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Competition between exotic and native insects for seed resources in trees of a Mediterranean forest ecosystem

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Abstract

The seeds of both cedar-of-Lebanon (*Cedrus libani*) and Cyprus cedar (*Cedrus brevifolia*) are attacked in their natural range by a specialised chalcid, *Megastigmus schimitscheki*. From 1995 to 1999, seeds were screened for insect damage in the main cedar plantations of southern France, as well as in the stands where cedar is mixed with firs (*Abies* spp.). X-rays were used to identify chalcid-infested seeds from which the insects were then reared. The surveys revealed the presence of *M. schimitscheki* in all the stands of Atlas cedar, *Cedrus atlantica*, planted at Mt Ventoux, southeastern France. The chalcid also infested seeds of an exotic fir, *Abies pinsapo*, planted in the same area. However, it has not yet reached the cedar plantations in southwestern France, where the seeds are colonised by a related exotic insect, *Megastigmus pinsapinis*, originating from North Africa. The latter species was common in cedar seeds at Mt Ventoux in the early 1990s but seems to have been supplanted by *M. schimitscheki* in the invasion zone. A native chalcid species, *Megastigmus suspectus*, was also shown to have shifted to a slight extent from a native fir, *A. alba*, onto cedar. The presence of three chalcid species competing for cedar seed resources may result in a substantial decline of the regeneration potential of that tree species. At Mt Ventoux, up to 92.6% of the cedar seeds were attacked, with 86.8% due to *M. schimitscheki*. The survey also revealed the widespread presence of another North American chalcid, *Megastigmus rafni*, in the fir stands of southern France.

Introduction

Worldwide exchange and trade of tree materials is rapidly increasing with the development of plantations and ornaments using exotic tree species. 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). 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 long-horned beetle (*Anoplophora glabripennis* [Motsch]), chestnut blight (*Chryphonectria parasitica* [Murr.] Barr.), and pine shoot moth (*Rhyacionia buoliana* [Denis and Schiff.]) caused irreparable damage to forested ecosystems and landscape trees in North America whilst the recent arrival of the pine nematode, *Bursaphelencus xylophilus* (Steiner and Buhrer) Nickle, in Portugal constitutes a considerable threat to the European forests (for a review of invasive forest pests, see a CD-Rom archive of the Internet forum 'Risks of exotic forest pests and their impact on trade'; American Phytopathogical Society 2001).

Invasive forest pests can use a number of pathways (e.g., importation of logs, chips, solid wood packaging and propagative materials), but seed-borne organisms have been neglected. Such organisms are not easily surveyed because of their cryptic way of life, and their impact is thus difficult to estimate. However, a recent survey of insects related to tree seeds in the West Palaearctic revealed that 8 of the 21 species in the seed chalcid genus *Megastigmus* Dalman (Hymenoptera: Torymidae) were introduced and became established in the region through seed trade, mostly from North America (Roques and Skrzypczyńska 2003). These invasions have modified considerably the species composition and levels of impact of seed insects on both native and exotic trees. In Europe, North Africa and Asia Minor, the exotic chalcids have colonised 29 species of native conifers, 43 species of exotic introduced conifers, 28 species of Rosaceae and 9 species of Anacardiaceae. Negative impacts on both natural forest regeneration and insect biodiversity are expected, especially through competition for seed resources (e.g., five invasive species as opposed to one native species in fir seeds).

From this point of view, the entomofauna exploiting cones and seeds of true cedars (*Cedrus* spp.) constitutes an interesting model although it has received relatively little attention in the natural range. In Turkey, a group of three, apparently host-specific species was reported on cedar-of-Lebanon, *C. libani* A. Rich. (Çanakcioglü 1959; Fabre et al. 1994; Alptekin et al. 1997). This includes two species attacking both cone tissues and seeds (*conospermatophages*; Turgeon et al. 1994), *Barbara osmana* Obraztsov (Lepidoptera: Tortricidae) and *Ernobius anatolicus* Johnson (Coleoptera: Anobiidae), and a chalcid specialising in seed exploitation (*spermatophage*; Turgeon et al. 1994), *M. schimitscheki* Novitzky (Hymenoptera: Torymidae). The latter, also observed in Lebanon on *C. libani* (Fabre et al. 1994), is the only recognised insect species from cones of *C. brevifolia* (Hook.f.) A. Henry, a cedar endemic in Cyprus (Hussey 1957). In North Africa, cones of Atlas cedar, *C. atlantica* (Endl.) G. Manetti ex. Carrière, host an entomofauna very similar to that observed on Cedar-of-Lebanon. Three conospermatophages, *Dioryctria peltieri* De Joannis, *Assara praestantella* (Lucas) (Lepidoptera: Pyralidae), *E. fructuum* Peyer. (Coleoptera: Anobiidae), and a spermatophage, *M. pinsapinis* (Hoffmeyer), were reported from Morocco (El Hassani and Messaoudi 1986; Roesler and Luquet 1987; Pintureau et al. 1991; Fabre et al. 1999) and Algeria with the exception of *A. praestantella* (Pintureau et al. 1991; Bouaziz and Chakali 1998; Fabre et al. 1999). The insects exploiting cones of Himalaya Cedar (*C. deodara* [Roxb. Ex. D. Don] G. Don), a species native of central Asia, have never been studied in detail. Only two conospermatophages, *Dioryctria abietella* Denis and Schiffermüller and *Cateremna cedrella* Hampson (Lepidoptera: Pyralidae) have so far been identified (Cheema and Syed 1973; Chacko 1979).

Although cedar stands, mainly *C. atlantica*, had been extensively planted since the 19th century on the northern side of the Mediterranean, especially in southern France, the colonisation of these exotic trees by insects had received little attention until the 1980s, when the increasing importance of cedar for reforestation of the Mediterranean area led to consideration of all factors affecting natural regeneration. At that time, an exhaustive inventory of the cone and seed pests in the French stands revealed the widespread presence of *M. pinsapinis,* which was probably introduced from North Africa along with seeds of Atlas cedar (Roques 1983; Fabre 1986; Pintureau et al. 1991). Besides the chalcid, a native species of *Dioryctria* (Lepidoptera: Pyralidae) was occasionally observed to have included cedar in its host range besides fir (*A. alba* Miller) (Roques 1983). However, a few specimens of another exotic chalcid, *M. schimitscheki*, were unexpectedly observed emerging from seeds of *A. pinsapo* Boissier collected in 1994 at Mt Ventoux, southeastern France. The observation led to a new extensive survey of seed insects in the cedar stands and in the associated fir stands of southern France from 1995 to 1999.

The survey aimed at (i) defining the present range of *M. schimitscheki* and its impact on the potential for natural regeneration of the cedar stands; (ii) comparing the biological characteristics observed in the invasion zone with those noted in the original natural range of Asia Minor; (iii) finding out its competitive status compared with other species exploiting the same seeds, especially *M. pinsapinis*; (iv) investigating whether the shift of *M. schimitscheki* on *A. pinsapo* is stable, and whether the insect could colonise other species of conifers in the introduction zone.

Materials and methods

Study sites and cone collections

Table 1 shows the location of the surveyed stands, which cover most of the French Mediterranean area, extending from the southeastern Alps to the Spanish border. The survey included the six most important stands of *C. atlantica* planted in France, and four 'cedar–fir' mixed stands. These were either cedar stands mixed with a few firs or pure fir stands situated near cedar stands. Firs included a native species, *A. alba*, and two exotic species introduced from Spain (*A. pinsapo*) and Greece (*A. cephalonica* Loudon), respectively. Cone samplings were carried out in every stand at least twice between 1995 and 1999. Because *M. schimitscheki* was first observed at Mt Ventoux, a more extensive survey was carried out in that area (Table 1). From 1995 to 1999, cones were collected from a total of 12 plots of *C. atlantica* (1 plot in 1995 and 1996, 2 in 1997 and 1998 and 8 in 1999), one plot of *A. pinsapo* (every year from 1994 to 1997 and in 1999) and one plot of *A. alba* (1997 and 1999).

The number of cones collected per stand varied between 8 and 139 according to the size of the annual cone crop. As far as possible the collection was made randomly from two to five different cone-bearing trees. Cones were collected during October, when the seeds had reached maturity but before the cones had disarticulated.

Insect rearings

Immediately after being collected the cones were brought back to the laboratory where they were individually disarticulated and the wings of the seeds removed by hand. In order to fit with the natural conditions encountered in southern France during winter, the seeds were then stored in a climatic chamber at 5 ± 1 °C until the end of March. Immediately on being removed from the climatic chamber each seed sample was placed in an emergence box stored in a climatic chamber at a constant temperature of 20 ± 1 °C until

Table 1. Location of the stands of Atlas cedar (*C. atlantica*) and of firs (*A. alba*, *A. cephalonica*, and *A. pinsapo*) surveyed for seed infestation by insects in southern France during 1995–1999.

Stand number	Region	Stand	Tree species	Latitude N	Longitude W	Altitude (m)
1	Mt Ventoux	Bédouin Forest-Collet de Roland	*A. pinsapo*	44°07′33″	5°15′21″	780
2	Mt Ventoux	Bédouin Forest-Collet de Rolland	*C. atlantica*	44°07′33″	5°15′29″	800
3	Mt Ventoux	Bédouin Forest-Jas des Abeyts	*C. atlantica*	44°07′15″	5°16′01″	790
4	Mt Ventoux	Bédouin Forest-Jas des Abeyts	*C. atlantica*	44°07′05″	5°15′55″	740
5	Mt Ventoux	Bédouin Forest-Font de Canaud	*C. atlantica*	44°06′23″	5°15′58″	660
6	Mt Ventoux	Bédouin Forest-Font de Canaud	*C. atlantica*	44°06′44″	5°16′19″	766
7	Mt Ventoux	Bédouin Forest-Chapelle Saint-Jean	*C. atlantica*	44°06′28″	5°13′02″	920
8	Mt Ventoux	Bédouin Forest-Combe d'Ansis	*C. atlantica*	44°07′45″	5°15′26″	833
9	Mt Ventoux	Bédouin Forest-Plaine de l'escalier	*C. atlantica*	44°03′18″	5°15′15″	885
10	Mt Ventoux	Bédouin Forest-Jas du Mourre	*C. atlantica*	44°03′19″	5°16′23″	1065
11	Mt Ventoux	Ventoux Forest-2^{e}Plateforme	*C. atlantica*	44°09′35″	5°09′19″	670
12	Mt Ventoux	Ventoux Forest-Bram-Fam	*C. atlantica*	44°09′58″	5°09′48″	710
13	Mt Ventoux	Ventoux Forest-Ramayette	*C. atlantica*	44°10′14″	5°11′51″	930
14	Mt Ventoux	Ventoux Forest-Combe Mt Serein	*A. alba*	44°11′06″	5°14′16″	1100
15	Southeastern Alps	Issole Forest-La Reynière	*A. alba* *C. atlantica*	43°59′05″	6°30′55″	1100
16	Southeastern Alps	Issole Forest-L'Allier	*A. alba* *C. atlantica*	44°00′49″	6°27′55″	1600
17	Eastern Pyrenees	Marcelly	*A. alba* *A. cephalonica* *C. atlantica*	43°21′15″	2°29′07″	610
18	Eastern Pyrenees	Arques	*A. alba* *A. pinsapo* *C. atlantica*	42°55′58″	2°24′17″	550–750
19	Cévennes	Barjac	*C. atlantica*	44°18′51″	4°22′05″	170
20	Lubéron	Ménerbes	*C. atlantica*	43°47′48″	5°14′28″	680

the end of October. During this period, adult emergence was recorded daily. At the end of October the seeds were again placed in a climatic chamber until the end of March in the following year, then once more put into emergence boxes at 20 °C. The number of adults emerging after one year of prolonged diapause was recorded. The same procedure was followed over three successive years in order to determine the extent of prolonged diapause.

Measurement of the specific importance of the seed chalcid species

The relative importance of each chalcid species was estimated initially by the total number of adults that emerged per seed lot. In addition, for the batches collected in 1995 and 1996, the seeds in each emergence box were examined, and the number of adult wasps which had not been able to emerge from the seeds, or had died by becoming stuck in the exit hole, was counted. The counts were used to calculate the proportion of each species among the chalcids in each batch of seeds. Percentage attack was calculated by dividing the total number of adults (those that had emerged for the 1997 and 1998 batches; those that had emerged and those that had died in the emergence boxes for the 1995 and 1996 batches) by the total number of seeds collected. However, this was only a rough estimate since it did not take into account the larvae which had possibly died in the seeds and whose presence cannot be detected except by X-raying. The batches of seeds collected in 1999 were examined with X-rays (Faxitron – 43855®; 15 Kv, 3 mA, 3 min 30 s) using X-ray sensitive films (Kodak ‘Industrex M’®).

The number of filled, empty and larva-infested seeds was counted (Figure 1). The total percentage of attack was then calculated by dividing the number of infested seeds by the number of filled seeds plus the infested ones. However, chalcids cannot be identified or sexed through observations of larvae on X-ray plates. Therefore, the percentage attack attributable to each species was calculated by multiplying the proportion of each species represented among the adults that emerged by the overall percentage of seeds that were damaged, assuming that the larvae which died within the seeds (and thus did not become adults) were randomly distributed among species.

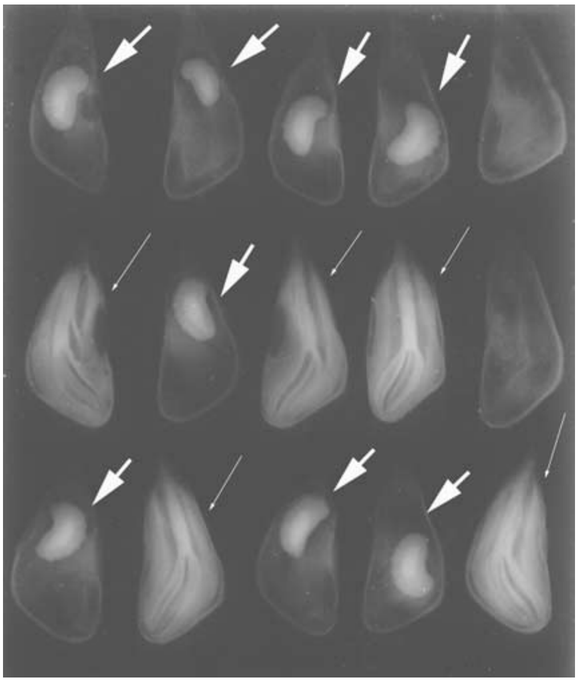

Figure 1. Radiographic picture of seeds of *Cedrus atlantica* showing seeds infested by *Megastigmus* larvae (thick arrow), filled, sound seeds (thin arrow), and empty, aborted seeds (no arrow).

Results

Present invasive range of Megastigmus schimitscheki *in France*

Adult females of *M. schimitscheki* were first observed in 1995 at Mt Ventoux where they emerged on 18 April from *A. pinsapo* seeds collected during the autumn of 1994, at a height of 800 m, in the Bédoin forest at a place known as the ‘Collet de Roland’ (Table 2). Additional adults were then obtained from seeds of both *A. pinsapo* and *C. atlantica* collected in 1995 at the same place. Between 1996 and 1998, the colonisation extended to three other stands of *C. atlantica* growing at heights of 600–900 m on the forest of Mt Ventoux (Table 1). In 1999, all the mature stands of *C. atlantica* surveyed on the communal forest of Bédoin had seeds attacked by *M. schimitscheki*. In contrast, the chalcid was not observed in the stands of a native fir, *A. alba*, located on the northeastern slopes of Mt Ventoux. The other stands surveyed in southern France did not reveal any additional invasions of *M. schimitscheki*. In particular, the chalcid was not observed in the cedar stands of

Table 2. Seed damage by *Megastigmus* seed chalcids and emergence of adult chalcids in the stands of *Cedrus atlantica*, *Abies alba* and *A. pinsapo* surveyed from 1995 to 1999 at Mt Ventoux, southeastern France. Stand numbers refer to Table 1. Adult emergences of each seed batch are summed over three consecutive years.

Crop year	Number of cones analysed	Stand	Host species	Total infested seeds (%)	*M. pinsapinis*			*M.rafni*			*M. schimitscheki*			*M. suspectus*		
					Infested seeds (%)	Nb ♂ em.	Nb ♀ em.	Infested seeds (%)	Nb ♂ em.	Nb ♀ em.	Infested seeds (%)	Nb ♂ em.	Nb ♀ em.	Infested seeds (%)	Nb ♂ em.	Nb ♀ em.
1995	30	2	*C. atlantica*	0.2^{a}	—	—	—	—	—	—	0.2	—	7	—	—	—
1996	78	2	*C. atlantica*	15.0^{a}	4.1	—	280	—	—	—	10.8	431	314	0.1	—	4
1997	30	2	*C. atlantica*	<0.1^{b}	—	—	—	—	—	—	<0.1	1	—	—	—	—
1997	30	11	*C. atlantica*	0.6^{b}	—	—	—	—	—	—	0.6	3	13	—	—	—
1998	15	12	*C. atlantica*	19.0^{b}	—	—	—	—	—	—	19.0	155	96	—	—	—
1998	9	13	*C. atlantica*	11.0^{b}	6.9	—	55	—	—	—	4.0	23	9	—	—	—
1999	19	9	*C. atlantica*	17.1^{c}	12.2	—	10	—	—	—	4.9	3	1	—	—	—
1999	14	3	*C. atlantica*	52.7^{c}	0.5	—	1	—	—	—	52.2	60	48	—	—	—
1999	29	4	*C. atlantica*	47.7^{c}	—	—	—	—	—	—	47.7	18	3	—	—	—
1999	7	5	*C. atlantica*	34.5^{c}	0.9	—	1	—	—	—	33.6	14	23	—	—	—
1999	6	6	*C. atlantica*	70.0^{c}	—	—	—	—	—	—	70.0	33	51	—	—	—
1999	12	7	*C. atlantica*	28.7^{c}	—	—	—	—	—	—	28.7	25	27	—	—	—
1999	10	8	*C. atlantica*	23.8^{c}	—	—	—	—	—	—	23.8	3	2	—	—	—
1999	8	10	*C. atlantica*	92.6^{c}	5.8	—	15	—	—	—	86.8	92	131	—	—	—
1994	139	1	*A. pinsapo*	2.3^{a}	—	—	—	0.2	2	25	0.4	—	54	1.7	16	187
1995	42	1	*A. pinsapo*	2.3^{a}	—	—	—	2.3	26	177	<0.1	—	1	<0.1	—	3
1996	30	1	*A. pinsapo*	0.1^{a}	—	—	—	—	—	—	—	—	—	0.1	—	2
1997	30	1	*A. pinsapo*	1.0^{b}	—	—	—	0.9	1	22	—	—	—	0.2	—	4
1997	30	14	*A. alba*	<0.1^{b}	—	—	—	<0.1	—	1	—	—	—	—	—	—
1999	10	1	*A. pinsapo*	1.3^{c}	—	—	—	1.3	13	5	—	—	—	—	—	—
1999	10	14	*A. alba*	0.5^{c}	—	—	—	0.5	—	1	—	—	—	—	—	—

[a] Percentage of damaged seeds estimated by the ratio: number of emerged adults/total number of seeds per lot.

[b] Percentage of damaged seeds estimated by the ratio: number of adults emerged and dead on emergence/total number of seeds per lot.

[c] Percentage of damaged seeds calculated by the ratio: number of infested seeds visible under X-ray/total number of seeds per lot.

Lubéron which are geographically very close (37 km) to those of Mt Ventoux (Table 3).

Competition between Megastigmus chalcids *for the cedar seed resource and impact on the regeneration potential of cedars*

Three species of *Megastigmus* were observed in seeds of *C. atlantica* in southern France: two exotic species, *M. schimitscheki* and *M. pinsapinis*, and a native species normally related to fir, *M. suspectus* Borries. *M. pinsapinis* was by far the dominant species in the stands outside Mt Ventoux since *M. suspectus* was only found in a ratio of approximately 1 : 100 and *M. schimitscheki* was absent (Table 3). In all the stands, the overall percentage of infested seeds never reached 10%. In contrast, *M. schimitscheki* largely dominated at Mt Ventoux, *M. pinsapinis* being more abundant in only 2 of the 14 samples. At Mt Ventoux, the levels of percentage damage varied from 0.1% to 15% between 1995 and 1998, when only adult emergences were recorded (Table 2). On average *M. schimitscheki* attacked 10.8% of the cedar seeds in 1996, 0.3% in 1997 and 12.5% in 1998 while these proportions were 4.1, 0 and 3.5, respectively, for *M. pinsapinis* during the same years. *M. suspectus* was only observed in 1996 at Mt Ventoux where it infested only 0.06% of the seeds.

In 1999, the X-ray examinations revealed a considerably higher percentage of infested seeds, exceeding 20% in all the sites where *M. schimitscheki* dominated (Table 2). The seed damage reached up to 92.6% in a stand (Jas du Mourre), 86.8% of was due to *M. schimitscheki*. Including the empty seeds, the cone crop in the latter stand thus resulted in only 3.8% filled, healthy seeds, i.e. approximately 3–4 seeds capable of germinating per cedar cone. On average,

Table 3. Percentage of seeds of *Cedrus atlantica* and *Abies* spp. attacked by *Megastigmus* spp. observed between 1995 and 1999 in the stands surveyed in southern France not including Mt Ventoux. Stand numbers refer to Table 1. Adult emergences of each seed batch are summed over three consecutive years.

Crop year	Number of cones analysed	Stand	Host species	Total infested seeds (%)	*M. pinsapinis*			*M.rafni*			*M. schimitscheki*			*M. suspectus*		
					Infested seeds (%)	Nb ♂ em.	Nb ♀ em.	Infested seeds (%)	Nb ♂ em.	Nb ♀ em.	Infested seeds (%)	Nb ♂ em.	Nb ♀ em.	Infested seeds (%)	Nb ♂ em.	Nb ♀ em.
1995	9	16	*C. atlantica*	0.0[a]	—	—	—	—	—	—	—	—	—	—	—	—
1996	29	16	*C. atlantica*	0.0[a]	—	—	—	—	—	—	—	—	—	—	—	—
1996	89	19	*C. atlantica*	4.0[a]	4.0	—	311	—	—	—	—	—	—	<0.1	—	3
1996	45	20	*C. atlantica*	3.3[a]	3.3	—	133	—	—	—	—	—	—	<0.1	—	1
1997	30	15	*C. atlantica*	0.0[b]	—	—	—	—	—	—	—	—	—	—	—	—
1997	30	16	*C. atlantica*	0.0[b]	—	—	—	—	—	—	—	—	—	—	—	—
1997	24	17	*C. atlantica*	5.6[b]	5.6	—	124	—	—	—	—	—	—	—	—	—
1997	30	18	*C. atlantica*	0.0[b]	—	—	—	—	—	—	—	—	—	—	—	—
1997	30	19	*C. atlantica*	2.0[b]	2.0	—	53	—	—	—	—	—	—	—	—	—
1997	30	20	*C. atlantica*	0.0[b]	—	—	—	—	—	—	—	—	—	—	—	—
1998	15	17	*C. atlantica*	9.2[b]	9.2	1	120	—	—	—	—	—	—	—	—	—
1998	15	18	*C. atlantica*	0.0[b]	—	—	—	—	—	—	—	—	—	—	—	—
1998	15	20	*C. atlantica*	0.0[b]	—	—	—	—	—	—	—	—	—	—	—	—
1995	40	15	*A. alba*	0.1[a]	—	—	—	0.1	2	2	—	—	—	—	—	—
1995	28	16	*A. alba*	0.3[a]	—	—	—	0.3	3	19	—	—	—	—	—	—
1996	50	16	*A. alba*	0.1[a]	—	—	—	0.1	—	12	—	—	—	<0.1	—	1
1997	30	15	*A. alba*	0.0[b]	—	—	—	—	—	—	—	—	—	—	—	—
1997	15	18	*A. alba*	5.2[b]	—	—	—	5.2	19	50	—	—	—	—	—	—
1999	13	16	*A. alba*	0.0[c]	—	—	—	—	—	—	—	—	—	—	—	—
1997	23	17	*A. cephalonica*	0.6[b]	—	—	—	0.6	3	9	—	—	—	-	—	—
1997	15	18	*A. pinsapo*	16.1[b]	—	—	—	16.1	90	131	—	—	—	—	—	—

[a–c]Estimate of the percentage of damaged seeds; refer to Table 1.

M. schimitscheki attacked 43.4% of the seeds in 1999 while *M. pinsapinis* only infested 2.4%.

Competition between Megastigmus chalcids *for the fir seed resource*

Among the seeds collected from *Abies* spp., three species of *Megastigmus* were identified: *M. suspectus*, *M. schimitscheki* and an additional exotic species native to North America, *M. rafni* Hoffmeyer. *M. rafni* was largely dominant in all the fir stands located outside Mt Ventoux whatever the species and the year (Table 3). At Mt Ventoux the situation was different and *M. suspectus* was the dominant chalcid in the seed samples from *A. pinsapo* collected in 1994 and 1996 whereas *M. rafni* was dominant in the samples collected in 1995, 1997 and 1999 (Table 2). A greater proportion of *M. schimitscheki* adults than *M. rafni* adults emerged from the seeds collected in 1994, but the proportion of *M. schimitscheki* declined in 1995 and none emerged from the seeds collected during the subsequent years.

Sex ratio, period of adult emergence and prolonged diapause of the seed chalcids

Only females of *M. schimitscheki* emerged from *A. pinsapo* (Table 2). In contrast, the sex ratio ♂ : ♀ of the specimens emerged from *C. atlantica* varied from 0.23 up to 1.37. With the exception of one male, only females of *M. pinsapinis* and *M. suspectus* were obtained from *C. atlantica*. Quite all the adults of *M. suspectus* emerged from *Abies* seeds were females except in the 1994 sampling where males accounted for 7.9% of the emergences from *A. pinsapo*. The sex ratio of *M. rafni* was usually in favour of females in *Abies* seeds.

M. schimitscheki emerged over a 12–15-day period, with a clear protandry (Figure 2). The emergence of *M. pinsapinis* females took place some days later than those of *M. schimitscheki*. All the chalcid species showed prolonged diapause (Table 4) except for *M. suspectus* on cedar, but in this particular case the species was represented by only eight specimens. About 20% of the individuals of *M. schimitscheki*

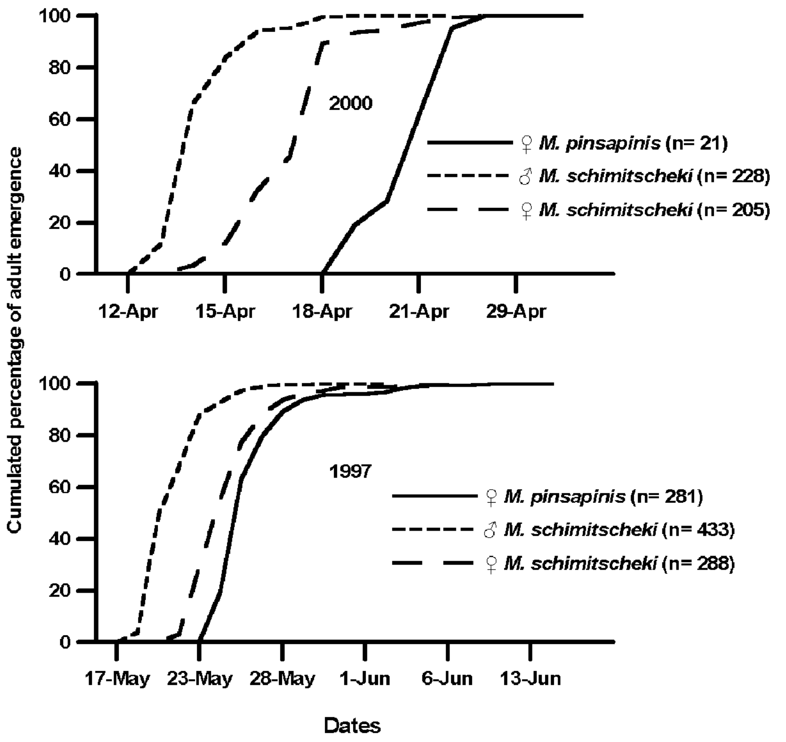

Figure 2. Cumulative adult emergence of *Megastigmus schimitscheki* and *M. pinsapinis* observed in 1997 and in 2000 from seeds of *Cedrus atlantica* collected at Mt Ventoux. The seeds were placed into climatic chambers under 20 °C from 8 May 1997 and 4 April 2000 onwards.

Table 4. Importance of prolonged diapause in the *Megastigmus* species attacking seeds of *Cedrus* and *Abies* spp. in southern France between 1995 and 1999. The values correspond to the average percentage of adult emergence and the numbers into brackets to the total number of adults emerged from the seed samples.

Megastigmus species	Host species	% Adults emerged after 1 year	% Adults emerged after 2 years	% Adults emerged after 3 years
M. schimitscheki	*C. atlantica*	80.8 (1172)	2.9 (42)	16.4 (239)
M. schimitscheki	*A. pinsapo*	89.1 (49)	10.9 (6)	0.0 (0)
M. pinsapinis	*C. atlantica*	99.2 (1081)	0.6 (6)	0.3 (3)
M. suspectus	*C. atlantica*	100 (8)	0.0 (0)	0.0 (0)
M. suspectus	*A. pinsapo*	62.7 (133)	37.3 (79)	0.0 (0)
M. rafni	*A. pinsapo*	42.9 (216)	56.3 (283)	0.8 (4)
M. rafni	*A. alba*	38.5 (52)	61.5 (83)	0.0 (0)
M. rafni	*A. cephalonica*	100 (12)	0.0 (0)	0.0 (0)

infesting cedar stayed in diapause for 2 or 3 years but only ca. 10% did so when developing on fir. *M. pinsapinis* exhibited a very low rate (<1%) of prolonged diapause. In contrast, prolonged diapause was much more prominent in the two other species attacking firs, *M. suspectus* and *M. rafini*, emergences after two years of diapause being most usual in the latter species.

Discussion

The study confirmed that the exotic cedar seed chalcid, *M. schimitscheki*, has become established in southern France, at Mt Ventoux. The absence of *M. schimitscheki* from the large survey of cedar seeds carried out in that area as well as in other stands of southern France at the end of the 1980s indicated that it was introduced between 1990 and 1993 along with the importation and sowing of seeds of *C. libani* collected in the native range of that cedar. *M. schimitscheki* was first described from the Elmali Avlan cedar stand in Turkey (Novitzky 1954), but appeared to be distributed throughout the range of *C. libani* in both Turkey (Çanakçioglü 1990; Fabre et al. 1994) and Lebanon (Forest of Barouk; Fabre, unpublished observations), and in Cyprus on *C. brevifolia* (Forest of Paphos; Hussey 1957). French foresters carried out several trials using seeds of *C. libani* originating from Turkey in the early 1990s at Avignon, near Mt Ventoux.

M. schimitscheki was shown to utilise seeds of Atlas cedar and *A. pinsapo*, both non-native conifer species introduced from Morocco and Spain, respectively. Damage to cedar seeds appeared higher, at least in 1999, on Atlas cedar in the invasion area than on cedar-of-Lebanon in the natural Turkish stands where *M. schimitscheki* destroyed an average of 20% of the seeds (Fabre et al. 1994). However, the spatial progression of the invasion seems to have been relatively slow. Since the presumed date of introduction (i.e., 6–9 years ago), the insect has become common at Mt Ventoux but has not reached the cedar stands in surrounding areas more than 30 km away. Over a period of two successive years (1994–1995), a few *M. schimitscheki* were also observed in seeds of *A. pinsapo* in mixed fir–cedar stands at Mt Ventoux but no more individuals emerged from this fir species, nor from the native *A. alba*. In the native area, *M. schimitscheki* was never observed on fir although mixed stands of *A. cilicica* (Antoine and Kotschy) Carrière and *C. libani* growing in the Turkish Antitaurus (Alptekin et al. 1997) were specifically investigated in 1991 and 1993 (Fabre, unpublished observations).

The biological patterns of the individuals colonising *Cedrus* in the invasion zone did not differ significantly from those reported by Özkazanç (1979) and Çanakçioglü (1990) in Turkey. In the native range, the adult emergence period was observed to coincide with the 9th month of development of the cedar cones and the beginning of seed development. Emergence may start by early April and end by mid-June depending on altitude and location of the stand but generally extends over about 15 days at any one site. We observed the same duration when the seeds were kept in climatic chambers under constant temperatures. The balanced sex ratio usually observed on *Cedrus* in the invasion zone was also close to that reported for the Turkish stands (88.5♂♂ : 100♀♀ on average; Fabre et al. 1994) although it was clearly in favour of males in a few stands, indicating arrhenotoky as is usual in *Megastigmus* (Roques and Skrzypczyńska 2003). Diapause was reported to extend over two successive winters in Turkey whilst it could be prolonged over one or two additional years for some larvae infesting the cedar seeds at Mt Ventoux. However, these observations need to be interpreted with caution because the seeds with diapausing larvae were kept under artificial, constant conditions.

The individuals emerging from seeds of *A. pinsapo* showed some differences in biological patterns when compared to those observed from *Cedrus*. Only females were observed to emerge and most of them (89%) developed in 1 year without prolonged diapause. All insects emerged after 2 years whilst 16.5% of the adults emerged after 3 years in the population infesting cedar seeds even though the diapausing insects were stored under the same artificial conditions. These differences in biological characteristics as well as the absence of emergence from fir seeds since 1995 indicated that the shift of *M. schimitscheki* to *A. pinsapo* may have been among particular, scarce genotypes which have subsequently disappeared.

Up to now, only one seed chalcid species, *M. pinsapinis*, had been reported from the cedar stands planted in France. Described originally on *A. pinsapo* (Hoffmeyer 1931), it was found to be present throughout the natural range of *C. atlantica* in North Africa, from the Rif mountain in Morocco to the mountains of Chréa, Aurès and Little Kabylia in Algeria (El Hassani and Messaoudi 1986; Pintureau et al. 1991; Bouaziz and Chakali 1998; Fabre et al. 1999), which probably constitutes its native area (Roques and Skrzypczyńska 2003). On the other hand, *M. pinsapinis* was not reported from the fir species endemic to Algeria (*A. numidica* de Lannoy ex. Carrière) and Morocco (*A. marocana* Trabut) even though these firs form mixed stands with Atlas cedar (Fabre, unpublished data).

M. pinsapinis was probably introduced into France along with cedar seeds which have been imported regularly from North Africa for over a century. *M. pinsapinis* was observed for the first time in 1947 from cedar seeds collected at Apt, a stand close to Mt Ventoux (Berland 1950). By the 1980s, cedar stands throughout France were colonised by the wasps, including the northern arboreta of Les Barres near Paris and Amance near Nancy (Roques 1983; Fabre 1986; Pintureau et al. 1991; Fabre et al. 1999; Roques and Skrzypczyńska 2003). In these arboreta, *M. pinsapinis* also infested, but at lower levels, *A. nordmanniana* (Steven) Spach, *A. pinsapo* and *A. alba* (Roques and Skrzypczyńska 2003). Our survey confirmed that *M. pinsapinis* occurred throughout the range of introduction of cedar in France, except in the plantations of the southeastern Alps (Issole Forest) and the eastern Pyrenees (Marcilly) where it had, however, been observed previously (Fabre 1986; Pintureau et al. 1991).

Comparisons between stands showed that the percentage of cedar seeds infested by *M. pinsapinis* was notably higher between 1978 and 1983 when levels of damage ranged from 0.1% and 57.9% (Fabre 1986, 1989), whereas levels of damage only reached a maximum of 9.2% during our survey. Percentage damage by insects specialised in cone and seed exploitation is highly variable with year, usually being inversely correlated to annual host abundance (Roques 1983). However, average seed damage by *M. pinsapinis* was limited to 2.4% in 1999 at Mt Ventoux while the cone crop was very light. The same year, more than 45% of the seeds were destroyed by chalcids, with *M. schimitscheki* causing most of the damage. These observations indicate that the recently introduced species has displaced the resident one but this result needs confirmation. Since the two species occupy the same ecological niche, the early emergence and oviposition of *M. schimitscheki* females may explain its possible competitive superiority. The imbalance was enhanced because general population levels were considerably lower in *M. pinsapinis*. Although both species are capable of prolonged diapause, specific strategies may be different. Seed infestation by *M. schimitscheki* was highly variable from year to year but continuously observed every year from 1995 to 1999. Therefore, significant adult emergences yearly occurred during the whole period. In contrast, the absence of seeds infested by *M. pinsapinis* in the batches collected in 1995 and 1997 suggested that the major part of the larvae of generations 1994 and 1996 stayed into prolonged diapause during these years.

The shift of a native chalcid species, *M. suspectus*, from fir (*A. alba*) to cedar was demonstrated for the first time, albeit at very low levels of infestation. This occurrence at Mt Ventoux can be easily explained because stands of *A. alba* and *C. atlantica* are geographically close. However, there are no firs mingled with the cedar stands, or in pure stands, within a radius of several kilometres around the cedar stands of the Lubéron and Barjac where *M. suspectus* was also found.

Mt Ventoux is the only place where three species of the genus *Megastigmus* are in competition for the use of the cedar seed resource. The consequences of these interactions still have to be worked out, but the increase in the number of spermatophagous insects on cedar is likely to result in a decrease of its capacity for natural regeneration which was up to now one of the main advantages accounting for the prodigious extension of this species in Mt Ventoux massif and throughout the whole of the French Mediterranean area.

This study revealed that *M. rafni* was present in all the fir stands that were surveyed, both native or exotic and growing mixed with cedar or near cedar stands. Originating from Canada and the United States, this species attacks the seeds of several fir species (*A. concolor* [Gordon and Glend.] Lindl. ex F.H. Hildebr., *A. grandis* [Douglas ex D. Don] Lindl., *A. magnifica* A. Murray) in its native natural range (Hedlin et al. 1980). Discovered as early as the 1950s inside batches of North American seeds arriving in Great Britain, it very quickly colonised the American firs planted in that country (Hussey 1952). However, *M. rafni* seemed insignificant and even absent as far as continental Europe was concerned until the 1990s, when it became considered a serious pest attacking seeds destined for the Christmas tree industry of Euro-Caucasian (*A. alba*, *A. nordmanniana*) and North American (*A. grandis*, *A. procera* Rehder) origin in Denmark (Ochsner and Jensen 1998). In France this study, together with further data obtained from natural stands of *A. alba* (Roques and Skrzypczyńska 2003; Auger-Rozenberg, unpublished observations) indicates that *M. rafni* is displacing the native species, *M. suspectus*, at least in the southern and eastern parts of the country.

The results presented here bring to light new evidence concerning the phylogenetic relationships between the genera *Cedrus* and *Abies*. Remarkably, practically all the chalcid species in the genus *Megastigmus* develop in the seeds of trees that are linked with a particular vegetal genus, except in five cases, three of which involve a transfer from cedar to fir or *vice versa* (Roques and Skrzypczyńska 2003). Spermatophagous insects such as *Megastigmus* are completely dependent upon their hosts for their development without any possibility of escape, except for the imaginal phase. The evolutionary relationships underlying the host changes in the insects imply a significant phylogenetic proximity among the plants.

Besides seed chalcids and cone insects, vertebrates such as birds and mammals are known to affect the tree regeneration process by consuming and/or dispersing the seeds. Yet, the interactions between the two groups are poorly understood for conifer seeds (Smith and Balda 1979). In the surveyed cedar plantations, pre-dispersal seed predators essentially involve red squirrels (*Sciurus vulgaris* L.) and crossbills (*Loxia* spp.) whilst post-dispersal predators consist of wild boars (*Sus scrofa* L.), bank voles (*Clethrionomys glareolus* [Schreber]), finches (*Fringilla* spp.) and ants (*Formica* spp.). Because the *Megastigmus* species exploit seeds before the cones are mature, they are usually ahead of birds and mammals. In spruce forests, abundance and foraging activity of species specialised on seeds such as crossbills and bank voles is related to the size of seed crops (Holimon et al. 1998; Selås et al. 2002). Therefore, the dynamics of these species may be negatively influenced by large pre-dispersal damage due to seed chalcids, especially during years of poor cone crop, but it is also possible that they use chalcid larvae as an alternate source of food.

From the plant viewpoint, Hulme (2002) suggested that pre-dispersal predators may influence seed dispersal through at least three mechanisms: (i) by reducing crop sizes, they decrease the probability of seeds being dispersed, irrespective of the dispersal mechanism; (ii) density-responsive seed-dispersers may visit fruit crops diminished by seed predators less frequently than they do for larger crops; and (iii) pre-dispersal predators not only may cause the fruit they damage to be rejected by vertebrate seed-dispersers but may also lead to reduced feeding rate on undamaged fruits. Traveset (1993) observed only weak interactions between a related seed-chalcid species, *M. pistaciae* Walker and the avian seed-consumers of a Mediterranean shrub, *Pistacia terebinthus* L. but in *Juniperus communis* L. the infestation of seeds by *M. bipunctatus* (Swederus) promotes the rejection of juniper berries by avian seed-dispersers (García et al. 1999). Similarly, foresters were used for a long time to collect cones of Douglas-fir in squirrel caches because squirrels appear to select cones less infested by a Douglas-fir seed chalcid, *M. spermotrophus* Wachtl (A. Roques, unpublished observations). Indeed, seed insects may have evolved avoidance mechanisms in response to vertebrate seed predators that might attack them. A pine seed chalcid, *M. albifrons* Walker, causes the seed coat to fuse to the subtending scale in ponderosa pine. Therefore, the seed cannot fall when the cone opens, nor the seed be pulled from the cone by birds or squirrels (Smith and Balda 1979).

However, Hulme (2002) pointed out that high seed predation rates do not necessarily translate into dramatic reduction in plant populations. Even moderately high seed loss may have little impact on demography, especially when seed losses to predators are buffered by a large persistent seed bank and seed predators are satiated by large seed crops. Persistent seed banks are of limited occurrence in both fir and cedar because the seeds have a limited survival in the forest soil (B. Fady, personnal communication). Mast seeding is observed every three to four years in *C. atlantica* at Mt Ventoux (Toth 1984). Is it sufficient to satiate the seed predators when the invasion by *M. schimitscheki*, and the subsequently high level of seed damage, is likely to have perturbed the preceding relationships between seed chalcids and vertebrate seed consumers? The large annual variations in *Megastigmus* infestation tends to support the hypothesis but confirming requires to precise the interactions *Megastigmus*–vertebrate–cedar seed, and more especially whether the vertebrate consumers can discriminate between infested and sound seeds.

In conclusion, the introduction of exotic seed chalcids into Europe is not really surprising. Indeed, up to now conifer seeds can be imported to Europe without any particular phytosanitary check and it is quite likely that other spermatophages of exotic origin have been or will be introduced if no controls are exercised. Although the potential insect invaders related to forest seeds as well as the possible routes of invasion are quite well known (Roques and Skrzypczyńska 2003), the development of preventative 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 (e.g., X-raying) is undertaken at seed importation. Because of the obvious risks due to infested seeds being deposited on the ground which could allow adults to escape over a period of several years in the light of diapause phenomena, we might reasonably suggest that only pre-germinated seeds should be used in nurseries. The seeds should be placed in layers at 4–5 °C and those that fail to germinate should be destroyed. Risk assessment should also rely on some ecological characteristics that may favour or not the establishment and spread of invasive spermatophages, such as the presence or absence of tree species congeneric to the native host and the importance of the native fauna related to cones and seeds. 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 seed predators or from being a superior competitor to native spermatophages. Some tree species with already significant damage may thus face severe problems for natural regeneration. The invasion could also constitute a threat to biodiversity of animals mostly relying on seed resources for food, which makes them vulnerable to any factor that reduces the size of seed crops.

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