



Potential invasion of China by exotic insect pests associated with tree seeds

ALAIN ROQUES^{1,*}, JIANG-HUA SUN², MARIE-ANNE AUGER-ROZENBERG¹ and OUYANG HUA³

¹Station de Zoologie Forestière, Institut National de la Recherche Agronomique (INRA), Avenue de la pomme de pin, BP 20619, F-45166 Olivet Cedex, France; ²Institute of Zoology, Chinese Academy of Sciences, 100080 Beijing, China; ³Institute of Geographic Sciences and Natural Resources, Chinese Academy of Sciences, 100101 Beijing, China; *Author for correspondence (e-mail: alain.roques@orleans.inra.fr; fax: +33-2-38417879)

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Abstract. A total of 39 insect species, mostly seed chalcids in the genus *Megastigmus* (Hymenoptera), but also midges (Diptera), are listed as potential seed-borne invaders of Chinese conifers. Although the number of native seed insects per conifer genus does not differ between China and other biogeographical regions, there are significantly fewer seed insects associated with each conifer genus in China than potential invaders. The eventual success of the invaders is likely to depend on the presence of native Chinese conifers that are congeneric with the original host, or on the presence of the original host as an exotic. When a substantial entomofauna is already associated with cones, competition for seed resources may limit the potential impact of invaders because seed insects are usually the last organisms to colonize the cone. A survey of 26 fir species, both native and introduced to Europe, showed that overall seed infestation by five species of exotic chalcids is negatively correlated to levels of damage by native insects, except on the original hosts of the chalcids. Similar patterns are hypothesized for native firs, spruces, Douglas firs, and larches in China. Uncontrolled importation of seeds and nuts of broad-leaved trees could also facilitate the introduction of seed chalcids, seed bruchids, tortricid moths and nut weevils into China. Only six species of seed chalcids are present in China, out of the 72 known to attack broad-leaved seeds over the world.

Introduction

As a result of technological advances and of globalisation trade, forest products are moved around the globe with an ever-increasing speed and frequency. This movement has precipitated a substantial increase in biological invasions by allowing organisms to pass the natural barriers that limit their dispersal (Liebhold et al. 1995). Forest pests can move between countries via a number of pathways including importation of logs, chips, solid wood packaging and propagative materials (for a review see a CD-ROM archive of the Internet forum 'Risks of Exotic Forest Pests and their Impact on Trade'; The American Phytopathological Society 2001). During the past century, the introduction of exotic forest pests into highly vulnerable tree populations has resulted in severe ecologic, aesthetic and economic impacts. For example, the European gypsy moth (*Lymantria dispar* [L.]), balsam woolly adelgid

(*Adelges piceae* [Ratzeburg]), Asian longhorned beetle (*Anoplophora glabripennis* [Motsch]) and pine shoot moth (*Rhyacionia buoliana* [Denis and Schiff.]) caused irreparable damage to forested ecosystems and landscape trees in North America (Mattson 1997; Britton and Sun 2002), as did introduced tree diseases such as chestnut blight (*Chryphonectria parasitica* [Murr.] Barr.) (Schumann 1991).

Although worldwide exchange and trade of tree reproductive materials is rapidly increasing with the development of plantations and ornamentals using exotic tree species, little information is available about associated invaders. Such exchanges actually favor the invasion of new pests, because phytosanitary regulations are limited or non-existent in many countries. Two categories of organisms are recognized: (i) seed-borne insects and mites, because isolated seeds are preferred to whole cones and fruits for trade of conifers and of most broadleaved tree species; and (ii) soil-borne pests associated with bareroot and seedling containers.

A conservative estimate based on a literature search indicated that 30 exotic insect species damaging seed cones and other forest tree fruits had already been introduced into and become established in North America by the 1990s (Mattson et al. 1994). In the West Palearctic, a recent survey revealed that invasions of exotic seed pests of the genus *Megastigmus* Dalman (Hymenoptera: Torymidae) have considerably modified the species composition and levels of impact of seed insects on both native and exotic trees (Roques and Skrzypczyńska 2003). Of a total of 21 species of *Megastigmus* observed in this region, 38% (i.e. eight species) were introduced through seed trade mostly from North America (seven species). In Europe, North Africa and Asia Minor, these introduced chalcids have colonised 29 species of native conifers, in the genera *Abies*, *Cedrus*, *Cupressus*, *Juniperus*, *Larix*, and *Picea*, 43 species of exotic introduced conifers, 28 species of Rosaceae (*Amelanchier*, *Rosa*, *Sorbus*) and nine species of Anacardiaceae (*Pistacia*, *Schinus*). These changes have negatively impacted on both natural regeneration of native forests and seed crops in seed orchards designed to produce genetically superior tree seeds (Roques and Raimbault 1985). Invasive *Megastigmus* in the West Palearctic also pose threats to insect biodiversity with which they interact through competition for seed resources (e.g., five invasive species versus one native species in fir seeds).

In China, exotic forest pests have gained attention with the recent introduction of highly destructive species, such as the fall webworm, *Hyphantria cunea* (Drury), the red turpentine beetle, *Dendroctonus valens* LeConte, and pinewood nematode, *Bursaphelenchus xylophilus* (Steiner et Buhner) Nickle (Britton and Sun 2002). Besides those few cases, little is known about other exotic pests, especially those potentially associated with tree propagative materials. However, the increasing government efforts of planting trees to restore the deforested land in order to improve the environmental conditions, especially the ecological restoration project in South Western China that is being carried out in the 'West Development Programme', could risk more biological invasions, including exotic insects that damage tree seed crops, since a lot of planting species are introduced without proper risk assessment. Therefore, this paper reviews the potential pests associated with seeds that might invade China and identifies conditions that favour establishment of such invaders in Chinese forests.

Potential pest invaders associated with conifer seeds

To date, more than 400 species of phytophagous insects and mites are known to exploit seed cones of world conifers (Turgeon et al. 1994). However, only the species spending their entire development (egg to pupa) as endophytes within seeds (known as '*spermatophages*'; Turgeon et al. 1994) constitute a real threat of invasion, because seeds and not whole cones are used in trade exchanges. Actually no insects strictly developing in cone tissues but not entering seeds have been recognised as invaders, whereas numerous species developing within seeds have been introduced to other continents, especially from North America to Europe (Roques 1983). A total of 56 conifer spermatophages are recognised worldwide, the dominant group being the seed chalcid wasps (Hymenoptera: Chalcidoidea) with 51 species in the genus *Megastigmus* (Torymidae; Grissell 1999; Roques and Skrzypczyńska 2003). A few other chalcids in the family Torymidae (*Torymoides piceae* Kamijo and *Torymus tsugae* Yano; Noyes 1998) and Eurytomidae (*Eurytoma laricis* Yano = *E. bouceki* Skrzypczyńska; Noyes 1998), a cynipid wasp (Hymenoptera: Cynipidae – *Austrocynips* sp.; Riek 1971), and a few seed midges [Diptera: Cecidomyiidae – *Plemeliella abietina* Stein. (Roques 1983) and *Mayetiola carpophaga* Tripp (Hedlin et al. 1980)] are also recognized together with several mites in the genus *Trisetacus* (Nalepellidae = Eryiophiidae; Smith 1977, 1979), especially infesting junipers and cypresses.

Nearly all the spermatophages develop in seeds of plant species in only one genus, except for four *Megastigmus* species which utilise two closely related genera; notably *M. amicum* Bouček on *Cupressus* and *Juniperus*; *M. atedius* Walker on *Picea* and *Pinus*; and *M. suspectus* Borries and *M. pinsapinis* Hoffmeyer on *Cedrus* and *Abies* (Roques and Skrzypczyńska 2003). However, recent genetic investigations suggest that the populations developing on two different conifer genera may actually correspond to separate *Megastigmus* species (M.-A. Auger-Rozenberg and A. Roques, unpublished data). In parallel, nearly 80% of the conifer species serve as hosts to at least one spermatophage (Turgeon et al. 1994), and it is likely that most conifer seed lots contain spermatophages when not cleaned using appropriate methods. Usually, these pests cannot be detected by examining the outside of the seeds and only show up when X-rayed. Thus, without X-ray surveys infested seeds are likely to go undetected.

Because of the relative dominance of seed chalcids within the conifer spermatophages, they require special attention. The lifecycle of all seed chalcids is roughly similar to that of the Douglas fir seed chalcid, *Megastigmus spermatrophus* Wachtl (Figure 1). Using its long ovipositor, the female lays an egg directly into the seed where the larva develops completely. After having entirely consumed the endosperm and embryo, the mature larva overwinters within the seed. Besides being spermatophagous, three other biological characteristics contribute to the invasiveness of seed chalcids: (i) an ability to extend larval diapause in seeds for up to 4 years in most species (Turgeon et al. 1994), allowing them to bridge periods where seeds are unavailable because of the masting phenomenon which is common in forest trees (Silvertown 1980); (ii) parthenogenesis (the females can reproduce

without males); and (iii) an ability of some species to develop within unfertilised seeds (e.g. *M. spermatrophus*; Niwa and Overhulser 1992; Rappaport et al. 1993).

Table 1 provides details of the spermatophagous species per conifer genus in China and the species which are potential invaders from other parts of the world (compiled from Roques et al. 1995; Xu and He 1995; Xu et al. 1998; Noyes 1998; Grissell 1999; Roques and Skrzypczyńska 2003). Large seed samples collected between 1997 and 2002 did not disclose any spermatophages associated with some relict genera present in China (e.g., *Glyptostrobus*, *Taiwania*, *Foekenia*, *Calocedrus*, *Taxus*, *Cephalotaxus*) (Roques and Pan, unpublished data), but up to three species were found in each of the main conifer genera. Although the present record of 17 conifer spermatophages in China (of which some new species of seed chalcids are currently being described; Roques and Pan, unpublished data) is probably an underestimate, the number of native spermatophages per conifer genus does not differ between China and other biogeographical regions (Table 1; Wilcoxon sign rank tests: China – West Palearctic: $P = 0.250$; China – Nearctic: $P = 0.320$; China – remainder of East Palearctic: $P = 0.500$). However, there are significantly fewer spermatophages associated with each conifer genus in China than potential invaders (Wilcoxon sign rank test: $P = 0.008$). It is thus estimated that at least 39 species

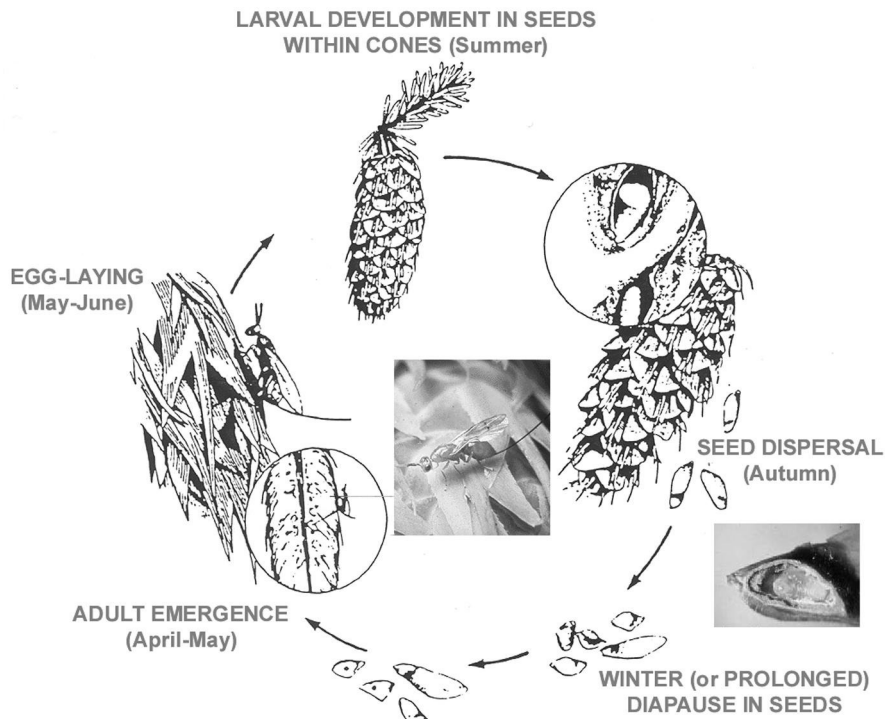


Figure 1. Lifecycle of the Douglas fir seed chalcid, *Megastigmus spermatrophus* Wachtl (adapted from Hedlin et al. 1980).

Table 1. Seed infestation of Chinese conifers by spermatophages (SP) compared to the numbers of native spermatophages observed in other regions of the world and potentially invading species, not yet recorded from China.

Tree genus	No. SP in China	Chinese species	No. SP in West Palearctic	No. SP in East Palearctic ^a	No. SP in Nearctic	No. of potential invaders	Potentially invading species	Continent and countries to be surveyed for seed importation
<i>Abies</i>	2	<i>M. lasiocarpae</i> ^b ; <i>Megastigmus</i> sp. (Yunnan)	2	1	6	7	<i>M. firmae</i> ; <i>M. milleri</i> ; <i>M. pinsapinis</i> ; <i>M. pinus</i> ; <i>M. rufi</i> ; <i>M. specularis</i> ; <i>M. suspectus</i> ; <i>Megastigmus</i> sp. (Mexico)	Europe, Japan, North America, Mexico
<i>Cedrus</i>	n.p.	–	2	0	n.p.	2	<i>M. pinsapinis</i> ; <i>M. schimitscheki</i>	North Africa, Asia Minor (introduced into France)
<i>Larix</i>	2	<i>M. pictus</i> ; <i>Eurytoma laricis</i>	2	2	1	2	<i>M. laricis</i> ; <i>M. inamurae</i>	North Europe, North America, Japan
<i>Picea</i>	2	<i>M. ezomatsuanus</i> ; <i>M. likiangensis</i>	2	2	3	6	<i>M. atedius</i> ; <i>M. caperatus</i> ?; <i>M. strobilobius</i> ; <i>Torymides piceae</i> ; <i>Plenetiella abietina</i> ; <i>Mayetiola carpophaga</i>	Europe, Japan, North America
<i>Pinus</i>	0	–	0	0	2	2	<i>M. albifrons</i> ; <i>M. atedius</i>	Southern USA, Mexico, Central America
<i>Pseudotsuga</i>	2	<i>M. pseudotsugaphilus</i> ; <i>Megastigmus</i> sp. (Zhejiang)	n.p.	0	2	2	<i>M. spermatrophus</i> ; <i>M. spermatrophus nigrodorsatus</i>	North America (introduced into Europe, New Zealand)
<i>Tsuga</i>	0	–	n.p.	2	2	4	<i>M. hoffmeyeri</i> ; <i>M. tsugae</i> ; <i>M. tsugaphilus</i> ; <i>Torymus tsugae</i>	North America, Japan
<i>Cupressus</i>	2	<i>M. carinus</i> ; <i>M. ducouxiana</i>	3	1	0	4	<i>M. amicum</i> ; <i>M. atlanticus</i> ; <i>M. cupressi</i> ; <i>M. wachli</i>	Southern Europe, North Africa, India
<i>Juniperus</i>	4	<i>M. pingii</i> ; <i>M. rigidae</i> ; <i>M. sabiniae</i> ; <i>Megastigmus</i> sp. (Yunnan)	2	5	0	8	<i>M. atedius</i> ; <i>M. bipunctatus</i> ; <i>M. certus</i> ; <i>M. fidus</i> ; <i>M. gravis</i> ; <i>M. juniperi</i> ; <i>M. somaliensis</i> ; <i>M. valdus</i>	Europe, Asia Minor, Central Asia, Eastern Africa
<i>Chamaecyparis</i>	0	–	n.p.	1	1	2	<i>M. chamaecyparidis</i> ; <i>M. thuyoides</i>	Japan, Canada
<i>Thuopsis</i>	0	–	n.p.	1	n.p.	1	<i>M. thuyopsis</i>	Japan
<i>Cryptomeria</i>	1	<i>M. cryptomeriae</i>	n.p.	1	n.p.	0	–	–
<i>Araucaria</i>	n.p.	–	n.p.	n.p.	n.p.	1	<i>Austrocyrtops</i> sp.	Papua-New Guinea
Unknown	2	<i>M. cellus</i> ; <i>M. pseudomali</i>	n.p.	n.p.	n.p.	0	–	–
Total	17		13	16	17	41 (39) ^c		

^a Remainder of the East Palearctic without China; ^b Species possibly introduced from North America; ^c For totals, note that *M. atedius* and *M. amicum* can colonize 2 conifer genera. Data compiled from Roques et al. (1995), Xu and He (1995), Xu et al. (1998), Noyes (1998), Grissell (1999), Roques and Skrzypczynska (2003); Roques and Pan, unpublished data). *Megastigmus* is abbreviated by *M.*; n.p.: no native conifers in the genus.

Table 2. Average percentage of seeds infested by native and exotic insects during 1994 on the fir species, *Abies* spp., planted at the Les Barres arboretum, North-Central France.

Abies species	Origin	Seed damage by introduced seed chalcids					Seed damage by native insects			Total	
		Nearctic species					M. suspectus		Total native		
		M. milleri	M. spectularis	M. pinus	M. rafni	M. pinsapinis	Total introd.	Cone insects			
A. alba Mill.	WP	1.1	0.2	0.4	3.1	0.9	5.7	12	36.4	48.4	54.1
A. borisi-regis Matf.	WP	0	0	0	0	0	0	15.2	42.0	55.2	55.2
A. bommilleriana Matf.	WP	0.2	0.1	0.9	1.3	0	2.5	12.4	63.6	76.0	78.5
A. cephalonica Loud.	WP	0	0	0	1	0	1.0	13.1	43.0	56.1	57.1
A. cilicica (Ant. et Kotschy) Carr.	WP	0	0	0.4	1.2	0	1.6	11.0	62.6	73.6	75.2
A. equi trojani Asch. et Sint.	WP	0	0	0	1	0	1.0	13.2	61.8	75.0	76.0
A. marocana Trabut	WP	0	0	0	3.9	0	3.9	0.0	22.7	22.7	26.6
A. nebrodensis (Lojac.) Mattei	WP	0	0	0	0.3	0	0.3	10.1	56.5	66.6	66.9
A. nordmanniana (Steven) Spach	WP	0.1	0.4	2.8	3	0.2	6.5	11.1	39.1	50.2	56.7
A. numidica Carr.	WP	0	0	3	1.9	0	4.9	12.9	23.9	36.8	41.7
A. pinsapo Boissier	WP	0.8	0.1	0.7	1.1	0.4	3.1	14	49.7	63.7	66.8
A. holophylla Maxim.	EP	0	0.1	0	0	0	0.1	0	61.5	61.5	61.6
A. homolepis Sieb. et Zucc.	EP	0.8	0.3	0	0.2	0	1.3	8.2	42.4	50.6	51.9
A. koreana Wils.	EP	0	0.1	0	4.1	0	4.2	0	36.1	36.1	40.3
A. nephrolepis Maxim.	EP	0	0.2	0	0	0	0.2	6.8	49.3	56.1	56.3
A. pindrow Royle	EP	0	0	0	5	0	5.0	0	17.4	17.4	22.4
A. sachalinensis (Schmidt) Mast.	EP	0	4.0	0	0	0	4.0	0	24.5	24.5	28.5
A. sibirica Ledeb.	EP	0	3.0	0	0	0	3.0	0.7	33.2	33.9	36.9
A. veitchii Lindl.	EP	0	3.0	0	0.8	0	3.8	3	37.0	40.0	43.8
A. amabilis (Dougl.) Forbes	NA	0	7.0	0	0	0	7.0	0	35	35	42
A. balsamea (L.) Mill.	NA	9.2	4.0	0	0	0	13.2	0	42.2	42.2	55.4
A. concolor (Gord.) Engelm.	NA	6.2	1.7	8.4	9.1	0	25.4	1.9	60.1	62	87.4
A. grandis Lindl.	NA	7.1	0	10.6	7.9	0	25.6	3.9	60.5	64.4	90
A. lasiocarpa (Hook.) Nutt.	NA	0	7.2	5.5	0	0	12.7	0	54.3	54.3	67
A. magnifica A. Murr.	NA	12.6	0	0	0	0	12.6	0	48.2	48.2	60.8
A. procera Rheder (= nobilis Lindl.)	NA	0	0	14.2	8.9	0	23.1	0	61.2	61.2	84.3

Region of origin of *Abies* spp.: WP: West Palearctic; EP: East Palearctic; NA: Nearctic.

(excluding seed mites) of seed-borne insects have the potential to be introduced to China with conifer seeds (Table 1).

However, the establishment and spread of exotic seed pests in an area of introduction largely depends on the presence of native tree species in the same genus as the original host, because all the conifer spermatophages are strictly host-specific at the tree genus level (cf. above). When there are no native tree species congeneric to the original host, the spermatophages cannot become established unless the original host or a congeneric is introduced simultaneously. In these cases, the introduced pests tend to be more abundant because there are no native or introduced competitors or parasitoids (Roques 1998). Under these circumstances damage to the seed crop is much more prevalent than in native areas. For example, the Douglas fir seed chalcid, *M. spermotrophus*, was probably introduced during the last part of the 19th century along with Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, from Western North America to Europe and New Zealand where no native species of *Pseudotsuga* occurs (Roques and Skrzypczyńska 2003). At present, *M. spermotrophus* usually infests more than 50% of the Douglas fir seeds in most of the European plantations, especially in the seed orchards (Lessmann 1974; Roques 1981; Candau et al. 1996; Jarry et al. 1997). Besides pollination and germination problems, chalcid impact seems to be a principal factor limiting natural regeneration of Douglas fir in Europe (Roques 1981). In contrast, seed damage by *M. spermotrophus* is generally lower than 10% in the native American range (Rappaport and Roques 1991). In China, a similar situation might be observed with exotic true cedars (*Cedrus* spp.) if an exotic cedar seed chalcid is accidentally transferred from North Africa and Asia Minor, or via Europe where two such chalcids have already been introduced (Roques and Skrzypczyńska 2003).

When suitable tree host genera exist in the area of introduction, the exotic chalcid usually shifts to these (Roques 1983). Competition with native cone insects, however, may limit the chalcid's impact because cone insects have usually consumed most of the seeds before the chalcid oviposits, as has been shown for *Picea* spp. in Europe (Da Ros et al. 1993). In order to investigate this hypothesis, the impact of introduced fir seed chalcids was surveyed during 1994 in a French arboretum ('Les Barres', North-Central France) where a large number of native and exotic fir species (*Abies* spp.) have been planted. Depending on the species cone crop, 5 to 20 mature seed cones were randomly collected before disarticulation on two trees per fir species, including 11 species native to the West Palearctic, eight species introduced from the Eastern Palearctic, and seven species introduced from the Nearctic. All the cones were dissected scale by scale in order to estimate the number of seeds preyed by larvae of cone moths and cone flies; then, the externally undamaged seeds were X-rayed to measure the number and percentage of filled, empty, and chalcid- or midge-infested seeds. The infested seeds were finally reared in individual tubes stored in an outdoor insectary. Because of possible diapause, adult emergence was surveyed until 1998, and the adults were then identified to species. For each insect and tree species, the percentage damage was expressed as the ratio of the number of attacked seeds over the total number of seeds because of possible development of chalcids within unpollinated, unfertilised seeds.

Four chalcid species introduced from the Nearctic (*M. milleri* Milliron, *M. pinus* Parfitt, *M. rafni* Hoffmeyer, and *M. specularis* Walley) and one introduced from North Africa (*M. pinsapinis* Hoffmeyer) were observed, but they had to share resources with a native chalcid (*M. suspectus*) and five other cone insects that destroy the seeds earlier in the season (two cone flies, *Strobilomyia carbonaria* [Ringdahl] and *Earomyia impossibile* Morge; two cone moths, *Barbara herrichiana* Obraztsov and *Dioryctria abietella* [Denis and Schiff.]; and a midge, *Resseliella piceae* Seitner; Roques 1983). All of the fir species except the Greek species, *Abies borisii-regis* Mattf., were colonized by at least one exotic chalcid species (Table 2). However, the levels of damage they caused never exceeded 15%. Host colonization also differed between the exotic chalcid species. The region of origin of the fir species did not seem to affect the level of seed infestation by *M. milleri* (Kruskal–Wallis one-way AOV: $H = 5.009$, $P = 0.082$), *M. pinsapinis* ($H = 4.427$, $P = 0.109$), *M. rafni* ($H = 1.665$, $P = 0.435$), and *M. specularis* ($H = 5.698$, $P = 0.058$). In contrast, *M. pinus* infested significantly fewer seeds on the firs from the East Palearctic than on those of Nearctic origin (Kruskal–Wallis one-way AOV followed by comparison of mean ranks; $H = 7.378$, $P = 0.025$).

As a result, total seed infestation by exotic chalcids was significantly higher on

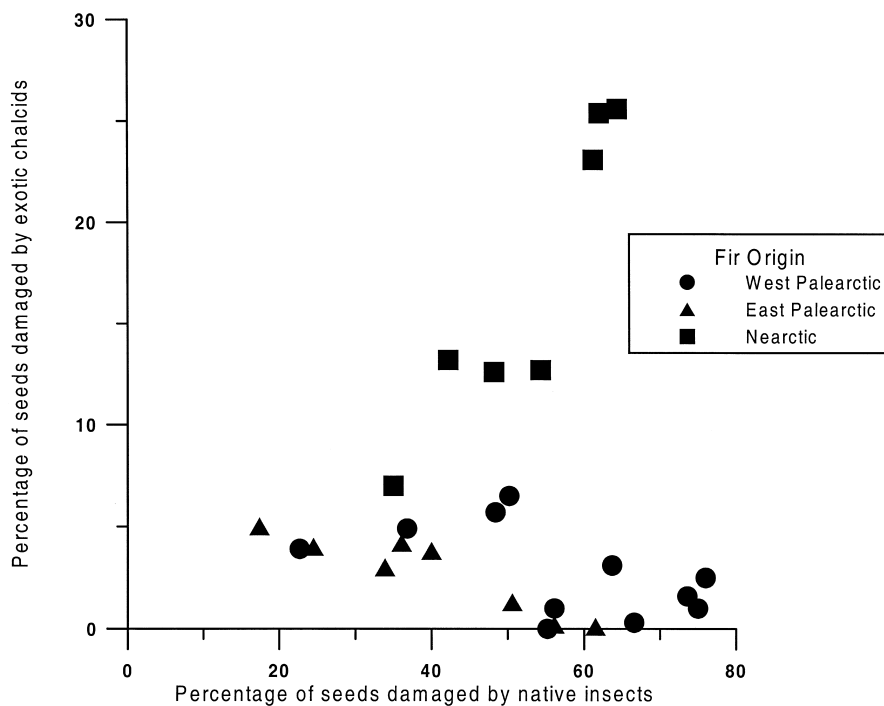


Figure 2. Relationship between the overall percentage of seeds infested by exotic chalcids versus percentage of seeds destroyed by native insects in fir species of different geographical origins planted at the Les Barres arboretum, France, during 1994.

the Nearctic firs than on those originating from both the West and the East Palearctic ($H = 14.783$, $P = 0.000$) and exceeded 20% on seeds of *A. grandis* Lindl., *A. concolor* (Gord.) Lindl. and *A. procera* Rheder. On the other hand, the native seed chalcid, *M. suspectus*, preferred the fir species native to the West Palearctic ($H = 15.064$, $P = 0.000$), but the total seed damage by native insects (cone insects plus *M. suspectus*) did not differ among geographic origins of the firs ($H = 4.833$, $P = 0.089$), ranging from 17.4% up to 76.0% of the seeds according to fir species. The introduced chalcids distorted this damage pattern because of proportionately higher levels of infestation on the Nearctic firs, which are their native hosts (except for *M. pinsapinis*). Thus, total seed damage was significantly higher on Nearctic firs, of which three species showed more than 80% of attacked seeds, compared to firs originating from the East Palearctic ($H = 8.243$, $P = 0.016$). No differences were observed between both regions and the West Palearctic. When all the fir species were considered, plotting the percentage of seed damage caused by exotic chalcids against the total damage caused by native insects did not reveal any relationship (Figure 2; Spearman rank correlations, $r' = -0.267$, $P = 0.187$), but the two variables were significantly negatively correlated as soon as the Nearctic firs were removed from the analysis (Spearman rank correlations, $r' = -0.623$, $P = 0.005$). Damage by native insects thus limited seed infestation by exotic chalcids, except on the original hosts of these chalcids.

It must be stressed that larval populations of cone and seed insects, and subsequent damage, fluctuate substantially with annual variations in cone abundance (Turgeon et al. 1994). This is especially verified in seed chalcids where an inverse relationship exists between the level of seed infestation and the annual change in crop size (Candau et al. 1996). In the studied arboretum, the cone crop size largely decreased from an average of ca. 25 cones per tree in 1993 to 8.5 cones per tree in 1994. This change in crop size probably resulted in a higher level of cone occupancy by insects in 1994, which in turn might have affected chalcid distribution among the fir species.

A similar limitation in impact of exotic spermatophages is expected in China on native firs, spruces (*Picea* spp.), Douglas firs (*Pseudotsuga* spp.), and larches (*Larix* spp.), because a substantial entomofauna is associated with cones of these conifers (Fang et al. 1989) and the seed resource is already heavily utilised before exotic spermatophages can attack the cones when seeds begin to mature (i.e., later than most of the other species).

For example, cones and seeds of Siberian larch, *L. gmelini* Rupr. (Kusen.), are attacked in Northeastern China by at least 13 species, including six species of larch cone flies in the genus *Strobilomyia* (Diptera: Anthomyiidae), several moths (*Cydia illutana* [Herrich-Schäffer] and *Retinia perangustana* Snellen), seed midges (*Reseliella* spp. and *Asynapta* spp.), and two native seed chalcids (*Megastigmus pictus* [Förster] and *Eurytoma laricis*) (Fang et al. 1989; Zhang et al. 1991; Sun et al. 1994; Roques et al. 1995). The overall percentage of damage to cones varies between 60 and 100%, often exceeding 90% (Yao et al. 1991). The introduction of a new, exotic spermatophage may significantly worsen the already substantial impact of native insects only if the female is capable of detecting the few seeds left undamaged at

cone, tree and stand level. This may occur when long-term evolutionary links exist between the conifer and spermatophyte species – i.e., when the introduced insect encounters one of its original hosts as was the case for the Nearctic firs and their related chalcids – but *Megastigmus atedius* Walker, a North American spruce chalcid introduced to Europe, also showed such capabilities when it shifted on Oriental spruce, *Picea orientalis* (L.) Link. (Da Ros et al. 1993).

In contrast, when the native cone entomofauna is limited the invader could have a large impact on seed crops. A species recently introduced from Asia Minor to France in the 1990s, *M. schimitscheki* Novitzky, became highly damaging in a few years within the main *Cedrus* stands of southeastern France where only one insect species was previously observed (Fabre and Roques, unpublished data). Such a situation could be expected with the introduction into China of exotic seed chalcids associated with hemlocks (*Tsuga* spp.), cypresses (*Cupressus* spp.), and some junipers (*Juniperus* spp.). All these tree species have only low numbers of native cone insect species (Roques et al. 1995). Special attention should be paid to pines (*Pinus* spp.), false cypresses (*Chamaecyparis* spp.) and arborvitaes (*Thuja* spp.), whose seed niche is unoccupied in China because several candidate invaders exist in other continents (Table 1).

The lifecycle of *Trisetacus* mites is synchronised with that of the host seeds, and the various life stages are present within seeds from initiation to dispersal. However, mites do not survive for long within seeds that have been extracted from the cones (Roques 1983) and there is less opportunity for them to translocate in seed lots.

Some insect species associated with seeds drop to the ground as mature larvae to

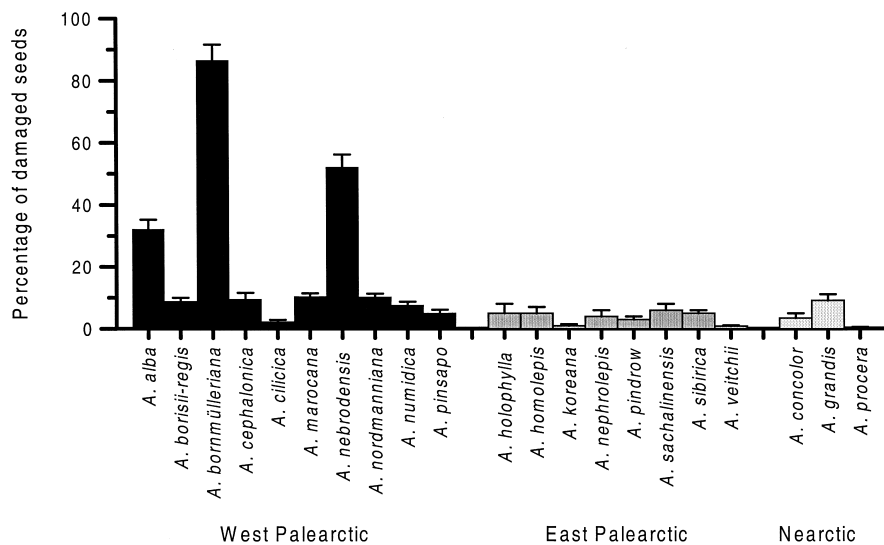


Figure 3. Average seed damage (\pm standard error) by a seed midge, *Resseliella piceae* Seitner, observed during 1989–1990 on native and exotic fir species (*Abies* spp.) planted at the Les Barres arboretum (North-Central France).

Table 3. Seed chalcids associated with broadleaved tree species at world level compared to the number of species already present in China (in bold) (data compiled from Noyes 1998).

Tree family (genus)	Seed chalcid genus	Chalcid family	Number of species (present in China)
Aceraceae (<i>Acer</i>)	<i>Torymus</i>	Torymidae	1
Anacardiaceae (<i>Pistacia</i> , <i>Rhus</i>)	<i>Eurytoma</i>	Eurytomidae	4
Anacardiaceae (<i>Pistacia</i> , <i>Rhus</i>)	<i>Megastigmus</i>	Torymidae	4/ 1
Annonaceae (<i>Annona</i> , <i>Cymbopetalum</i>)	<i>Bephratelloides</i>	Eurytomidae	4
Annonaceae (<i>Annona</i>)	<i>Striaeurytoma</i>	Eurytomidae	1
Aquifoliaceae (<i>Ilex</i>)	<i>Bootania</i>	Torymidae	2
Aquifoliaceae (<i>Ilex</i>)	<i>Megastigmus</i>	Torymidae	1
Aquifoliaceae (<i>Ilex</i>)	<i>Torymus</i>	Torymidae	1
Boraginaceae (<i>Cordia</i>)	<i>Eurytoma</i>	Eurytomidae	1
Ephedraceae (<i>Ephedra</i>)	<i>Blascoa</i>	Pteromalidae	1
Ephedraceae (<i>Ephedra</i>)	<i>Eurytoma</i>	Eurytomidae	1
Euphorbiaceae (<i>Euphorbia</i>)	<i>Bruchophagus</i>	Eurytomidae	1
Euphorbiaceae (<i>Euphorbia</i>)	<i>Eurytoma</i>	Eurytomidae	1
Euphorbiaceae (<i>Mallotus</i>)	<i>Homodecatoma</i>	Eurytomidae	1/ 1
Hamamelidaceae (<i>Casuarina</i>)	<i>Bootanelleus</i>	Torymidae	1
Hamamelidaceae (<i>Distylus</i>)	<i>Megastigmus</i>	Torymidae	1
Lecythidaceae (<i>Eschweilera</i>)	<i>Tanaoneura</i>	Tanaostigmatidae	1
Leguminosae (<i>Acacia</i>)	<i>Bruchophagus</i>	Eurytomidae	1
Leguminosae (<i>Albizia</i>)	<i>Risbecoma</i>	Eurytomidae	1
Leguminosae (<i>Albizia</i>)	<i>Megastigmus</i>	Torymidae	1
Leguminosae (<i>Cajanus</i>)	<i>Tanaostigmodes</i>	Tanaostigmatidae	1
Leguminosae (<i>Caragana</i>)	<i>Bruchophagus</i>	Eurytomidae	1/ 1
Leguminosae (<i>Caragana</i>)	<i>Eurytoma</i>	Eurytomidae	2/ 2
Leguminosae (<i>Dalbergia</i>)	<i>Megastigmus</i>	Torymidae	1
Leguminosae (<i>Inga</i>)	<i>Tanaoneura</i>	Tanaostigmatidae	1
Leguminosae (<i>Inga</i>)	<i>Tanaostigma</i>	Tanaostigmatidae	1
Leguminosae (<i>Mimosa</i>)	<i>Risbecoma</i>	Eurytomidae	1
Leguminosae (<i>Robinia</i>)	<i>Bruchophagus</i>	Eurytomidae	1
Leguminosae (<i>Robinia</i>)	<i>Eurytoma</i>	Eurytomidae	1
Leguminosae (<i>Sesbania</i>)	<i>Bruchophagus</i>	Eurytomidae	1
Leguminosae (<i>Sesbania</i>)	<i>Eurytoma</i>	Eurytomidae	1
Leguminosae (<i>Sophora</i>)	<i>Bruchophagus</i>	Eurytomidae	1
Leguminosae (<i>Sophora</i>)	<i>Eurytoma</i>	Eurytomidae	1
Myrtaceae (<i>Eugenia</i>)	<i>Anselmella</i>	Eulophidae	1
Pandanaceae (<i>Pandanus</i>)	<i>Bootania</i>	Torymidae	3
Rosaceae (<i>Amelanchier</i>)	<i>Megastigmus</i>	Torymidae	1
Rosaceae (<i>Amygdalus</i>)	<i>Eurytoma</i>	Eurytomidae	5
Rosaceae (<i>Cotoneaster</i>)	<i>Megastigmus</i>	Torymidae	1
Rosaceae (<i>Crataegus</i>)	<i>Megastigmus</i>	Torymidae	1
Rosaceae (<i>Crataegus</i>)	<i>Torymus</i>	Torymidae	2
Rosaceae (<i>Malus</i>)	<i>Megastigmus</i>	Torymidae	1
Rosaceae (<i>Pourthiaea</i>)	<i>Megastigmus</i>	Torymidae	1
Rosaceae (<i>Prunus</i>)	<i>Megastigmus</i>	Torymidae	1
Rosaceae (<i>Rosa</i>)	<i>Megastigmus</i>	Torymidae	4/ 1
Rosaceae (<i>Sorbus</i>)	<i>Megastigmus</i>	Torymidae	2
Rosaceae (<i>Sorbus</i>)	<i>Torymus</i>	Torymidae	3
Rosaceae (<i>Spiraea</i>)	<i>Megastigmus</i>	Torymidae	2

pupate and therefore are not easily transferred with seed crops. However, early seed collection before larval drop-down may cause contamination of consignments of seeds, essentially by seed midges; e.g. *Resseliella* spp. on *Abies* spp. and *Larix* spp. Like seed chalcids, *Resseliella* spp. are oligophagous species capable of surviving on new hosts that are congeneric with the original one. A survey of the colonization potential of a fir seed midge, *R. piceae* Seitner from Europe, was carried out in the same arboretum as above where cones were collected by mid-October on 21 *Abies* species (10 from the West Palearctic, eight from the East Palearctic, and three from the Nearctic) during both 1989 and 1990. Depending on the species cone crop, 5–10 cones were randomly collected per tree on two trees per species, and treated as for fir seed chalcids (cf. above). Numerous midge larvae were still present within seeds at this time. These larvae were shown to survive on most of the fir species (Figure 3). However, they caused limited levels of damage except on *A. alba* Mill., *A. bornmülleriana* Matf. and *A. nebrodensis* (Lojac.) Mattei, three species originating from the West Palearctic. Colonisation was significantly lower on the species from the East Palearctic and Nearctic America than those from the West Palearctic (Kruskal–Wallis one-way AOV followed by comparison of mean ranks; $H = 9.199$, $P = 0.010$). These results suggest that the potential threat from the introduction of such midges in China is not very important.

Problems in cleaning seeds after harvest may also result in additional invaders; e.g. species pupating within cones, where the cocoons are attached to the seeds. This is probably how the Port-Orford cedar seed midge, *Janetiella siskyiou* Felt., was transferred from North America to Europe (Roques 1983), and this could happen with the Chinese *Chamaecyparis* spp. The removal of galled seeds from seed lots to be imported is also essential to prevent introductions of these species; e.g. *Conartaria oregonensis* Foote on *Pseudotsuga* (Hedlin et al. 1980), *Kaltenbachiola* spp. on *Picea* (Roques 1983; Turgeon and de Groot 1992).

Potential pest invaders associated with seeds and nuts of broadleaved trees

The seeds of broadleaved trees are infested by a variety of insects, especially seed chalcids of the families Eurytomidae, Tanaostigmatidae, and Torymidae, and by seed beetles (Bruchidae) especially in Leguminosae. A compilation of the tree seed chalcids using the data from Noyes (1998) revealed 72 species, of which only six are currently present in China (Table 3). However, as for conifers it is likely that the present records largely underestimate the Chinese fauna infesting broad-leaved trees. As is the case with conifers, the possibility for an exotic seed pest of broadleaved trees becoming established depends on the presence of tree species that are congeneric to the original host. For example, *Bootanellus orientalis* (Mathur et Hussey), a species exploiting specifically the seeds of *Casuarina* (Hamamelidaceae), was introduced along with its host from the Australian-Pacific region to India, North America and Cuba (Grissell 1999) where *Casuarina* is exotic and *B. orientalis* readily became established. *Megastigmus aculeatus* (Swederus), a rose seed chalcid already introduced to China, is probably capable of shifting to all the native and exotic species of *Rosa*, being recorded from 23 species so far (Roques

and Skrzypczyńska 2003). The situation seems similar for seed chalcids attacking other Rosaceae (e.g., *Sorbus*, *Crataegus*), Anacardiaceae (e.g., *Pistacia*, *Rhus*) and legume trees (Leguminosae), because of the large species diversity of these tree families in China.

Unlike cones, entire nuts are used for trade of nut-bearing trees such as oaks (acorns), hazels, chestnuts, walnuts, pecans, hickory, tanoak, etc. Such nuts are normally hosts to weevils in the genus *Curculio* (Coleoptera: Curculionidae), moths in the genus *Cydia* (Lepidoptera: Tortricidae) and Cynipid wasps such as *Eumayria* spp. and *Callirithys glandium* (Giraud) (Hymenoptera: Cynipoidea). Except for most Cynipoidea, most of these species vacate the nuts as mature larvae to pupate in the ground during autumn, but some remain in nuts as late as December. Thus, nut harvesting may occur before larval drop-down, and larvae may be inadvertently included in the collection bags. When accidentally introduced with nut lots, these larvae first need to find a suitable site for pupation. As is the case for conifer spermatophages, the invasive patterns of these species then depend both on the presence of trees in the same tree genera as the original host and on the abundance of the native entomofauna already exploiting the nuts. Most of the genera of potential insect invaders already have representatives in China showing the same nut-feeding behaviour; e.g. *Curculio arakawai* Mats. et Kono, *C. chinensis* Chevrolat, *C. davidi* Fairmaire, *C. dieckmanni* Faust, *Cyllorhynchites ursulus* (Roel) in acorns of *Quercus* and *Quercobalanopsis* (Xiao 1992). Thus, the nut niche is already exploited and invaders may not induce large levels of damage unless they are able to become superior competitors to native species. Special attention should be given to the possible introduction of species in the genus *Conotrachelus* (Coleoptera: Curculionidae) with *Quercus* acorns from North America and Mexico (USDA 1985), because this taxon is not yet present in China.

Concluding remarks

Although the potential insect invaders related to forest seeds as well as the possible routes of invasion to China are well known (cf. Table 1), the development of preventive measures and early detection remains difficult. The cryptic way of life of these insects makes them difficult to detect unless large-scale sophisticated and expensive screening is undertaken at seed importation. Risk assessment could rely on some ecological characteristics that may or may not favour the establishment and spread of invasive spermatophages, such as the presence or absence of tree species congeneric to the native host in China and the importance of the native, specific entomofauna related to cones or nuts. However, since the host finding ability of each invader is not adequately understood, one cannot preclude an exotic spermatophage from aggravating seed damage caused by native cone insects or from being a superior competitor to native seed insects. Some tree species with already significant damage, e.g. Chinese larches, may thus face severe problems with natural regeneration. The apparent emptiness of the seed niche in many relict tree species still present in China may also offer establishment possibilities to exotic sper-

matophages. Such tree species require special attention because many of them are endangered.

In firs at least, observations in Europe showed that the Asian species were less colonized by exotic seed insects than those originating from other regions. There were also indications that the threat to insect biodiversity may be less than expected, with native species remaining dominant in most of the five cases where exotic chalcids were introduced. However, these observations were made under highly artificial conditions in an arboretum and recent observations suggest that there is an inverse relationship between the relative abundances of native and exotic chalcids in some natural fir stands of southern Europe (Roques and Skrzypczyńska 2003).

Finally, China may serve as a source of invasive spermatophages. The seed entomofauna of most tree species in China is still poorly known and there are probably many more than the 17 species of spermatophages currently recognised on conifers from the region. China is known to constitute the original evolutionary centre for many conifer species and most spermatophages are endemic of China or are only present in the East Palearctic. Uncontrolled importations of Chinese seeds to Europe and North America could result in new invasions with detrimental consequences.

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