Elimination of cone and seed pests by wildfire opened a five-year regeneration window in a non-regenerating incense-juniper (Juniperus thurifera L.) stand

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L'élimination des ravageurs des cônes et graines par un incendie accidentel a ouvert une fenêtre de régénération de cinq ans dans un peuplement de Juniperus thurifera *L. présentant des difficultés de régénération naturelle*

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Abstract

The sanitary status of seed cones of incense juniper, Juniperus thurifera, *has been surveyed from 2001 to 2011 in a relict population of the French Pyrenees (Rié Mountain, Haute-Garonne, France) which has been severely affected by a wildfire during the summer 2003. Damage to seed and cones was compared on the same trees before and following the 2003 fire. Before the fire, natural regeneration was severely hindered by the joint damage of a seed mite,* Trisetacus quadrisetus, *and a seed chalcid,* Megastigmus thuriferana *which limited to 25-55 the number of sounds seeds falling on the ground per tree. The fire destroyed a large part of the stand but simultaneously killed most of insect seed predators. No flowering was observed the following year (2004), thus contributing to eliminate the remaining predators. In spite of large annual fluctuations, more than 200 sound seeds were dispersed on the average per tree in 2006 and 2009,* i.e. *4-10 times more than before the fire. Seed chalcids and mites only began to recolonize the stand during summer 2008, probably originating from nearby stands of* J. thurifera *(chalcids) or* J. communis *(mites). Although the pest populations regularly increased every year, cone damage remains concentrated on less than ten trees. Unexpected events such as wildfires may thus play a regulating role upon seed predation by arthropods and opened a regeneration window of five years at least, as it can be observed from the sudden appearance of numerous seedlings during this period.*

Keywords: pests, *Juniperus thurifera*, seed cones, seeds, natural regeneration, fire.

Résumé

L'évolution du potentiel de régénération naturelle de la population pyrénéenne relique de Juniperus thurifera *de la montagne de Rié (Haute-Garonne, France) a été surveillée de 2001 à 2011, avant et après l'incendie qui a*

Mots clés : ravageurs, *Juniperus thurifera*, galbules, graines, régénération naturelle, incendie.

détruit une large partie de ce peuplement en 2003. La production de galbules, leur état sanitaire de la floraison à la maturité, et le nombre de graines viables résultantes ont été mesurés chaque année sur les dix mêmes branches de dix arbres différents. Avant l'incendie, l'impact conjugué du chalcidien des graines, Megastigmus thuriferana*, et des acariens des galbules,* Trisetacus quadrisetus*, réduisait de manière drastique le potentiel de régénération naturelle du Genévrier thurifère, avec seulement 25 à 55 graines pleines tombant au sol en moyenne par arbre. L'incendie de 2003, survenu pendant une période où les ravageurs ne pouvaient s'échapper des galbules, a conduit à l'élimination complète de leurs populations sur le site. Après une année de reprise sans floraison, l'absence des ravageurs s'est traduite par une augmentation significative du potentiel de régénération du thurifère par rapport à la situation prévalant avant l'incendie. Malgré des variations interannuelles de fructification, plus de 200 graines pleines sont tombées en moyenne au sol par arbre fructifère en 2006 et en 2009, soit de quatre à dix fois plus qu'en 2002-2003. La recolonisation du site par les chalcidiens et acariens n'a commencé qu'à l'été 2008, probablement à partir de populations voisines de* J. thurifera *(chalcidiens) ou* J. communis *(acariens). Malgré une augmentation progressive des populations de ravageurs, les dégâts restent concentrés jusqu'à maintenant sur moins de dix arbres. L'incendie paraît avoir ainsi joué un rôle régulateur sur la prédation des graines par les ravageurs, avec l'apparition d'une fenêtre de régénération de l'ordre de cinq années comme l'attestent les nombreuses jeunes plantules apparues sur le site après l'incendie.*

Introduction

Many factors are susceptible to affect the natural regeneration of conifer trees (Rodrigo *et al.* 2004; Verheyen *et al.* 2009). Among them, arthropod damage to cones and seeds during the pre-dispersal phase may be considered to play a key role because it may severely decrease the annual number of seeds then available for germination (Turgeon *et al.* 1994). Extensive surveys of the impact of cone and seed pests were carried out since a long time in economically important species of the family Pinaceae (*e.g.*, *Abies*, *Larix*, *Picea*, *Pinus*, and *Pseudotsuga* spp.; for a review, see Turgeon *et al.* 1994). In contrast, little remains known about the damage due to the fauna exploiting the seed cones of Cupressaceae, with the exception of evergreen cypress, *Cupressus sempervirens* L. (Guido *et al.* 1998; Battisti *et al.* 1999, 2003; Roques *et al.* 1999), and common juniper, *Juniperus communis* L. (Garciá, 1998, 2001; Garciá *et al.* 2000, 2002; Falke, 2004; Rouault *et al.* 2005; Verheyen *et al.* 2009). Conservation purposes recently led to investigate whether the arthropods damaging seeds could constitute, besides the effects of human activity, an aggravating factor hindering the preservation of some endangered Cupressaceae species such as the Atlas cypress, *Cupressus atlantica* Gaussen, and the incense juniper, *Juniperus thurifera* L. (El Alaoui El Fels & Roques 2006a).

For example, insects and mites developing in cones of *J. thurifera* have to been shown to limit drastically the number of viable seeds susceptible to be dispersed in the Atlas Mountains of Morocco (El Alaoui El Fels *et al.* 1999a; El Alaoui El Fels & Roques 2006b). In these areas, pest damage was observed to decrease the average number of sound seeds to less than 0.2 per cone, resulting in a very low probability of regeneration because of the subsequent action of other mortality factors following germination (El Alaoui El Fels *et al.* 1999a). A similar high impact of cone and seed pests was also noticed in other parts of the patchy range of this juniper species such as the French Alps and Corsica (Roques *et al.* 1984) and the French Pyrenees (Roques & Auger-Rozenberg 2006). In both Morocco and France, the natural regeneration of native stands usually appeared very limited, and even quite non-existent in most cases. In contrast, the recruitment of young seedlings was commonly observed in Spain although overall pest damage did not seem to differ significantly from the value observed in Morocco (El Alaoui El Fels *et al.* 1999b). Indeed, Roques & El Alaoui El Fels (2002) showed that the number of viable seeds remaining in cones following pest damage is positively correlated with the initial number of seeds; thus, an initial number of seeds per cone higher in the Spanish stands than in the Moroccan and French ones may partly explain the observed differences in natural regeneration. For the same reasons, *J. oxycedrus* L. and *J. phoenicea* L. may be favored by their higher number of seeds when they grow in sympatry with *J. thurifera* (Roques & El Alaoui El Fels 2002).

In many conifers, 'masting' (*i.e.*, the synchronous production of large seed crops at variable intervals; Silvertown 1980), is a common reproductive phenomenon. Seed production is highly irregular in both space and time, which results in large annual variations in seed predation with an inverse relationship between the damage percentage and the change in cone crop size from the past year to the current year (Turgeon *et al.* 1994; Poncet *et al.* 2009; Auger-Rozenberg & Roques 2012). In some years, a sudden, sharp increase in cone abundance is likely to outpace the increase in arthropod populations and their ability to attack cones, and as a result a large quantity of seeds would escape from predation and contribute to the regeneration process (Predator Satiation hypothesis; Janzen 1971; Silvertown 1980). However, an 8-year study in the Middle Atlas Mountain revealed a quite different figure in *J. thurifera*. The fluctuations in the annual cone abundance appeared limited whereas cone damage varied quite in parallel but never dropped below 30% (Roques & El Alaoui El Fels 2002). It has been hypothesized that unpredictable events such as late frosts, which may suddenly kill the available flowers, or wildfires, are susceptible to break such equilibrium between juniper cones and the populations of associated arthropods, and thus favor natural regeneration (Roques & Auger-Rozenberg 2006).

An occasion to study this process has been given by the occurrence in summer 2003 of a wildfire which destroyed the major part of a rather isolated stand of *J. thurifera* in the French Pyrenees, which had been previously monitored for arthropod damage (Cambecèdes *et al.* 2005). Before the fire, only three phytophagous species attacked cones and seeds in this stand, which corresponded to a low species richness compared to Morocco (8 species), the Alps and Spain (4 species) (Roques & Auger-Rozenberg 2006). Only two of these species were effectively affecting seed yield. A seed chalcid, *Megastigmus thuriferana* Roques et El Alaoui (Hymenoptera: Torymidae), is specialized in the exploitation of seeds of *J. thurifera* (Auger-Rozenberg *et al.* 2006). Using its ovipositor, the female chalcid lays eggs directly into the seeds where the whole larval development will take place, with only one larva per seed. The mite, *Trisetacus quadrisetus* Thomas (Acarina: Eriyophiidae), is galling the seeds which then protrude noticeably through cone surface (El Alaoui El Fels & Roques 2006a). However, this species is oligophagous, being also observed on other junipers such as *J. communis* L. *J. sabina* L., *J. oxycedrus*, and *J. phoenicea* (Roques 1983). The third species, a scale, *Carulaspis juniperi* (Bouché) (Hemiptera: Diaspididae), is observed on all juniper species in Europe (Graora *et al.* 2010). It develops and feeds on the outer part of the cone of *J. thurifera* but it seems to have no impact on seed viability (Roques & Auger-Rozenberg 2006). Because the three species were either too tiny to move or larvae concealed in seeds when the fire occurred, the major part of their populations could not escape the burning or the too hot temperatures observed in the areas that were not completely burnt. The few survivors disappeared during the following year because no cones were available at all in the stand (Roques & Auger-Rozenberg 2006). It has thus been hypothesized that a regeneration window may exist if the stand succeeds in flowering again before the cone and seed pests recolonize it. Wildfires are known to be responsible for massive seed release in conifer species with serotinous cones (Baskin & Baskin 1998). However, the relationships with cone and seed consumers were little investigated except in a few angiosperms with seed capsules. In the Australian *Eucalyptus baxteri* (Benth.) Maiden & Blakely ex J.M. Black and *Casuarina pusilla* Macklin, massive seed release following fire can lead to predator satiation and large subsequent recruitment of seedlings (Andersen 1987).

Therefore the objectives of our study were to 1) to test whether the disappearance of cone and seed pests following the 2003 wildfire resulted in a significant increase in the number of sound seeds available for germination; 2) to monitor the possible recolonization of the stand by the pests and to assess the time during which the stand would remain free of any pest; and 3), to measure the dynamics of seed damage after recolonization.

Material and methods

Monitoring of cone and seed damage before and following the 2003 wildfire

The monitoring procedure followed the one described by Roques & Auger-Rozenberg (2006) in order to survey the complete development of a cone generation, from initiation to seed maturity. In 2002, 15 trees with female cones were randomly selected in the stand,

and two branches per tree were tagged in early June. The total number of 1st- and 2nd-year cones present on the tree was visually estimated. The position of all of the 1st-year cones present of the tagged branches was mapped, and their sanitary status checked. All the 2nd-year cones (*i.e.*, from generation 2001) present on the tagged branches were then collected and dissected to identify possible damage to species. Their seeds were extracted and individually radiographed in order to measure the respective numbers of filled, empty and infested seeds. Seed radiography was carried out using a Faxitron 43855® apparatus (15Kv, 3mA, 3'30'') and X-ray sensitive films (Kodak® "Industrex M"). The infested seeds were placed in individual rearing boxes stored in an outdoor insectary located at INRA, Orléans, France (47°83'N, 1°91'E, 107 m elevation), according to the method defined by Roques & Skrzypczyńska (2003). Adult emergence was surveyed over the two years following seed collection because of a possible prolonged diapause.

The same trees and branches were visited again in late October to check the survival of the 1st-year cones and to assess possible damage. The following year, the surviving cones having turned to 2nd-year cones on the tagged branches were counted, collected and treated as above whereas the newly- appeared 1st-year cones were counted and mapped.

However, the 2003 fire resulted in the complete burning of six of the tagged trees whilst the branches of four more trees did not resprout the years after. Thus, only five of the original trees were available for further monitoring. Because no flowering occurred in 2004, we could only add in June 2005 ten more flowering trees, which were selected at random. These 15 trees (five original and ten added in 2005) were monitored similarly as above two times a year from 2005 to 2011.

In order to get a more precise spatial estimation of the recolonization of the stand by cone pests, 12 additional trees were sampled in 2011, with a collection of 30 1st-year and 30 2nd-year cones per tree. All the cones were dissected, and their seeds X-rayed, in order to assess the presence and numbers of cone pests.

Data analysis

The following variables were measured every year on each tagged branch and their mean values were compared between the periods preceding and following the 2003 fire: 1) number of 1st-year cones initiated in spring; 2) percentage of 2nd-year cones remaining on branch at maturity in autumn with regard to the initial number of 1st-year cones; 3) percentage of cones damaged by herbivores; 4) specific percentage of cone damage per herbivore species; 5) mean number of seeds per cone; 6) proportion of sound, infested and empty seeds; 7) mean number of filled seeds. Seed damage was calculated as the ratio of infested seeds on the number of seeds considered as available for pest development, *i.e.* filled seeds plus infested seeds (Roques & Skrzypczyńska 2003). Then, the total number of filled seeds potentially- dispersed per tree was extrapolated from the percentage of sound seeds per branch and the total number of 2nd-year cones remaining on tree at maturity. In order to harmonize the assessments, the data will be presented by cone generation; *i.e.* generation 2001 will correspond to 1st-year cones analyzed in 2001 but to 2nd-year cones and seed yield analyzed in 2002. Because neither the overall seed damage nor the specific damage followed a normal distribution (Kolmogorov-Smirnov test), the comparisons were done using a non-parametric Kruskal-Wallis test.

Results

Annual variation in flowering magnitude and in size of the final crop before and following the 2003 fire

The mean number of 1st-year cones per branch largely varied between years, with intervals of 2-3 years between years of large flowering (Figure 1). Less than forty 1st-year cones were observed per branch before the 2003 fire. No flowering at all occurred the year following the fire (2004) but 1st-year cones appeared again in 2005 at a magnitude larger than previously. Then, periods of low flowering alternated with years of large flowering to culminate with ca. seventy 1st-year cones per branch in 2011.

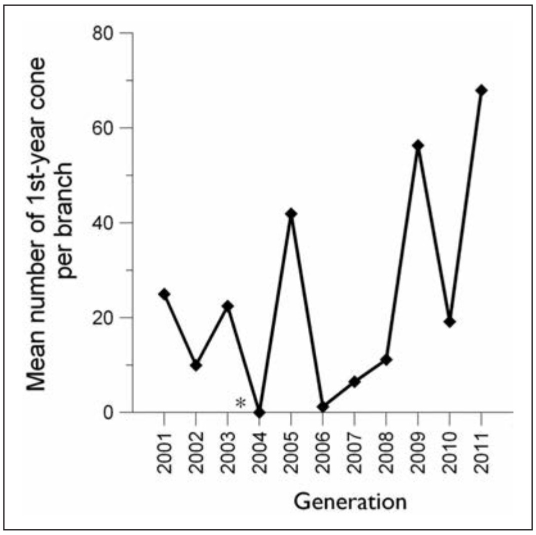

Figure 1 – Annual variation in the mean number of 1^st^-year cones having appeared from spring 2001 to spring 2011 on the branches surveyed at Rié. *: Fire occurrence.

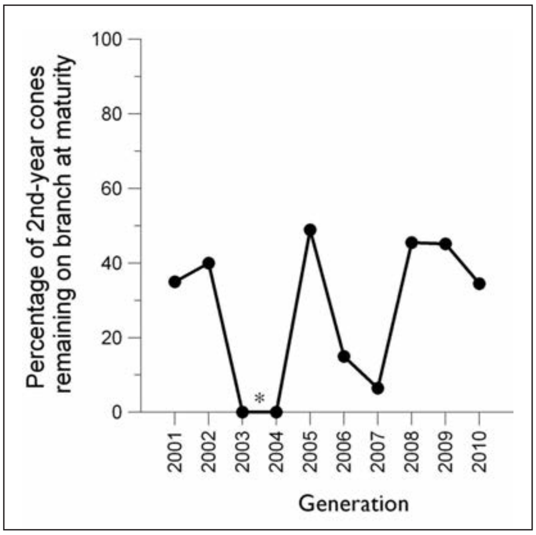

Figure 2 – Annual variation in the proportion of 2nd-year cones remaining at maturity on the branches surveyed at Rié from 2001 to 2011. Data are presented by cone generation, meaning that generation N corresponds to mature cones still present on branches in autumn N + 1. *: Fire occurrence.

The percentage of 2nd-year cones remaining on branch at maturity was not different before and after the fire (Figure 2). About 35 to 49% of the initial number of cones survived during the years of large initial crop but the survival was less than 15% when the initial crop was low.

Annual variation in cone damage before and following the 2003 fire

Cone damage was significantly different before and after the fire for both 1st-year and 2nd-year cones (Figure 3). Before the fire occurred, more than 20% of the 1st-year cones were observed to be attacked every year by mites (Figure 3A), and a large number of them probably dropped to the ground before reaching the 2nd-year of development. At maturity, 35 to 45% of the 2nd-year cones remaining on branch were attacked by either mites or chalcids (Figure 3B). After the fire, no chalcid and mite damage was observed until 2009 where a few (12.3%) 2nd-year cones of the generation 2008 were observed to be attacked by these species. However, large numbers of cone scales were observed during the meantime with a culmination in 2008 where up to 80% of the 2nd-year cones of the generation 2007 were infested (Figure 3B).

From 2009 on, mite damage on 1st-year cones as well as chalcid and mite damage on 2nd-year cones regularly progressed every year.

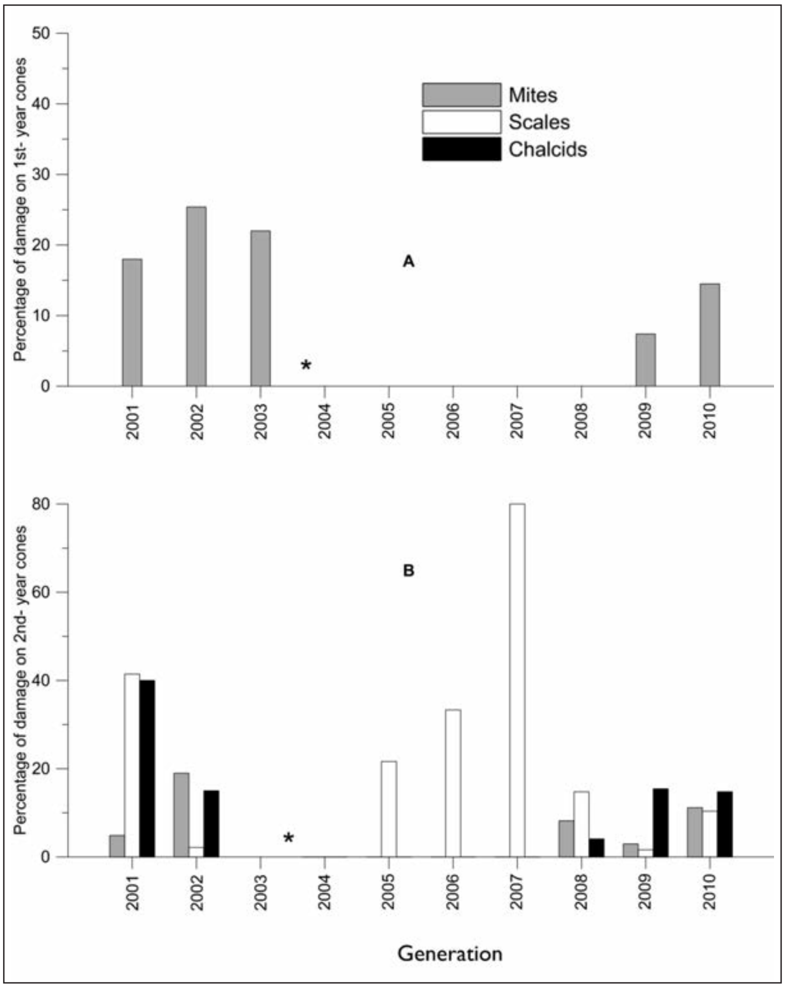

Figure 3 – Cone damage caused by the different species of arthropods on the branches surveyed at Rié from 2001 to 2011. A– Damage to 1st-year cones; B– Damage to 2nd-year cones. Data are presented as in Figure 2. *: Fire occurrence.

However, overall damage remained still lower than in the generations 2001-2003, and did not exceed 14.5% in 1st-year cones (Figure 3A) and 26.0% in 2nd-year cones when mite and chalcid damage are added (Figure 3B).

Before the fire, all of the surveyed trees were attacked by either chalcids or mites. After the fire, the number of infested trees remained low (eight in total) after the pests have reappeared since 2009. Three of the 15 surveyed trees were attacked in 2009 (generation 2008), only one in 2010 (generation 2009), but the infestation extended to six trees in 2011 (two from the original survey and four from the additional collection of 12 trees). Only one tree was attacked every year during these three years (Figure 4). Mites recolonized a total of seven trees up to now whereas chalcids were observed on two trees, only one tree sharing both pests.

Annual variation in dispersal of sound seeds before and following the 2003 fire

The total number of seeds per mature cone averaged 2.58 ± 0.06 for the generations 2001 and 2002 preceding the fire. The values observed in the years following the fire were not significantly different (average 2005-2010: 2.51 ± 0.05; Kruskal-Wallis test; $P = 0.076$).

Before the fire, the percentage of filled seeds did not exceed 20% of the total seeds whereas it was always higher for the generations 2005 to 2008 (*i.e.*, mature seeds of years 2006 to 2009), reaching up to 45% for the generation 2008 (Figure 5A). This percentage largely decreased during the two following years. In contrast, empty seeds represented more than 40% of the total seeds whatever the year, and more especially in 2011 (generation 2010) where they accounted for up to 87% of the total seeds.

Mites and chalcids were destroying up to 40% of the total seeds in 2002 (generation 2001) but then, any damage disappeared until 2009 (generation 2008). In the following years, the proportion of infested seeds increased again but never exceeded 15% of the total seeds. When only sound and infested seeds were considered, seed damage decreased by 42.4 to 64.8% the expected seed yield before the fire (Figure 5B). After a 5-year period where this damage was nil, it only decreased by 24.1% the expected seed yield of the generation 2008 but in the following years the values became similar to these observed before the fire.

The presence of scales on the outer part of cones did not affect negatively seed health. A specific analysis carried out on a lot of 150 2nd-year cones of the generation 2005 even revealed that cones colonized by scales contained significantly more seeds (3.2 ± 0.2 vs. 2.5 ± 0.2 in cones without scales; Kruskal-Wallis test; $P = 0.0199$), and included a higher percentage of sound seeds (59.9 ± 7.9% vs. 13.8 ± 3.2%; Kruskal-Wallis test; $P = 0.0000$). A similar analysis was carried out in 2010 on cones infested by seed chalcids in the single tree they infested during that year. Only one seed was attacked in 38 (81%) of the 47 infested cones whereas eight cones showed two infested seeds (17%), and only one cone had three seeds attacked (2%). The cones attacked by chalcids also contained significantly more seeds (3.72 ± 0.18) than the healthy ones (2.03 ± 0.15) (Kruskal-Wallis test; $P = 0.0000$).

The total number of filled seeds was extrapolated to an average of less than 55 per tree before the fire (Figure 6). After the fire, this average number increased to more than 200 in 2006 (generation 2005) and 2009 (genera-

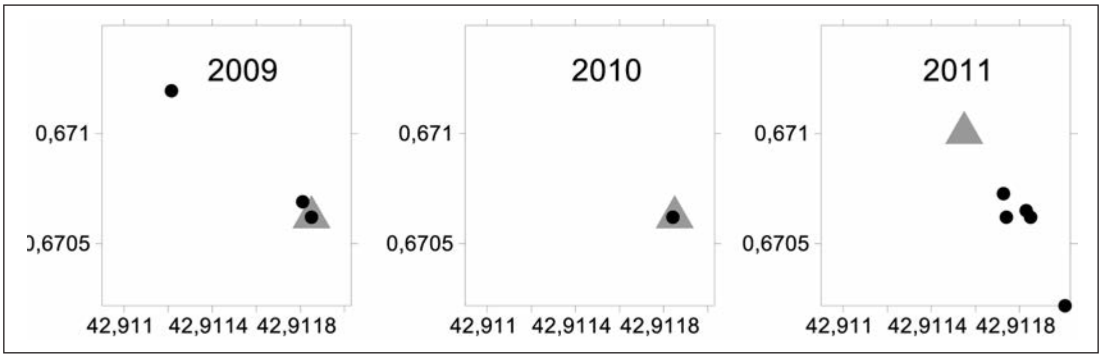

Figure 4 – Spatial position of the trees recolonized after the fire by the chalcid **Megastigmus thurifera** ***(triangle) and the mite*** **Trisetacus quadrisetus** ***(circle).***

tion 2008) when the pests were not present or just began to recolonize. Then, it decreased again during the following years. However, large variations were observed between trees, the number of filled seeds susceptible to be dispersed per tree varying from 0 to 350. Considering all the surveyed trees, up to 3600 filled seeds were available for dispersal in 2006 (generation 2005) and still more than 2000 in 2009 (generation 2008) (Figure 6).

Discussion

Our survey showed that the 2003 wildfire resulted in a complete disappearance for a 5-year period of the pests affecting seed cones during the pre-dispersal phase. A few individuals might have survived to fire and high temperatures in areas which were little burnt but the null crop observed in 2004 led the populations to disappear since no prolonged diapause allowing an escape in time is apparently existing in these species (Roques, unpublished. results). Because the *Megastigmus* larvae observed in seeds in June 2009 were necessarily issued from eggs deposited during July 2008, the recolonization by chalcids probably began at that time. It is likely that the recolonizing chalcids originated from nearby populations developing on *J. thurifera* at Bezins-Garraux and St Béat, two small stands distant of ca. 5 km, where 4-5% of the cones were observed to be attacked by chalcids in 2006-2007 (Roques, unpublished results). Mites were first observed during spring 2009 on both 1st-year and 2nd-year cones but it is not known whether they can directly attack 2nd-year cones (*i.e.* in 2009) or if they must first develop in 1st-year cones (*i.e.*, attack in 2008). These oligophagous mites may have switched from cones of *Juniperus communis*, several shrubs of this species present in the same valley having not been affected by the fire. Another oligophagous species common on junipers, the scale *Carulaspis juniperi,* profited from the absence of the major pests to occupy the emptied niche. Scales re-appeared as soon as cones were available in 2005 and their populations colonized up to 80% of the cones in 2008. Mendel *et al.* (1997) also noticed that a scale insect, *Matsucoccus josephi* Bodenheimer & Harpaz, rapidly recolonized the young seedlings which have appeared following a wildfire in a stand of Aleppo pine,

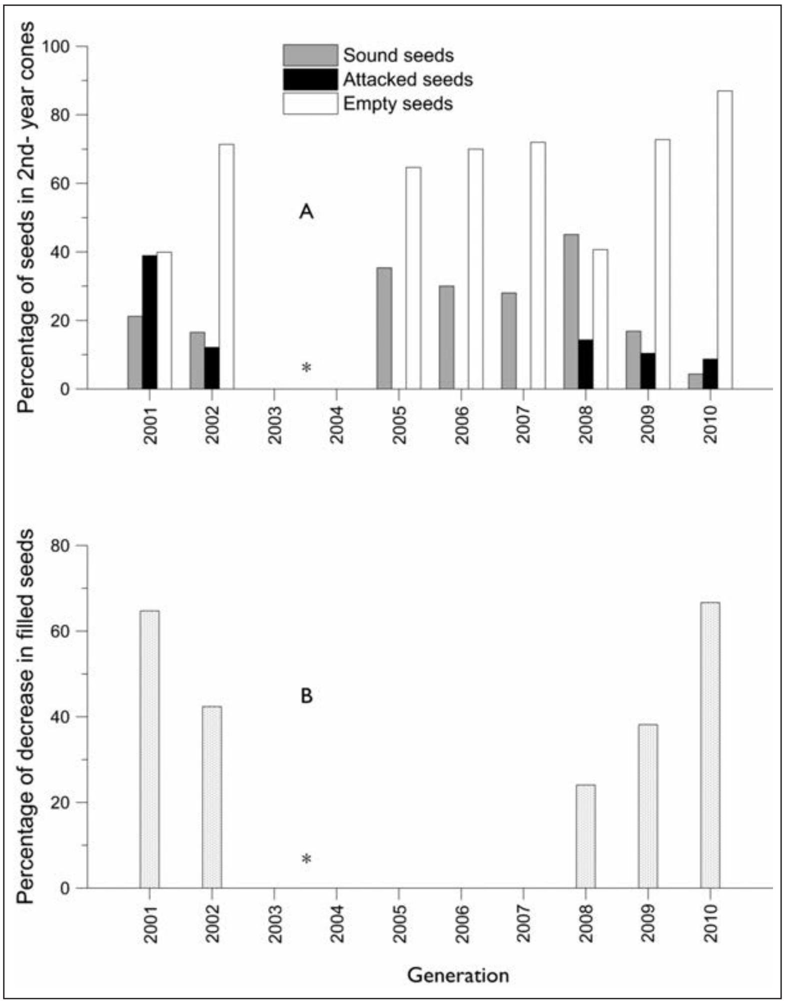

Figure 5 – Annual variation in the sanitary status of the seeds present in the 2nd-year cones remaining at maturity on the branches surveyed at Rié from 2001 to 2011. A– Proportion of sound, infested and empty seeds vs. total seeds; B– decrease in seed yield due to pests. Data are presented as in Figure 2. *: Fire occurrence.

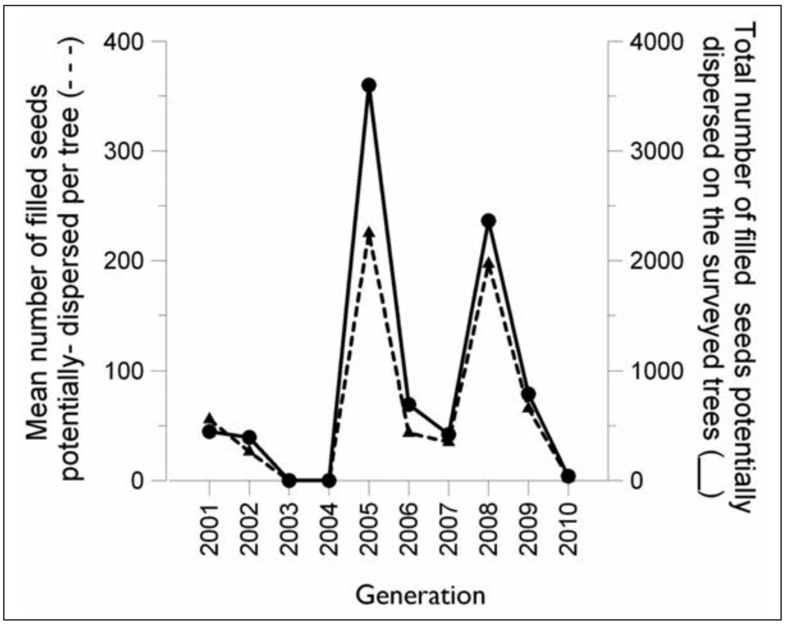

Figure 6 – Extrapolation of the annual numbers of filled seeds potentially dispersed by the surveyed trees from 2001 to 2011. Data are presented as in Figure 2.

Pinus halepensis Mill. Thus, cone scales were apparently much more mobile at the adult stage than the other species. However, their importance rapidly decreased when chalcids and mites reappeared. Moreover, we confirmed that the scales have no impact on seeds but prefer to attack cones with a higher seed content and a higher number of filled seeds. A similar selection process seemed to occur for *Megastigmus*. The cones attacked by chalcids also contained significantly more seeds than the uninfested ones present on the same tree. This did not seem true for mites but large differences in mite damage were noticed between trees, similarly as Guido *et al.* (1995) observed for a congeneric mite, *Trisetacus juniperinus* Nalepa, attacking cones of evergreen cypress, *Cupressus sempervirens*.

The disappearance of chalcid and mite pests immediately resulted in a significant increase in the number of sound, filled seeds susceptible to be dispersed, the more as a very large flowering occurred two years after the fire (a delayed consequence of the fire?). Then, the recolonization process by cone pests was rather slow, and only affected a limited number of trees which were rather spatially concentrated until 2011 when mites expanded significantly but not chalcids. As a consequence of this slow recolonization, in spite of annual fluctuations in the flowering magnitude the canopy seed bank extrapolated per tree was every year from 2006 to 2010 larger than the values observed before the fire, and especially 4 to 10 times larger in 2006 and 2008, respectively. However, the high proportion of empty seeds limited the potential size of the canopy seed bank in most years. This was especially true in 2011 where quite no seeds were dispersed whilst the pest damage was still low. The causes could not be identified yet but they were apparently not related to fire occurrence. The large variation in the proportion of empty seeds among trees (*e.g.*, ranging from 47 to 100% of the total seeds in 2010) led to hypothesize pollination problems, genetic incompatibility, or inbreeding.

As a probable consequence, new seedlings began to be observed at a high frequency since 2006 on. A survey in 2010 noticed 261 seedlings with a stem diameter smaller than 2 cm (Cambecèdes *et al*. 2010). Although a few may have pre-existed to the fire, it is likely that most of these seedlings were issued from seeds having germinated after the fire. In 2010, this category of seedlings predominated, representing 30.8% of all *J. thurifera* trees in the pure stand whereas they accounted for less than 10% in 2001 (Cambecèdes *et al.* 2010). Although the canopy seed bank was much larger during the years following the fire, it could not be excluded that some new seedlings were issued from the ground seed bank constituted before the fire. However, to sustain this hypothesis there was no data about the germinating capability of *J. thurifera* seeds following a wildfire. In the congeneric *J. phoenicea*, tests using buried seeds showed a rapid decrease in seed viability after a fire, 46% of the buried seeds remaining viable after 1 year but less than 5% after 2 years (Clemente *et al*. 2004).

The effects of fire will also depend on when the burn occurs within a plant's reproductive life cycle compared to the dynamics of pest populations. Thus, Peters *et al.* (2005) suggested that masting is a key process that interacts with fire to shape stand composition in boreal mixedwoods of white spruce, *Picea glauca* (Moensch) A. Voss. Small mammals, insects, and birds consumed most seeds in years with low to moderate cone crops, and spruce density was significantly lower after fires that occurred 1-3 years before a mast year than after fires occurring during mast years.

Besides wildfires, it can be noticed that prescribed burning was used as a management method to control populations of cone beetles (*Conophthorus* spp.; Coleoptera: Scolytidae) affecting seed production in white (*Pinus strobus* [L.]) and red (*P. resinosa* Ait.) pines in North America (Miller 1978; Wade *et al.* 1989). Miller (1978) showed that burning of naturally accumulated fuels in red pine stands significantly increased by 11-45% the number of cones free of all cone-destroyers. However, prescribed litter burning in *J. thurifera* may have little effect on the population density of cone and seed pests because their life cycle usually takes place in the cones remaining on tree, and rarely in these fallen on the ground. Evaluating the effects of seed predators on post-dispersal seed removal and early seedling establishment of *Pinus nigra*, Ordóñez & Retana (2004) also showed that recently burnt areas were the most favorable habitat for recruitment. These areas have both the lowest vegetation cover and the lowest abundance of granivorous ants because there was mortality after fire and new colonizers had not yet established. Another mechanism has been shown in the Australian *Eucalyptus baxteri* and *Casuarina pusilla* where fire induces a massive seed release, then resulting in predator satiation and large subsequent recruitment of seedlings (Andersen, 1987). In contrast, although fire usually destroys most of the original insect communities in the ecosystem, some pre-adapted species have developed strategies to take advantage of the newly created, competition- free environment, comprised of pre-killed trees. Cerambycids (*e.g.* from genera *Acmaeops, Arhopalus*, and *Monochamus*), and Buprestids (*e.g.* from genera *Melanophila* and *Buprestis*) are well-known examples of such pyrophilous species, some attracted to smoke and some by heat (Boulanger & Sirois 2007; Saint-Germain *et al.* 2008).

In conclusion, wildfires could constitute a key factor in the natural regeneration process by breaking the relative equilibrium existing between populations of cones and these of cone and seed pests, where most seeds are usually predated year after year. This disappearance of the cone pests would open a 'regeneration window'; in this case of 5 years at least taking into account the slow recolonization process by pests. Such sporadic regeneration events in particular years could explain why many stands are even-aged. Indeed, Gauquelin *et al.* (2003) observed that most trees in this stand were aged of less than 150 years before the 2003 fire, which is rather young with regard to the longevity on *J. thurifera* trees, and they suggested that successive wildfires might have occurred in the past centuries to shape the stand.

However, the overall regeneration process is much more complex, involving many other environmental factors affecting germination and seedling establishment and growth. For example, most trees of *Juniperus procera* C.F. Hochstetter ex. Endlicher failed to regenerate following forest fire in Saudi Arabia (Aref *et al.* 2011). Even forest species, that usually regenerate well after fire, such as *Pinus halepensis* or *Pinus pinaster*, show irregular or low regeneration when post-fire environmental conditions are not favorable for seed germination (Rodrigo *et al.* 2004).

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