ELSEVIER

Available online at www.sciencedirect.com
SCIENCE DIRECT®

Journal of Stored Products Research 41 (2005) 31–45

Journal of
STORED
PRODUCTS
RESEARCH

www.elsevier.com/locate/jspr

Ecological factors associated with pest status in *Callosobruchus* (Coleoptera: Bruchidae): high host specificity of non-pests to Cajaninae (Fabaceae)

M. Tuda[a,]*, L.-Y. Chou[b], C. Niyomdham[c], S. Buranapanichpan[d], Y. Tateishi[e]

[a] *Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka 812-8581, Japan*
[b] *Department of Applied Zoology, Taiwan Agricultural Research Institute, Taichung, Taiwan 413, China*
[c] *Royal Forest Department, The Forest Herbarium, Chatuchak, Bangkok 10900, Thailand*
[d] *Department of Entomology, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand*
[e] *College of Education, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan*

Accepted 9 September 2003

Abstract

Larval host plants of six *Callosobruchus* species (Coleoptera: Bruchidae), including pest species, were discovered by collecting the seeds of wild (or inedible) and cultivated edible legumes in the field in Taiwan, Thailand, continental China, Myanmar, Nepal and the Philippines. A close relationship between Asian *Callosobruchus* species and the leguminous subtribe Cajaninae was revealed: *Rhynchosia* species were commonly used by three *Callosobruchus* species, wild and cultivated species of *Cajanus* and two *Dunbaria* species, respectively, by single species. Two Taiwanese species were confirmed to be conspecific with continental species. We further reviewed host legumes of 11 species of *Callosobruchus* including nine species of pests. There were significant positive correlations between geographic distribution range and host range at all three taxonomic levels of hosts. Principal component analysis on geographic distribution range, host range, altitude of distribution, utilizations of cultivated hosts, of Cajaninae and of Phaseolinae showed that the first axis (PC1) described 52% of total variance, which was related significantly with the frequencies of utilization of cultivated legumes (0.93), and of Cajaninae (*Cajanus*, *Dunbaria* and *Rhynchosia*) (−0.85). PC1 was also positively correlated with the frequency of utilization of Phaseolinae (*Vigna* and *Lablab*) (0.68), geographical range (0.67) and with host range (0.67) before Bonferroni corrections. Contrary to the polyphagy of the widely distributed pest *Callosobruchus*, non-pest species exhibited fidelity to single specific genera of wild or inedible legumes, and pests with limited distribution are specific to leguminous subtribes. Non-pests are characterized by tight association with Cajaninae. We concluded that specialization to non-economic Cajaninae prevents a species of *Callosobruchus* from becoming a pest of cultivated legumes.

---

*Corresponding author. Tel.: +81-92-642-3038; fax: +81-92-642-3040.
E-mail address: tuda@grt.kyushu-u.ac.jp (M. Tuda).

0022-474X/$ - see front matter
doi:10.1016/j.jspr.2003.09.003

Keywords: Host specificity of bean weevils; Leguminosae; Plant-insect relation; *Callosobruchus chinensis*; *Callosobruchus maculatus*

---

1. Introduction

Understanding ecological characters associated with pests is crucial not only for pest control but also for prediction of insects that have potential to become pests. While polyphagy and wide geographical distribution are common properties of stored-product pests, oligophagy is most ubiquitous in herbivorous insects. Selective pressures on diet breadth, or host range, have been proposed and discussed in recent years (e.g. Strong et al., 1984; Jaenike, 1990; Bernays and Chapman, 1994). Comparisons between closely related species have been effective in elucidating a set of characters associated with pests for this purpose.

Among stored-product pests, species of the genus *Callosobruchus* Pic (Coleoptera: Bruchidae) seriously damage beans or legume seeds, especially in warm parts of the Old World from which it originates (Borowiec, 1987; Udayagiri and Wadhi, 1989; Singal and Pajni, 1990). *Callosobruchus*, comprising at least 20 species, about three quarters of which are from Asia, is well studied for a few stored-bean pests, i.e. *Callosobruchus maculatus* (F.) and *Callosobruchus chinensis* (L.). These pest species have been reported from economic legumes and non-leguminous crops that are not necessarily their natural hosts. Economic edible legumes include a variety of beans (*Vigna*, *Phaseolus*, *Glycine*, *Lablab*, *Vicia*), peas (*Pisum*, *Cicer*, *Lens*, *Cajanus*), and peanut (*Arachis*), all of which are attacked by *Callosobruchus* pests under agronomic conditions. The bias in host information toward the pest species feeding on commercial edible seeds in the genus has prohibited a general understanding of the natural association of *Callosobruchus* species with their legume hosts.

The taxonomy and biology of beetles in the family Bruchidae have been studied in a unified effort in the New World (Southgate, 1979 and references therein), while the Old-World bruchids are either largely left unidentified or studied regionally (Japan and Taiwan by Chujo, 1937a,b; Morimoto, 1990; France by Hoffmann, 1945; Russia by Lukjanovich and Ter-Minassian, 1957; Egorov and Ter-Minassian, 1983; India by Arora, 1977; China by Juanjie et al., 1980; a review by Borowiec, 1987). As is typical of the life history of Bruchidae, larvae of *Callosobruchus*, an Old World genus, burrow into the legume seeds after hatching, consume the cotyledons, pupate, eclose as adults within the single seed, and emerge. Larval host plants remain unknown for most species in these regions (Udayagiri and Wadhi, 1989), partly because collections of these beetles are usually made by net-sweeping adults, which often feed on non-larval host plants as a source of nectar. The excellent review of Johnson (1981) sums up the present state of knowledge: the hosts of *Callosobruchus* belong predominantly confined to the leguminous tribe Phaseoleae (78.9% of reported feedings), in which the subtribe Phaseolinae is the most frequently used (64.4%), followed by the subtribes Cajaninae (7.7%) and Glycininae (6.7%). Most of the remaining records are from the tribe Fabeae (or Vicieae, 15.6%), which is in part due to an adaptation to agronomic practices (Johnson, 1981).

Our specific objective is to assess key ecological factors associated with cosmopolitan agricultural pests using *Callosobruchus*, which includes both pests and non-pests of legume seeds, as a model. To quantify biological and environmental interactions in each species, a reliable data set of host and distribution records is constructed, based on our investigation of larval host plants of *Callosobruchus* under natural and semi-natural conditions and a review of the literature.

2. Material and methods

2.1. Collection and identification

Mature seeds in pods of legumes from all three subfamilies, Papilionoideae, Mimosoideae and Caesalpinioideae (Fabaceae), were collected from the following Asian countries: Taiwan, Thailand, continental China, Myanmar, Nepal and the Philippines. Either about 80% of local populations or 1000 seeds, whichever was fewer, were collected from local populations of legumes. The bruchids emerging from these seeds were identified by comparison with holotypes and paratypes in the Natural History Museum London, the Museum National d'Histoire Naturelle, Paris, the National Museum of Natural History, Smithsonian Institution, Washington, DC, and the Laboratory of Entomology, Kyushu University, Fukuoka. The *Callosobruchus* species obtained in the Philippines was a female and identified based on a mitochondrial gene sequence.

2.2. Literature review on association with hosts

We reviewed the literature on *Callosobruchus* host legume associations and geographical distribution, taking into special account the geographical information of old records. For example, many cultivated varieties of legumes had been classified as independent species; old records of several cultivar 'species' of *Vigna* were here grouped into a single species, *Vigna unguiculata* (L.) Walp. Also, many *Phaseolus* species were renamed as *Vigna*, according to the present nomenclature. Host records without geographical information (c.f. Zacher, 1952) were omitted. Even with geographical information, records were excluded when hosts were not native to the regions and it was suspected that they were commercially imported from abroad (e.g. Luca, 1962). Experimental combinations of bruchids and hosts were also omitted (e.g. Bridwell, 1918). Records of *C. maculatus* and *C. chinensis* from *Vigna umbellata* (Thunb.) Ohwi et Ohashi in Myanmar (Ghosh, 1937), are doubtful because experimental results on the suitability of various *Vigna* species as hosts show that neither *C. maculatus* nor *C. chinensis* survived when fed on the wild and cultivated varieties of *V. umbellata* (Tomooka et al., 2000). Therefore, we did not include records from Ghosh (1937).

All insect specimens were deposited in the Laboratory of Entomology, Faculty of Agriculture, Kyushu University, Fukuoka, Japan. All seed specimens were retained by the first author and the plant specimens were deposited in the Herbarium of the Biological Institute, Tohoku University, Japan, the Herbarium of the College of Education, the University of the Ryukyus, Japan, and the University Museum, University of Tokyo, Japan. Plant specimens from Thailand were also deposited in the Herbarium of the Royal Forest Department, Chatuchak, Bangkok, Thailand.

2.3. Statistical analysis

A principal component analysis (PCA) was performed on the following variables: the number of tribes of first recorded hosts from different countries, the number of the records from different biogeographic regions from different tribes, the frequency of utilization of cultivated legumes, the frequency of utilization of the legume subtribe Phaseolinae (tribe Phaseoleae), the frequency of utilization of the legume subtribe Cajaninae (tribe Phaseoleae), and the mean altitude of distribution. Altitudes for records of distribution in Table 1 were used in the analysis and for those from Appendix A, means of the altitudes of 20 randomly chosen sites were applied, i.e. 951 m for Angola, 402 m for Cuba, 155 m for Ghana, 780 m for Oahu, Maui and Hawaii Islands, 315 m for Oahu, Molokai and Laysan Islands, 488 m for Oahu and Maui Islands, 649 m for India, 147 m for India and Sri Lanka, 415 m for Indonesia (Java), 243 m for Israel, 197 m for Mascarene Islands, 346 m for Niger, 559 m for Nigeria, 29 m for Senegal, 577 m for Sudan, 1046 m for Taiwan and China (Guizhou Province), 976 m for Tanzania, 1101 m for Uganda, 1121 m for Zambia and Zimbabwe, and 1214 m for Zimbabwe. Altitudes for no specific locality in such large regions as China, North America and Brazil were omitted in the analysis. Frequencies were calculated as arcsine transformed ratios to the total records. A Bonferroni multiple comparison was applied using $\alpha = 0.0045$ for PCA.

To test which taxonomic level of hosts contributes to expansion of distribution of *Callosobruchus* species, Spearman rank correlations were calculated between biogeographic range and host range at different hierarchical levels of host taxons. The rank correlation was also derived between variables used in PCA.

3. Results

Host and geographical distribution: Of more than 80 legume species collected, 11 species were identified as hosts of *Callosobruchus* (Table 1). Eight of these species belong to the subtribe Cajaninae and were widely used by *Callosobruchus* species; two *Dunbaria* species were utilized by *Callosobruchus utidai* Tuda (Tuda, 2003), *Rhynchosia minima* (L.) DC. f. *nuda* (DC.) Ohashi et Tateishi by *C. chinensis*, wild species of *Rhynchosia* and *Cajanus* by *Callosobruchus theobromae* (L.), two *Rhynchosia* species by *Callosobruchus latealbus* (Pic) and *Cajanus cajan* (L.) Millsp. by *Callosobruchus pulcher* (Pic) (Table 1). *Callosobruchus chinensis* was discovered in tropical Taiwan, *C. theobromae* in tropical Asia, *C. latealbus* in the East Asian highlands (200–1500 m), *C. utidai* in the South-Asian highlands (800–1200 m), *Callosobruchus* imitator Kingsolver from South Asian *Vigna* in the highlands (500–1500 m), and *C. pulcher* in the Philippines and in Hawaii (Table 1). Two Taiwanese species, *Callosobruchus taiwanensis* Chujo and *Callosobruchus albobasalis* Chujo, were confirmed to be conspecific with the continental species *C. theobromae* and *C. latealbus*, respectively. Based on the new distribution information and the synonymy, the distribution of *C. latealbus* is extended to Taiwan and that of *C. theobromae* to Taiwan and Thailand (Appendix A).

The number of biogeographic regions of distribution was positively correlated with host taxonomic groups at all three levels examined; genera ($r_s = 0.909$; $n = 11$; $P < 0.001$), tribes ($r_s = 0.897$; $n = 11$; $P < 0.001$), and subfamilies ($r_s = 0.747$; $n = 11$; $P < 0.02$) (Fig. 1). Frequency

Table 1
A list of host plants and distribution of *Callosobruchus* beetles that are studied in Asia

Bruchid beetle	Host plant	Locality of host plant (Collector, No., Date, Herbarium[a])
Callosobruchus chinensis (L.)	*Rhynchosia minima* (L.) DC. f. *nuda* (DC.) Ohashi et Tateishi*	Oluanpi, Pingtung, Taiwan, alt. ca. 100 m (Ohashi et al., 14630, 5 Nov., 1982, TUS) (Tuda, 15 Nov., 1995) Maopitou, Pingtung, Taiwan, alt. ca. 50 m (Tuda 62, 19 Oct., 1995, URO) (Tuda, 159, 9 Nov., 1997, URO)
Callosobruchus imitator Kingsolver	*Vigna angularis* (Willd.) Ohwi et Ohashi*	Ban Mae Sapok, Chiang Mai, Thailand, alt. ca. 1500 m (Buranapanichpan, Nov., 1999)
	V. umbellata (Thunb.) Ohwi et Ohashi	Anisakan, Pynoolwin, Mandalay Div., Myanmar*, alt. 800 m (Murata et al., 387, 8 Nov., 1999, TI, URO) Pang Mapha Distr., Mae Hong Son, Thailand, alt. ca. 800 m (Tuda et al., 65, 16 Dec., 1999)
	V. unguiculata (L.) Walp.	Pai, Mae Hong Son, Thailand, alt. ca. 500 m (Tateishi et al., 12 Nov., 1998)
Callosobruchus latealbus (Pic) (= *Callosobruchus albobasalis* Chujo)	*Rhynchosia volubilis* Lour.*	Chimei, Hualien, Taiwan*, alt. 200 m (Tateishi et al., 15685, 19 Nov., 1982, TUS) Mt. Ali-shan, Chiayi, Taiwan, alt.1450 m (Tateishi et al., 17946, 20 Aug., 1984, TUS) Wushantou, Tainan, Taiwan, alt. ca. 200 m (Tuda, 13 Nov., 1995)
	Rhynchosia acuminatifolia Makino*	Anlong, Guizhou Prov., China, alt. ca. 1200 m (Wu et al., 100134, 14 Oct., 1998, URO)
Callosobruchus theobromae (L.) (= *Callosobruchus taiwanensis* Chujo)	*Rhynchosia rothii* Benth. ex Aitch.*	Maopitou, Pingtung, Taiwan*, alt. ca. 50 m (Tateishi et al., 25221, 2 Nov., 1988, TUS and URO) Kenting, Pingtung, Taiwan, alt. 100–200 m (Tateishi et al., 25320, 4 Nov., 1988, TUS and URO)
	Cajanus scarabaeoides (L.) Thouars*	Maopitou, Pingtung, Taiwan, alt. ca. 50 m (Tuda, 14 Nov., 1995) Thoen, Lampang, Thailand*, alt. 190 m (Tateishi et al., 14 Nov., 1998) Mae Tha, Lamphun, Thailand, alt. ca. 300 m (Tateishi et al., 52101, 13 Dec., 1999, URO)
Callosobruchus utidai Tuda	*Dunbaria rotundifolia* (Lour.) Merr.*	Choyang–Poluwa Khola, Nepal*, alt. 800 m (Tateishi 8523, 9 Nov., 1981, TUS)
	Dunbaria podocarpa Kurz*	Mt. Doi Inthanon, Chiang Mai, Thailand*, alt. 1100–1200 m (Tateishi et al., 52192, 15 Dec., 1999, URO)
Callosobruchus pulcher (Pic)	*Cajanus cajan* (L.) Millsp.*	Batangas Prov., Luzon Isl., Philippines, alt. ca. 300 m (Nemoto et al., 10063, 26 Oct., 1998, TUS) Waimanalo, Oahu Isl., Hawaii, USA, alt. ca. 50 m (Tuda et al., 13 Feb., 2003)

Collection sites are Taiwan, Thailand, mainland China, Myanmar, Nepal and the Philippines. Unless otherwise noted, host species belong to the Leguminosae. Asterisks indicate new records of the bruchid species from the host or from the country. All insect specimens are deposited in the Laboratory of Entomology, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.

[a] Herbarium; TUS: Herbarium of the Biological Institute, Tohoku University, Sendai, Japan; URO: Herbarium of the College of Education, the University of the Ryukyus, Nishihara, Okinawa, Japan; TI: University Museum, University of Tokyo, Hongo, Tokyo, Japan.

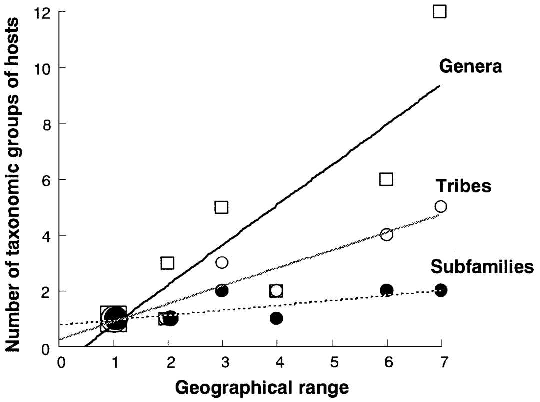

Fig. 1. Relation between ranges of hosts and geographic distribution in *Callosobruchus* beetles at different taxonomic levels; open squares indicate the numbers of host genera used by each species of *Callosobruchus*, open circles the numbers of host tribes, and closed circles the numbers of host subfamilies. Geographical range refers to the number of biogeographic regions of *Callosobruchus* species as shown in Table 2. The size of symbols refers to the number of data points overlapped.

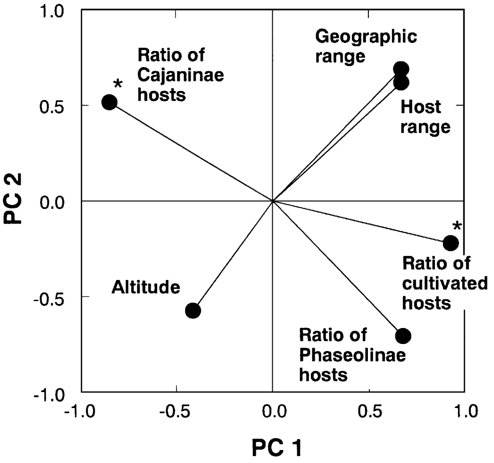

Fig. 2. Principal component analysis on variables for host range and geographic distribution in *Callosobruchus* species. The asterisks indicate variables significantly correlated with the first axis (PC1), after Bonferroni correction for multiple comparison.

of utilization of cultivated hosts was positively correlated with that of Phaseolinae ($r_s = 0.770$; $n = 11$; $P < 0.01$) and negatively with that of Cajaninae ($r_s = -0.820$; $n = 11$; $P < 0.005$). Utilizations of Phaseolinae and of Cajaninae were negatively correlated ($r_s = -0.961$; $n = 11$; $P < 0.001$).

Principal component analysis based on the records of bruchid-host association for each country (Fig. 2, Appendix A) showed that the first axis (PC1) described 52.1% of total variance (eigenvalue 3.13), which was related with the frequencies of utilization of cultivated legumes (0.930; $n = 11$; $P < 0.001$), of utilization of the legume subtribe Cajaninae (-0.848; $n = 11$; $P < 0.001$), of utilization of Phaseolinae (0.680; $n = 11$; $P < 0.02$), and the numbers of biogeographic regions (0.672; $n = 11$; $P < 0.02$) and tribes utilized (0.675; $n = 11$; $P < 0.02$) (Fig. 2). The second axis (PC2) described 33.3% total variance (eigenvalue 2.00), which was related with the frequency of utilization of Phaseolinae (-0.706; $n = 11$; $P < 0.01$), the numbers of biogeographic regions (0.687; $n = 11$; $P < 0.01$) and tribes utilized (0.618; $n = 11$; $P < 0.05$), and with altitudes (-0.576; $n = 11$; $P < 0.05$). Following Bonferroni corrections on multiple comparisons, the frequencies of utilization of cultivated legumes and of utilization of Cajaninae were significantly correlated with PC1, and none of the variables were significantly correlated with PC2.

4. Discussion

Utilization of a wide range of hosts and expansion of geographical distribution are associated ecological properties in *Callosobruchus* species (Fig. 1, Appendix A). Specifically, the widely distributed pests, *C. chinensis* and *C. maculatus*, by using non-Phaseoleae besides their original hosts belonging to the Phaseoleae, may have succeeded in being introduced to non-native regions. Such correlation between host range (or diet niche breadth) and geographic range size in phytophagous insects has been proposed by macroecological studies (e.g. Brändle et al., 2002). Insects often shift host preference across space (Leather, 1991; Thompson, 1994) and host range expansion at species level may better be interpreted as host shifts at local population level. This geographic range-host range association will be discussed further in Section 4.2.

The strong negative correlation between utility of the two host subtribes indicates that each *Callosobruchus* species is specific to a host subtribe. Pests are best defined by their heavy utilization of cultivated crops. This definition automatically associates Phaseolinae-feeding bruchids with pests because most legumes cultivated for food belong to the Phaseolinae, whereas Cajaninae-feeding bruchids are non-pests. The present analysis supports this prediction. In spite of such host specificity, only pests succeeded in expanding host range even to different subfamilies and families. A possible factor for this biased host expansion will be suggested in Section 4.1.

4.1. Host specificity (Table 2)

Contrary to the polyphagy of pest *Callosobruchus* species, non-pest species show fidelity to a specific genus of wild or inedible legumes (i.e. *C. latealbus* to *Rhynchosia* and *C. utidai* to *Dunbaria*) and locally distributed pests show fidelity to single leguminous subtribes (i.e. *C. theobromae* to Cajaninae, and *Callosobruchus rhodesianus* (Pic) and *C. imitator* to Phaseolinae) (Table 2, Fig. 2). Even in widely distributed pest species, their natural host ranges are within tribes of legumes, as in *C. chinensis* utilizing *Vigna* and *Cajanus* of the tribe Phaseoleae. Among *Callosobruchus* pests, species that have worldwide distribution are characterized by their utilization of wide ranges of hosts (Fig. 1). Expansion of host range can be due to the ability to feed and develop in dry, mature stage of hosts that are harder but contain reduced

Table 2
Summary of the numbers of records of geographical distribution and hosts of *Callosobruchus* species based on the data in Appendix A

Species	Geographical distribution							Host subtribes/tribes					
	TempNW	Neotrop	Afrotrop	MidEast	IndoChina	TropAsia	TempOW	Phaseol	Cajanin	Glycin	Fabeae	Cicer	Others
Widely distributed pests													
C. chinensis	3	1	1	5	19 (1)	3	3 (2)	14 (1)	7 (2)	1	6	4	3
C. maculatus	—	1	2	6	6	2	1	9	3	0	3	2	1
C. analis	—	—	3	—	7	2	—	5	1	2	0	3	1
C. phaseoli	—	3	3	1	2	—	—	8	0	0	0	1	0
Locally distributed pests													
C. theobromae	—	—	—	—	6 (3)	1	—	0	5 (3)	2	0	0	0
C. imitator	—	—	—	—	5	—	—	5	0	0	0	0	0
C. pulcher	—	1	—	—	—	1	—	0	2	0	0	0	0
C. subinnotatus	—	—	4	—	—	—	—	4	0	0	0	0	0
C. rhodesianus	—	—	2	—	—	—	—	2	0	0	0	0	0
Non-pests													
C. latealbus	—	—	—	—	4 (2)	—		0	2 (2)	0	0	0	0
C. utidai	—	—	—	—	2 (2)	—	—	0	2 (2)	0	0	0	0

TempNW: temperate New World, Neotrop: Neotropical, Afrotrop: Afrotropical, MidEast: Middle East, Tropical Asia, TempOW: temperate Old World. Phaseol: Phaseolinae, Cajanin: Cajaninae, Glycin: Glycininae, Cicer: Cicerieae. Phaseolinae, Cajaninae and Glycininae are subtribes in the tribe Phaseoleae. Numbers in parentheses indicate the numbers of reported associations with wild hosts.

allelochemicals, compared to young developing stage. This hypothesis should be tested in the future.

At the genus level, *Rhynchosia* and *Dunbaria* are frequently used as hosts not only by non-pests but also by pest species of *Callosobruchus* (Table 1, Appendix A). *Dunbaria* here for the first time recognized as a common wild host genus for *Callosobruchus*, and the close relationship between the Asian *Callosobruchus* species and the Cajaninae legumes are also revealed by the present study for the first time. The statement of Johnson (1981) that the hosts of *Callosobruchus* belong predominantly to the leguminous tribe Phaseoleae remains true.

4.2. Geographical distribution and host utilization (Table 2 and Appendix A)

As mentioned, host utilization cannot be considered separately from geographical distribution. Non-pests and some pest species with a limited distribution are characterized by association with the leguminous subtribe Cajaninae (i.e. *C. latealbus*, *C. utidai*, *C. theobromae*, and *C. pulcher*) (Table 2).

The Asian *Callosobruchus* species such as *C. latealbus* and *C. utidai* are not pests at the present because of their host specialization on Cajaninae (Table 2). This is probably because most species of Cajaninae are distributed only locally and have minor economic importance: *Dunbaria rotundifolia* (Lour.) Merr. and *Dunbaria podocarpa* Kurz are planted for medical use, *Cajanus scarabaeoides* (L.) Thouars for groundcover (in Australia), green manure (in Java) and medicine (Kondo et al., 1987). If the Cajaninae, by development and selection of cultivated varieties, attain greater universal economic importance, the current non-pest species will have the potential to become new pests. In Africa, *Bruchidius* and *Caryedon* species are predominant, feeding on its rich Mimosoideae (e.g. *Acacia*) and Caesalpinioideae (e.g. *Cassia*) flora and these bruchid genera are hardly observed to attack Phaseoleae legumes of the subfamily Papilionoideae. If Asian leguminous crops, represented by Phaseoleae, were introduced to Africa, they would not be attacked by the indigenous bruchids that feed on Mimosoideae and Caesalpinioideae but instead by indigenous and/or co-introduced *Callosobruchus* (e.g. Nahdy et al., 1998).

The current restricted distribution of some *Callosobruchus* species seems to reflect their limited physiological capability to withstand environmental variability to expand their host range. Three pest and non-pest species utilizing *Rhynchosia* as hosts can be compared in this respect. *Callosobruchus chinensis* utilizes pantropical *R. minima* and the other two natural hosts which do not overlap in geographical distribution. The distribution of *C. chinensis* is determined by its ability to withstand a wide range of temperatures and hosts. Yet, such species may better be considered as a mosaic of host-associated populations, each genetically differentiated (Tuda et al., 2003). The locally distributed pest *Callosobruchus theobromae* uses *Rhynchosia rothii* Benth. ex Aitch. and *Cajanus scarabaeoides*, both of which inhabit Indo-Malaya, with the latter species having a wider distribution extending to southern China and Australia. Since *C. theobromae* is not present in Australia (Appendix A), the present distribution of this bruchid may better be attributed to biogeographical history or physiological limits than to current host distribution. Nevertheless, it is quite possible that the locally distributed pest will catch up with the host distribution in the near future, if the host beans are frequently transported from its current habitat in Asia to Australia. *Callosobruchus latealbus*, utilizing *Rhynchosia*, was found only in the highlands of China, although the hosts are distributed widely from temperate to tropical regions in East Asia. Moreover, the temperate *Rhynchosia volubilis* Lour. has not yet been observed to be attacked by a bruchid (Tuda, personal observation). There may be a trade-off between reproductive ability and/or adaptation to environmental variation for habitat expansion and adaptation to the chemical composition of its host in such phytophagous insects, because *C. latealbus* is adapted to feed on the seeds of *R. volubilis*, known as an Oriental medicine and insecticide (Kondo et al., 1987).

4.3. Taxonomic consideration

In India *C. maculatus* has been misidentified as *C. analis* (Haines, 1989), while *C. imitator* may have been misidentified as *C. maculatus* and *C. analis* based on the elytral pattern and its utilization of commercial *Vigna* seeds in subtropical Asia, although its male genitalia are longer and more slender in comparison with the other two species.

In summary, the present study indicates that the high specificity of non-pest *Callosobruchus* to the legume subtribe Cajaninae prevents these species from becoming pests under current agricultural conditions. Because a future reduction in agricultural productivity induced by monoculture and intensive chemical use is anticipated, seeds of presently non-economic plant species may be utilized as new commercial food items. The results of this study impact on future screening of potential pest species of post-harvest legumes that would attain economic importance during expansion of human resources in Asia and in areas where these legumes are introduced.

Acknowledgements

We thank V. Bunsawat, S. Chatupamai, K. Chou, T. Jonganurak, C. Kamrat, S. Khaiam, P. Panyarat, W. Worn for cooperating in collecting legumes and obtaining permission for collecting legumes in national parks in Taiwan and in Thailand. Our sincere thanks also go to K. Kiritani and Y.I. Chu for their guide to the fauna of Taiwan, to T. Nemoto for providing collection information and to N. Berti, M. Cox, S. Shute and R. Thompson for their supervision at the Museum National d'Histoire Naturelle, Paris, and the Natural History Museum, London. K. Morimoto provided practical advice on the taxonomy of Bruchidae. This study was supported by the Fujiwara Natural History Foundation, the Sumitomo Foundation, and Grant-in-Aids for International Scientific Research (Field Research 09041145) and for Scientific Research (A)(08304049, 15208007), (B)(14405003) and for Young Scientists (B)(15770011) from MEXT.

Appendix A

Literature records on the host plants and distribution of *Callosobruchus* beetles. Only the first records of hosts for each country are listed. Unless otherwise stated, host species belong to the Leguminosae. Wild or inedible legumes are typed in bold (Table 3).

Table 3

Bruchid beetle	Host plant	Country recorded
Widely distributed pests		
Callosobruchus analis (F.)	*Acacia nilotica* (L.) Del. (as *Acacia arabica*)	Sudan (Peake, 1952)
	Cajanus cajan (L.) Millsp.	India (Arora, 1977)
	Cicer arietinum L.	Zambia and/or Zimbabwe (Mukherji and Chatterjee, 1951), India (Arora, 1977), Tanzania (Southgate, 1978)
	Glycine max (L.) Merr.	India (Arora, 1977), Indonesia (Java) (Haines, 1989)
	Vigna aconitifolia (Jacq.) Maréchal (as *Phaseolus aconitifolius*)	India (Arora, 1977)
	V. radiata (L.) Wilczek (as *Phaseolus aureus*)	Indonesia (Java) (Haines, 1989), India (Arora, 1977)
	V. unguiculata (L.) Walp. (as *V. catjang*)	India and Sri Lanka (Mukherji and Chatterjee, 1951)
	V. unguiculata var. *sesquipedalis* (L.) Ohashi (as *V. sinensis*)	India (Arora, 1977)
Callosobruchus chinensis (L.)	*Cajanus cajan* (L.) Millsp. (as *C. indicus*)	India (Mathur et al., 1958, Arora, 1977), Uganda (Nahdy et al., 1998), North America (Cushman, 1911), Brazil (Bondar, 1936), India and Sri Lanka (Mukherji and Chatterjee, 1951)
	Cassia javanica L.	India (Mathur et al., 1958)
	Cicer arietinum L.	North America (Cushman, 1911), India and Sri Lanka (Mukherji and Chatterjee, 1951), India (Mathur et al., 1958), Israel (Anton et al., 1997)
	Cyamopsis tetragonoloba (L.) Taubert	India and Sri Lanka (Mukherji and Chatterjee, 1951)
	Dunbaria villosa **(Thunb.) Makino**	**Japan** (Shinoda et al., 1991)
	Glycine max (L.) Merr. (as *G. hispida*)	Indonesia (Java) (Haines, 1989)
	Lens culinaris Medikus (as *L. esculenta*)	Israel (Anton et al., 1997), India and Sri Lanka (Mukherji and Chatterjee, 1951)
	Pisum sativum L.	India and Sri Lanka (Mukherji and Chatterjee, 1951), Israel (Anton et al., 1997)
	Rhynchosia minima **(L.) DC.**	**Taiwan** (present study)
	Senna tora (L.) Roxb. (as *Cassia tora*)	India (Arora, 1977)
	Vicia faba L.	China (all Provinces) (Juanjie et al., 1980), Israel (Anton et al., 1997)
	Vigna aconitifolia (Jacq.) Maréchal (as *Phaseolus aconitifolius*)	India and Sri Lanka (Mukherji and Chatterjee, 1951)
	V. angularis (Willd.) **Ohwi et Ohashi** (as *Phaseolus angularis*) (as *P. radiatus*)	China (all Provinces) (Juanjie et al., 1980), Japan (Utida, 1941)
	V. angularis **var.** ***nipponensis*** (Ohwi) Ohwi et Ohashi	**Japan** (Shinoda et al., 1991)
	V. mungo (L.) Hepper (as *P. mungo*)	India and Sri Lanka (Mukherji and Chatterjee, 1951)
	V. radiata (L.) Wilczek (as *Phaseolus aureus*)	Indonesia (Java) (Haines, 1989), India (Arora, 1977),

Table 3 (*continued*)

Bruchid beetle	Host plant	Country recorded
	(as *Phaseolus radiatus*)	North America (Cushman, 1911), China (all Provinces) (Juanjie et al., 1980)
	V. unguiculata (L.) Walp.	Indonesia (Java) (Haines, 1989),
	(as *Dolichos biflorus*)	India (Arora, 1977)
	V. unguiculata var. *sesquipedalis* (L.) Ohashi (as *V. sinensis*)	India and Sri Lanka (Mukherji and Chatterjee, 1951), China (all Provinces) (Juanjie et al., 1980), Israel (Anton et al., 1997)
Callosobruchus maculatus (F.)	*Acacia nilotica* (L.) Del. (as *Acacia arabica*)	Sudan (Peake, 1952)
	Cajanus cajan (L.) Millsp.	India (Arora, 1977),
	(as *C. indicus*)	Hawaii (Bridwell, 1919), Oahu, Maui and Hawaii (Nishida, 2002), Israel (Calderon, 1962)
	Cicer arietinum L.	India (Arora, 1977), Israel (Anton et al., 1997)
	Lens culinaris Medikus	Israel (Anton et al., 1997)
	Pisum sativum L.	India (Arora, 1977), Israel (Anton et al., 1997)
	Vigna angularis (Willd.) **Ohwi et Ohashi** (as *P. radiatus*)	Japan (Utida, 1941)
	V. mungo (L.) Hepper (as *P. mungo*)	India (Arora, 1977)
	V. radiata (L.) Wilczek	Indonesia (Java) (Haines, 1989),
	(as *Phaseolus aureus*)	India (Arora, 1977)
	V. unguiculata (L.) Walp.	Niger (Alzouma, 1981), Indonesia (Java) (Haines, 1989),
	(as *V. chinensis*)	Israel (Calderon, 1962)
	V. unguiculata var. *sesquipedalis* (L.) Ohashi (as *V. sinensis*)	India (Arora, 1977), Israel (Anton et al., 1997)
Callosobruchus phaseoli (Gyll.)	*Cicer arietinum* L.	Angola (Decelle, 1975)
	Lablab purpureus (L.) Sweet (as *Dolichos lablab*)	Brazil (Bondar, 1936), Mascarene Islands (Decelle, 1969), Angola (Decelle, 1975), India and Sri Lanka (Mukherji and Chatterjee, 1951), Hawaii, India, Cuba (Bottimer, 1961), Oahu, Molokai and Laysan (Nishida, 2002), Israel (Anton et al., 1997)
Locally distributed pests		
Callosobruchus imitator Kingsolver	*Vigna angularis* (Willd.) **Ohwi et Ohashi**	Thailand (present study), **Myanmar (**present study**),** China (no specific locality, Kingsolver, 1999), Thailand (present study)
	***V. umbellata* (Thunb.) Ohwi et Ohashi**	
	V. unguiculata (L.) Walp.	Thailand (Kingsolver, 1999; present study)
Callosobruchus pulcher (Pic)	***Cajanus cajan* (L.) Millsp.**	**Philippines (Luzon Isl.) (**present study**)**
	—	Hawaii (Oahu Isl.) (present study), Hawaii (Oahu and Maui, Nishida, 2002)
Callosobruchus rhodesianus (Pic)	*Vigna unguiculata* (L.) Walp.	Angola (Decelle, 1975), Zimbabwe (Ndlov and Giga, 1988)

Table 3 (*continued*)

Bruchid beetle	Host plant	Country recorded
Callosobruchus subinnotatus (Pic)	*Vigna subterranea* (L.) Verdcourt (as *Voandzeia subterranea*)	Nigeria (Prevett, 1966), Senegal (Decelle, 1969), Ghana (Appleby and Credland, 2001)
	Vigna unguiculata (L.) Walp.	Niger (Mbata, 1993)
Callosobruchus theobromae (L.)	*Cajanus cajan* (L.) Millsp. (as *C. indicus*)	India and Sri Lanka (Mukherji and Chatterjee, 1951), India (Vazirani, 1975)
	***C. scarabaeoides* (L.) Thouars**	**Taiwan** (present study), **Thailand** (present study)
	Glycine max (L.) Merr.	India (Arora, 1977), Indonesia (Java) (Haines, 1989)
	***Rhynchosia rothii* Benth. ex Aitch.**	**Taiwan** (present study)
Non-pests		
Callosobruchus utidai Tuda	***Dunbaria rotundifolia* (Lour.) Merr.**	**Nepal** (present study)
	***Dunbaria podocarpa* Kurz**	**Thailand** (present study)
Callosobruchus latealbus (Pic)	***Rhynchosia volubilis* Lour.**	**Taiwan** (present study)
	***Rhynchosia acuminatifolia* Makino**	**China** (**Guizhou Prov.**) (present study)
	—	China (no specific locality) (Pic, 1926)
	—	Taiwan and China (Guizhou Prov.) (Juanjie et al., 1980)

References

Alzouma, I., 1981. Observations on the ecology of *Bruchidius atrolineatus* Pic and *Callosobruchus maculatus* F. (Coleoptera, Bruchidae) in Niger. In: Labeyrie, V. (Ed.), The Ecology of Bruchids attacking Legumes (Pulses). Series Entomologica, Vol. 19, Dr. W. Junk, The Hague, pp. 205–213.

Anton, K-W., Halperin, J., Calderon, M., 1997. An annotated list of the Bruchidae (Coleoptera) of Israel and adjacent areas. Israel Journal of Entomology 31, 59–96.

Appleby, J.H., Credland, P.F., 2001. Bionomics and polymorphism in *Callosobruchus subinnotatus* (Coleoptera: Bruchidae). Bulletin of Entomological Research 91, 235–244.

Arora, G.L., 1977. Taxonomy of Bruchidae (Coleoptera) of northwest India. Part I. Adults. Oriental Insects Supplement 7, 1–132.

Bernays, E.A., Chapman, R.F., 1994. Host-Plant Selection by Phytophagous Insects. Chapman & Hall, New York.

Bondar, G., 1936. Notas biologicas sobre bruchideos observados no Brasil. Archivos do Instituto de Biologia Vegetal Rio de Janeiro 3, 7–44.

Borowiec, L., 1987. The genera of seed-beetles (Coleoptera: Bruchidae). Polskie Pismo Entomologiczne 57, 3–207.

Bottimer, L.J., 1961. New United States records in Bruchidae, with notes on host plants and rearing procedures (Coleoptera). Annals of the E ntomological Society of America 54, 291–298.

Brändle, M., Öhlschläger, S., Brandl, R., 2002. Range size in butterflies: correlation across scales. Evolutionary Ecology Research 4, 993–1004.

Bridwell, J.C., 1918. Notes on the Bruchidae and their parasites in the Hawaiian Islands. Proceedings of the Hawaiian Entomological Society 3, 465–505.

Bridwell, J.C., 1919. Some additional notes on Bruchidae and their parasites in the Hawaiian Islands. Proceedings of the Hawaiian Entomological Society 4, 15–20.

Calderon, M., 1962. The Bruchidae of Israel. Rivista di Parassitologia 23, 207–216.

Chujo, M., 1937a. Fauna Nipponica, Family Bruchidae. Sanseido, Tokyo (in Japanese).

Chujo, M., 1937b. Some additions and revisions of Bruchidae from the Japanese Empire. Transactions of the Natural History Society of Formosa 27, 189–200.

Cushman, R.A., 1911. Notes on the host plants and parasites of some North American Bruchidae. Journal of Economic Entomology 4, 489–510.

Decelle, J., 1969. Le Parc National du Niokolo-kobo (Senegal). Part III. XVII. Coleoptera: Bruchidae. Memoires de l'Institut Francais d'Afrique noire 84, 287–296.

Decelle, J., 1975. Les Coleopteres Bruchides d'Angola. Publicaçoes Culturais da Companhia de Diamantes de Angola 89, 13–32.

Egorov, A.B., Ter-Minassian, M.E., 1983. Bruchidae of east Siberia and far east of the USSR. Trudy Biologo-pochvennogo Instituta Akademii nauk SSSR.

Ghosh, C.C., 1937. The pulse beetles (Bruchidae) of Burma. Indian Journal of Agricultural Sciences 7, 395–412.

Haines, C.P., 1989. Observations on *Callosobruchus analis* (F.) in Indonesia, including a key to storage *Callosobruchus* spp (Col., Bruchidae). Journal of Stored Products Research 25, 9–16.

Hoffmann, A., 1945. Coleopteres bruchides et Anthribides. Faune de France 44, 1–184.

Jaenike, J., 1990. Host specialization in phytophagous insects. Annual Reviews of Ecology and Systematics 21, 243–273.

Johnson, C.D., 1981. Seed beetle host specificity and the systematics of the Leguminosae. In: Polhill, R.M., Raven, P.H. (Eds.), Advances in Legume Systematics Part 2. Royal Botanical Gardens, Kew, pp. 995–1027.

Juanjie, T., Peiyu, Y., Hongxing, L., Shuyong, W., Shengqiao, J., 1980. Economic Insect Fauna of China 18: Coleoptera: Chrysomeloidea (I). Science Press, Beijing (in Chinese).

Kingsolver, J.M., 1999. A new species of *Callosobruchus* (Coleoptera: Bruchidae) from Thailand and China. Entomological News 110, 209–213.

Kondo, N., Yuasa, H., Maekawa, F., 1987. Resource-Handbook of Legumes. Uchida Rokakuho Publishing, Tokyo (in Japanese).

Leather, S.R., 1991. Feeding specialization and host distribution of British and Finnish *Prunus* feeding Macrolepidoptera. Oikos 60, 40–48.

Luca, Y.de., 1962. Contribution aux Bruchides (Coleopteres) d'Algerie, leurs hotes, leurs parasites, leurs stations. Memoires de la Societe D'histoire Naturelle de L'Afrique du Nord 7, 1–120.

Lukjanovich, F.K., Ter-Minassian, M.E., 1957. Fauna of the USSR, 67: Coleoptera 24 (1), Seed beetles (Bruchidae). Zoologicheskii Institut Akademii nauk SSSR, Moscow (in Russian).

Mathur, R.N., Singh, B., Lal, K., 1958. Insect pests of flowers, seeds, and fruits of forest trees. Indian Forest Bulletin 223, 1–105.

Mbata, G.N., 1993. Some factors affecting oviposition and development of *Callosobruchus subinnotatus* (Pic) (Coleoptera: Bruchidae). Journal of Plant Diseases and Protection 100, 155–164.

Morimoto, K., 1990. A synopsis of the bruchid fauna of Japan. In: Fujii, K., Gatehouse, A.M.R., Johnson, C.D., Mitchel, R., Yoshida, T. (Eds.), Bruchids and Legumes: Economics, Ecology and Coevolution. Kluwer, Dordrecht, pp. 131–140.

Mukherji, S., Chatterjee, S.N., 1951. Morphology of the genital structures of some of the Bruchidae (Lariidae) of India and Ceylon and their taxonomic importance. Indian Journal of Entomology 13, 1–28.

Nahdy, M.S., Ellis, R.H., Silim, S.N., Smith, J., 1998. Field infestation of pigeonpea (*Cajanus cajan* (L.) Millsp.) by *Callosobruchus chinensis* (L.) in Uganda. Journal of Stored Products Research 34, 207–216.

Ndlov, T.M., Giga, D.P., 1988. Studies on varietal resistance of cowpeas to the cowpea weevil, *Callosobruchus rhodesianus* (Pic). Insect Science and its Application 9, 123–128.

Nishida, G.M., 2002. Hawaiian Terrestrial Arthropod Checklist 4th Edition.. Hawaiian Biological Survey and Bishop Museum, Honolulu.

Peake, F.G.G., 1952. On a bruchid seed-borer in *Acacia arabica*. Bulletin of Entomological Research 43, 317–324.

Pic, M., 1926. Nouveautes diverses. Melanges Exotico-Entomologiques 47, 1–32.

Prevett, P.F., 1966. Observations on the biology of six species of Bruchidae (Coleoptera) in northern Nigeria. Entomologist's Monthly Magazine 102, 174–180.

Singal, S.K., Pajni, H.R., 1990. Six new species of *Callosobruchus* Pic from India (Coleoptera, Bruchidae). Polskie Pismo Entomologiczne 59, 761–782.

Shinoda, K., Yoshida, T., Okamoto, T., 1991. Two wild leguminous host plants of the azuki bean weevil, *Callosobruchus chinensis* (L.) (Coleoptera, Bruchidae). Applied Entomology and Zoology 26, 91–98.

Southgate, B.J., 1978. New junior synonyms of *Callosobruchus analis* (F.) and *Callosobruchus dolichosi* (Gyll.) (Coleoptera: Bruchidae) with notes on distribution. Journal of Stored Products Research 14, 61–63.

Southgate, B.J., 1979. Biology of the Bruchidae. Annual Reviews of Entomology 24, 449–473.

Strong, D.R., Lawton, J.H., Southwood, R., 1984. Insects on Plants: Community Patterns and Mechanisms. Blackwell Scientific, Oxford.

Thompson, J.N., 1994. The Coevolutionary Process. University of Chicago Press, Chicago.

Tomooka, N., Kashiwaba, K., Vaughan, D.A., Ishimoto, M., Egawa, Y., 2000. The effectiveness of evaluating wild species: searching for sources of resistance to bruchid beetles in the genus *Vigna* subgenus *Ceratotropis*. Euphytica 115, 27–41.

Tuda, M., 2003. A new species of *Callosobruchus* (Coleoptera: Bruchidae) feeding on seeds of *Dunbaria* (Fabaceae), a closely related species to a stored-bean pest, *C. chinensis*. Applied Entomology and Zoology 38, 197–201.

Tuda, M., Wasano, N., Kondo, N., Horng, S.-B., Chou, L.-Y., Tateishi, Y., 2003. Habitat-related mtDNA polymorphism in the stored-bean pest *Callosobruchus chinensis* (Coleoptera: Bruchidae). Bulletin of Entomological Research 93.

Udayagiri, S., Wadhi, S.R., 1989. Catalog of Bruchidae. American Entomological Institute, Gainesville.

Utida, S., 1941. Studies on experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.) I. The effect of population density on the progeny populations. Memoirs of the College of Agriculture, Kyoto Imperial University 48, 1–30.

Vazirani, T.G., 1975. A contribution to the knowledge of oriental Bruchidae. Journal of the Bombay Natural History Society 72, 740–757.

Zacher, F., 1952. Die Nährpflanzen der Samenkäfer. Zeitschrift für Angewandte Entomologie 33, 460–480.