemala (HJ88)	N
L. trichodes (Jacq.) Benth. **M**	Honduras (HJ)	N

Status: N, native, **I**, introduced. †New host and/or country records. Tribe names: **I**, Ingeae, **M**, Mimoseae. ARC: ARC-PPRI (2003); DJ: Delobel and Johnson (1998); HJ88: Hetz and Johnson (1988); HJ: Hughes and Johnson (1996); Johns79: Johnson (1979); Johns89: Johnson (1989); J: Jones (1996); K: Kergoat *et al.* (2005); PJ: Pfaffenberger and Johnson (1976).

DISCUSSION

Host range of *Acanthoscelides macrophthalmus*

To our knowledge, *F. moluccana* is the first and only host for *A. macrophthalmus* besides *Leucaena* species. In contrast to its current wide geographical distribution, the diet breadth of *A. macrophthalmus* has remained narrow, utilizing almost only the Neotropical genus *Leucaena* except *Falcataria* (Table 3). The present result indicates that the bruchine seed predator has the potential to host shift to other mimosoid legumes. Utilization of the two different mimosoid tribes (i.e. Mimoseae and Ingeae) by a single species population is observed in a few other New World bruchines (appendix in Kergoat *et al.* 2007a), inferring that the host shift from *Leucaena* to *Falcataria* was not unpredictable. In fact, *Leucaena* is more closely related to Ingeae than to basal Mimoseae members, such as *Adenanthera* and *Entada*, according to recent molecular phylogenetic studies (Luckow *et al.* 2003; Sulaiman *et al.* 2003).

Falcataria moluccana is a multipurpose beneficial tree that has been spread to South-East Asia, India, China and Indian Oceanic Islands and introduced to tropical Africa and Pacific Islands including the Hawaiian Islands (Duke 1983; ILDIS World Database of Legumes, ver. 10.01, http://www.ildis.org). Climatic requirements of *F. moluccana* overlap with those of *L. leucocephala*, with the latter species tolerating colder and drier conditions as well (Duke 1983). Therefore, coexistence of the two species and consequent host shift by *A. macrophthalmus* are possible in the aforementioned introduced regions, if the seed predator has already invaded them.

Invasion of Asia by *Acanthoscelides macrophthalmus*

Acanthoscelides macrophthalmus has invaded widely across island and continental South Asia through the Far East, where its host *L. leucocephala* had been established

(Table 2). *Acanthoscelides macrophthalmus* has already been acknowledged to have invaded West Africa, feeding on the host plant (Delobel & Johnson 1998). In South Africa, this bruchine species has been deliberately introduced for control of *L. leucocephala* since 1999 (ARC-PPRI 2003; Olckers 2004). This is probably the first record of *A. macrophthalmus*' invasion of the Far East and South Asia and one of the earliest records of its invasion of Eurasia and Pacific Islands.

Acanthoscelides macrophthalmus is likely to have been introduced with *L. leucocephala* seeds, judging from the following three reasons: (i) it is specialized to *Leucaena* species in its native range (Table 3); (ii) *L. leucocephala* is the only *Leucaena* species that has been introduced to Asia; and (iii) airborne long-distance dispersal is highly unlikely in bean beetles (see references in Tuda *et al.* 2001).

Suitability of *A. macrophthalmus* as a control agent of *L. leucocephala*

Many leguminous plants serve as ornamentals, green manure, land cover, food crop and for erosion control. Human transportation of the seeds of such economic legumes can expand the distribution of not only the plants themselves (e.g. *Acacia mearnsii*, *Cytisus scoparius*, *Mimosa pigra*, *Prosopis glandulosa*, and *Pueraria montana* var. *lobata*) but also their internal seed predators like bruchines, protected and concealed inside the seeds. A recent example is the North American *Acanthoscelides pallidipennis* infesting *Amorpha fruticosa* seeds introduced to Europe and East Asia (Szentesi 1999; Tuda *et al.* 2001). Endophages tend to have narrower diet breadth than ectophages (Lewinsohn 1991; Gaston *et al.* 1992; Frenzel & Brandl 1998, but see Okamoto *et al.* 2008 for an example of the host range of ectophagous insects) and therefore are probably more suitable as biological control agents. Indeed, bruchine beetles have been suggested (Southgate 1979) and used as control agents of weedy plants (Julien 1992; van Klinken 2005; review in Tuda 2007). Furthermore, the present study indicates the possibility that *A. macrophthalmus* plays a twofold role of a pre- and post-dispersal seed predator.

Nevertheless, there remains a concern about the efficacy of *A. macrophthalmus* as a control agent: unexpected host expansion. Potential new host plants may not be indigenous but introduced ones as in the case of the bruchine control agent of *C. scoparius* (Fowler *et al.* 2000). Future experimental and observational studies are needed to clarify the ecology of host utilization and parasitoid accumulation process of *A. macrophthalmus* for effective biocontrol of the invading *L. leucocephala* that has become a pantropic species.

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