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Cone pests of stone pine in the Mediterranean Basin

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Abstract. Stone pines in the Mediterranean Basin are one of the most defended pines and only few pest species can cause damage, such as defoliators (*Thaumetopoea pytiocampa* (Schiff.)) or bark beetles (*Tomicus* sp. and *Ips sexdentatus* (Boern.)). In certain situations these insects can weaken or even cause tree mortality, but the main cause for concern are insects like *Pissodes validirostris* Gyll (Coleoptera:Curculionidae), *Dioryctria mendacella* Staudinger (Lepidoptera: Pyralidae) and *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae) that feed on cones and seeds, negatively impacting the economy. Two of the insect species are indigenous whereas the third, *L. occidentalis*, is an invasive species originating from America. During seed development substantial resources are used during embryogenesis as seeds provide a higher concentrated source of carbohydrates, fat and proteins and low water content, as compared with young needles. Species like *P. validirostris* and *D. mendacella* burrow through and feed on seed-bearing structures or cones, while *L. occidentalis* suck out the contents of seeds or seed-bearing structures as well as needles, flowers, shoots and twigs. At the same time, these specialized insects have developed diverse ecological strategies to complete their biological cycle. For example, *P. validirostris* completes its immature stages inside the cones, while *D. mendacella* larvae leave the cone to pupate in the soil, and *L. occidentalis* completes its development outside cones. In addition to direct consumption, insect attacks can cause fruit abortion or facilitate introduction of pathogens. For example, the sap-sucking insect *L. occidentalis* causes transmission of the fungus *Diplodia sapinea* (Fr.) Fuckel. Impacts of cone pests are related to reductions in seed production and productivity at the economic level and to reforestation and afforestation programs at the economic and ecological levels. In stone pine forests, phenology and seed production can be highly irregular in both space and time, directly affecting the pest population dynamics. In this paper we summarize the current knowledge on the more important cone pests in the Mediterranean Basin, emphasizing: (i) biological and ecological mechanisms involved in the establishment and spread of these species, (ii) the associated damages and, (iii) strategies available for integrated management with the objective of controlling pest populations.

Keywords. *Pinus pinea* – Seeds – Bioecology – *Pissodes validirostris* – *Dioryctria mendacella* – *Leptoglossus occidentalis*.

I – Introduction

Five regions of the world can be characterized by Mediterranean climate conditions (mild wet winters and warm dry summer conditions) and occur around the Mediterranean Sea (60%) and on portions of the southwest coasts of North America, South America, Australia, and Africa (Di Castri, 1991) (Fig. 1).

According to Quézel and Médail (2003), there are 6 bioclimatic types related to the main vegetation types of the Mediterranean basin (Fig. 2). The Mediterranean climatic zones represent about 2% of the Earth's land mass (World Conservation Monitoring Center, 1992) and are recognized centers of endemism and specialized vegetal communities, accounting for nearly 20% of plant diversity. Stone pines (*Pinus pinea* L.) are endemic to sclerophyll forests in sub-humid bioclimate zone of the Mediterranean Basin (600-800 mm of mean annual rainfall and 3-5 months without rainfall), according to Quézel and Médail (2003), together with *Pinus halepensis* Miller, *Pinus brutia* Ten., *Pinus pinaster* Aiton, *Pinus nigra* J.F. Arnold, *Cedrus* sp. and *Quercus* sp.

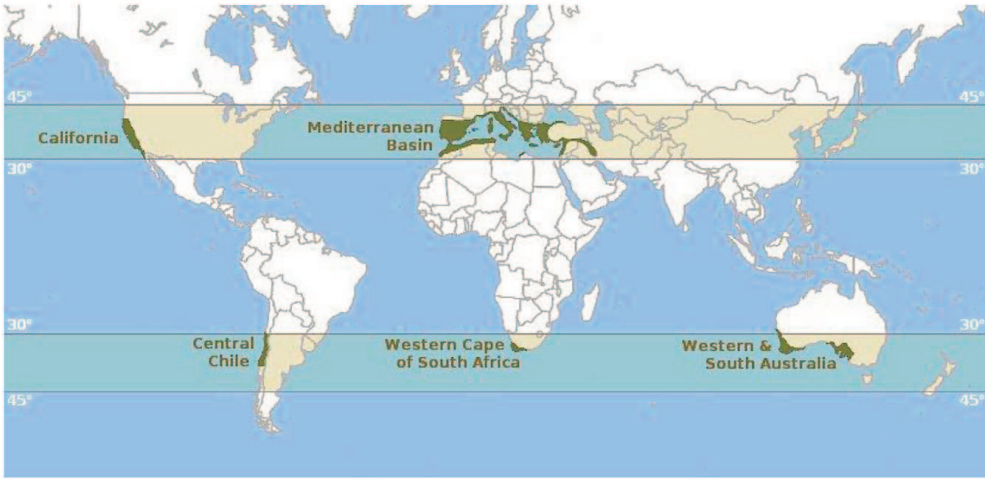


Fig. 1. Mediterranean regions in the world.

Bioclimate	Mean annual rainfall (mm)	Nb months without rainfall	Pine species				
			<i>P. halepensis</i>	<i>P. brutia</i>	<i>P. pinaster</i>	<i>P. pinea</i>	<i>P. nigra</i>
Per-Arid	< 100	11-12					
Arid	100-400	7-10	■				
Semi-Arid	400-600	5-7	■	■			
Sub-Humid	600-800	3-5	■	■	■	■	■
Humid	800-1000	1-3		■	■		■
Per-Humid	>1000	Less than 1					

Fig. 2. Bioclimate types and their relationship with main vegetation types of the Mediterranean basin (from Quézel and Médail, 2003).

A characteristic of the dynamics of Mediterranean forests is the intensity and frequency of long term disturbances, defined as temporary changes in the environmental conditions impacting the ecosystem due to complex multi factorial processes of biotic and abiotic origin (anthropogenic effect, pests and diseases, wildfire, drought and frost). These disturbances reshape biodiversity both in terms of composition and structure. However, in the Mediterranean Basin, the stone pine is one of the more defended pines against biotic and abiotic agents. *P. pinea* survival is increased by thick bark and protection of apical buds by terminal needles. Although *P. pinea* is characterised by low genetic variability (Mutke *et al.*, 2013), variation for adaptation to fire occurs both between and within tree species. Populations grown in areas of frequent fires appear more adapted than others (Lefèvre and Fady, 2016).

II – Main cone pests of the stone pine

There are only a few species that can cause damage to stone pine, such as defoliators (*Thaumetopoea pityocampa* (Schiff.)) or bark beetles (*Tomicus* sp. and *Ips sexdentatus* (Boern.)). In oc-

casual situations these insects can weaken or even cause tree mortality, but the main concern is for insects that feed on cones and seeds.

Fruiting structures of gymnosperms, i.e. seed cones, generally consist of a complex structure with diverse characteristics (bract, dwarf-shoot, ovules, seed wing, aril, and seed). Contributions of the different insect orders to diversity of insects attacking cones varies greatly among both host groups and genera (Fig. 3). In the Mediterranean Basin, Gymnosperms are colonized by five insect orders and the *Pinus* genus can be colonized by Lepidoptera (11 species), Hemiptera (1 species), Diptera (2 species) and Coleoptera (7 species) (Boivin and Auger-Rozenberg, 2016).

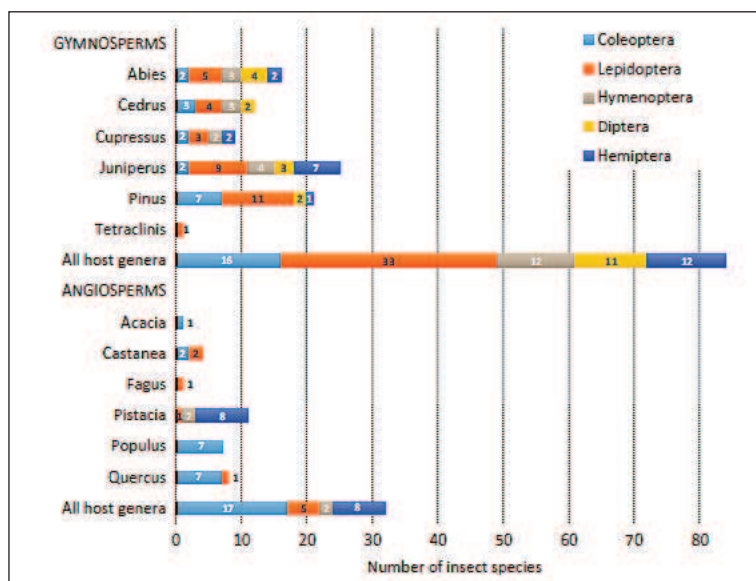


Fig. 3. Order level diversity according to host genera of the entomofauna of tree reproductive structures in the Mediterranean Basin (from Boivin and Auger-Rozenberg, 2016).

For *P. pinea* several conospermatophage species were identified, like *Ernobius impressithorax* Pic, *E. parens* (Mulsant and Rey), (Coleoptera: Anobiidae) and *Dioryctria pineae*. The main species in the Iberian Peninsula are *Pissodes validirostris* Gyll (Coleoptera:Curculionidae), *Dioryctria mendacella* Staudinger (Lepidoptera: Pyralidae) and *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae) which impact the economy. The first two species are indigenous to the Mediterranean basin, while the third is an invasive species originating from America.

Species like *P. validirostris* and *D. mendacella* burrow through and feed on seed-bearing structures or cones, while *L. occidentalis* suck out the contents of seeds or seed-bearing structures as well as needles, flowers or shoots and twigs.

1. Hosts and insect distribution

Phytophagous insects are known to preferentially colonize plants that are taxonomically related to their usual host.

P. validirostris (pine cone weevil) is a major cone pest of *Pinus* spp (except the Swiss stone pine *P. cembra* L.) (Dormont and Roques, 2001) having a large distribution from Europe to north east-

ern China (Annala and Hiltunen, 1977; Roques, 1976, 1983) (Fig. 4a). In Finland, the introduced pine *P. contorta* var. *latifolia* is a preferred host (Annala and Hiltunen, 1977).

D. mendacella (pine cone moth) can attack several pine species (*P. pinea*, *P. sylvestris*, *P. halepensis*, *P. brutia* and *P. pinaster*) (Gomez de Aizpurua, 1991; Knölke, 2007) with a more restricted distribution in Southern Europe and Northern Africa (Karsholt and van Nieuwerkerken, 2013) (Fig. 4b). It is found on *P. halepensis* (Nichane *et al.*, 2013) in Algeria.

P. validirostris and *D. mendacella* can attack several pine species but in Portugal they are found mainly on *P. pinaster* and *P. pinea*. In Spain, *P. validirostris* damages several species including *P. pinea*, *P. sylvestris*, *P. halepensis*, *P. nigra* and *P. pinaster* (Cadahia, 1981).

L. occidentalis is native to western North America, from British Columbia to Mexico in latitude, and from the Pacific Coast to Colorado in longitude (Koerber, 1963) (Fig. 4c). It can feed on several species of conifers (it can feed on seeds of over 40 hosts from different genus - *Pinus*, *Pseudotsuga*, *Tsuga*, *Picea*, *Abies*, *Cedrus*, *Juniperus* and *Pistacia*) (Bernardinelli and Zandigiacomo, 2001), *L. occidentalis* and has expanded eastward to the Atlantic Coast (McPherson *et al.*, 1990; Gall, 1992). In Europe, the species was first reported in Northern Italy in 1999 (Taylor *et al.*, 2001). It expanded its range very quickly and colonized all of Europe within ten years (Lesieur *et al.*, 2014), affecting a large host range including native pine species such as *P. sylvestris*, *P. pinaster*, *P. nigra*, *P. halepensis* and *P. pinea*, as well as *Picea abies* (L.) Karst, *Larix decidua* Mill., *Abies* spp., and *Juniperus* spp. in addition to introduced exotic conifers (*Cedrus* spp., *Pseudotsuga menziesii* (Mirb.)) (Taylor *et al.*, 2001; Fent and Kment, 2011; Tamburini *et al.*, 2012). Moreover, recent detections in Asia (China, Japan and South-Korea) (Zhu, 2010; Ishikawa and Kikuhara, 2009; Ahn *et al.*, 2013) and Northern Africa (Ben Jamaa *et al.*, 2013) highlight that the pest is a highly successful worldwide invader.

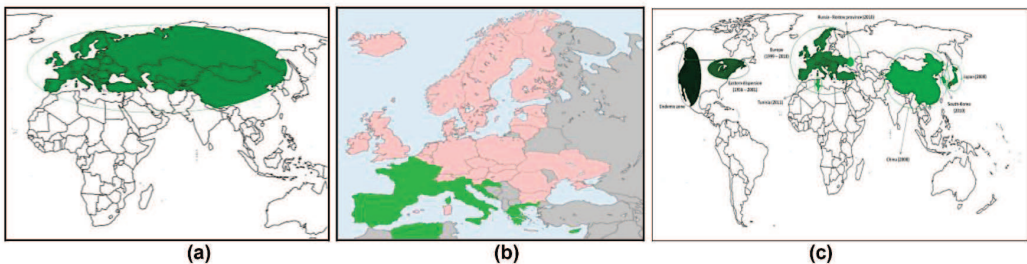


Fig. 4. World distribution of the main cone pests of the stone pine. (a) *P. validirostris*; (b) *D. mendacella*; (c) *L. occidentalis*.

2. Host-insect interrelationships

Compared to insects that attack other tree structures such as foliage, cone insects require more effective host recognition and more specific selection mechanisms that show high specificity towards cones. Several factors can be associated with the process of host selection (tree/stand characteristics, cones characteristics and cone production). At the same time, these specialized insects have developed diverse ecological strategies to disperse and complete their biological cycle (dispersal capacity, nutrition, biological cycle and natural enemies). The evolution of specialization is favored when pest development is dependent on a single plant organ or tissue for its life cycle (Gaston *et al.*, 1992). Overall, these patterns contrast with post-dispersal consumers that feed on a diverse and spatially heterogeneous resource that requires generalist feeding habits (Hulme, 1998).

However, for invasive species, like *L. occidentalis*, successful establishment depends of several factors related with new environments (high densities of favorable hosts, good climatic conditions),

their capacity to adapt (good dispersal, good strategies to find susceptible hosts, high capacities of adaptation to new hosts, no endemic predators or parasitoids) and high population levels. All of these factors have undoubtedly contributed towards the success of this pest in attacking conifer seeds in Europe and Asia.

Among the most important parameters which mediate and regulate the attacks of cone pests are tree and stand characteristics, cone characteristics, production and nutritional value, the insect's biology and dispersal capacity.

A. Tree/stand characteristics

Tree species, silhouette, size and shape play a key role in initiating long-range insect orientation. The contrast between the fruit or seed cone structure and foliage color may also act as a stimulus at the stand scale. Both visual and chemical cues operate sequentially or simultaneously in host location, insect response may also vary among sexes and may depend on the reproductive and nutritional status of individuals.

The variation between trees of the same population may be also due to the size and shape of the crown, motivated by age and social stratum to which the tree belongs; also they influence the quality of the station, the stand density and management techniques.

In many cases, plant chemistry may be responsible for the absence of insect attack on a given species (Bernays and Chapman, 1994). Such relationships were described for *P. validirostris*, a major cone pest of *Pinus* spp that does not attack Swiss stone pine (*P. cembra*) (Dormont and Roques, 2001). Further studies confirmed that this behavior is associated with cone volatile emissions (Dormont *et al.*, 1998; Dormont and Roques, 2001). However, second instar weevil larvae that were artificially introduced into Swiss stone pine cones were capable of developing to the adult stage, suggesting that it is only a question of host selection and that this pine species does not contain strong feeding deterrents that could prevent larval development. The greater susceptibility of *P. contorta* in Finland is also associated with differences in emission of volatile monoterpenes by foliage and especially to a lower content of α -pinene than for *P. sylvestris* (Brockerhoff *et al.*, 2004). However, it is unclear whether the effect of particular plant chemical defenses prevents insect colonization indefinitely, or simply delays it (Jones and Lawton, 1991).

Morphometric, behavioral and genetic (mtDNA) analyses showed that *P. validirostris* probably does not represent a single generalist species but rather consists of a complex of sibling species specialized to different host pines (Roques *et al.*, 2004). Two main groups of *P. validirostris* were identified corresponding to populations developing on northern and alpine pines of the *syvestris* section (*P. sylvestris*, *P. uncinata*, *P. nigra*) and on Mediterranean pines (*P. pinaster*, *P. pinea*), respectively (Roques *et al.*, 2004).

B. Cone characteristics

One of the main strategies for insects that depend on a single plant organ or tissue for development, is the synchronization between their biological cycle and cone development. The relationships between seed cone phenology and time of colonization have been reported for several Mediterranean conifers of the genus *Abies* sp. *Cupressus* sp. and *Juniperus* sp., and for only for two pine species, *P. brutia* and *P. nigra* (Roques *et al.*, 2005). These influence insect species in which both oviposition and larval development occur on immature fruiting structures (*P. validirostris* and *D. mendacella*), as there may be strong selection for synchronizing insect life history with the target stage of the host plant (McClure *et al.*, 1998; Harman, 1999).

Cone phenology in stone pine forests can be influenced by several environmental factors like weather conditions during flowering and cone development, giving rise to irregular behavior over

both space and time. A similar effect is due to physical damage caused by hail, as the scales affected no longer grow or develop their pinions, leaving a sunken navel on the mature cone.

In the Mediterranean area most of the insect colonization occurs during the second year of cone development, which corresponds to cone growth, although some species may also attack during the first year of development. For short-distance selection, the cone or seed size, structure and chemistry determine the short-range detection and host suitability for mating, feeding and ovipositing by the different pests (Turgeon *et al.*, 1994).

It is possible that for some insects, ovarian maturation may be stimulated by the presence of seed cones in the suitable development stage, thereby assuring synchrony between egg production and adequate oviposition sites as has been shown for *P. validirostris* (Roques *et al.*, 2005). In fact, the *P. validirostris* oviposition period is relatively limited in time (about a month) and coincides with a specific cone phenological phase (Roques, 1976).

On the other hand, *L. occidentalis* develops entirely outside the cones with a strong capacity of mobility even for earlier stages. This insect is very polyphagous for several conifers and can feed on different cone development phases. Therefore, this insects appears to have less specialized relations with its hosts, although it possesses infra-red (IR) radiation receptive organs to use as host-finding cues towards pine cones, which are warmer and emit more near-, mid- and long-range IR than needles (Takács *et al.*, 2009).

C. Production of cones

Insect species that cannot shift to alternative hosts when resource supply is low and when intra- or interspecific competition increases, life histories are under strong selection to offset such heterogeneity in resource availability.

Long term studies on *Juniperus thurifera* growing in Morocco have revealed that fluctuations in cone abundance generally reflect the substantial annual variation in larval populations of cone pests (Roques *et al.*, 2005) (Fig 5).

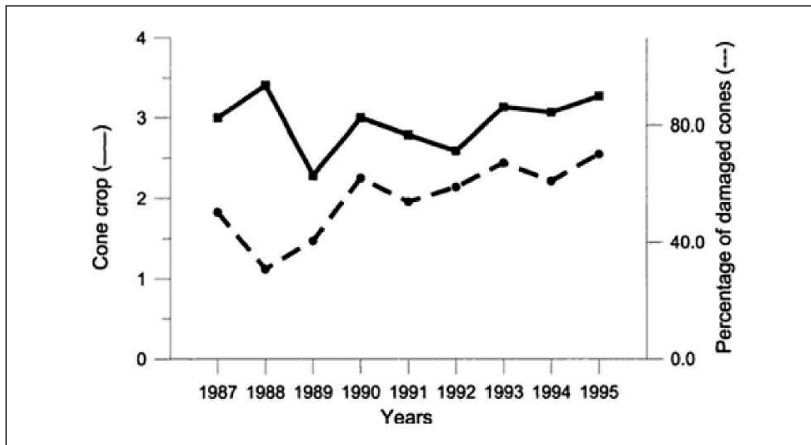


Fig. 5. Comparative variations in annual cone crop and annual pest damage on *Juniperus thurifera* at Tizrag (High Atlas, Morocco) from 1987 to 1995. Cone crop is estimated using a qualitative scale: 1 - slight, 2 - medium, 3 - heavy, 4 - bumper. (Roques *et al.*, 2005 modified from El Alaoui and Roques, 2005).

D. Nutritional value of the seeds / cones

During seed development, trees invest substantial resources for embryogenesis. The high nutritional value of fruiting structures is generally associated with a greater investment of plants in physical or chemical defense mechanisms than on vegetative tissues (Janzen, 1971). For example, *P. sylvestris* seeds during cone lignification (phase V) provide a concentrated and rich source of carbohydrates (61%), fat (4%) and proteins (10%) with a low water content (12%), compared to young leaves (4%, 1%, 5% and 76%, respectively) (Jordano, 2000) (Fig. 6).

Internal biochemical changes in cones occur at different stages of development. Water content shows a high increase since the resumption of activity in the second year of cones growth of *P. sylvestris*, with the higher levels in early June before the lignification process (phase IV). Concentrations of cellulose and hemicelluloses are inversely proportional to the concentration of water. Early June corresponds to the period when food reserves are at their maximum, and also to the peak of biological activity of most cone pests.

The cone therefore provides a particular insect habitat in permanent evolution (change of physical and chemical characteristics) while simultaneously being a direct or indirect source of food. However, insects can target very early developmental stages of tree reproductive structures such as male and female flowers (Turgeon *et al.*, 1994). Insects also attacking fruiting structure display two different feeding habits to acquire nutrients from their host plants.

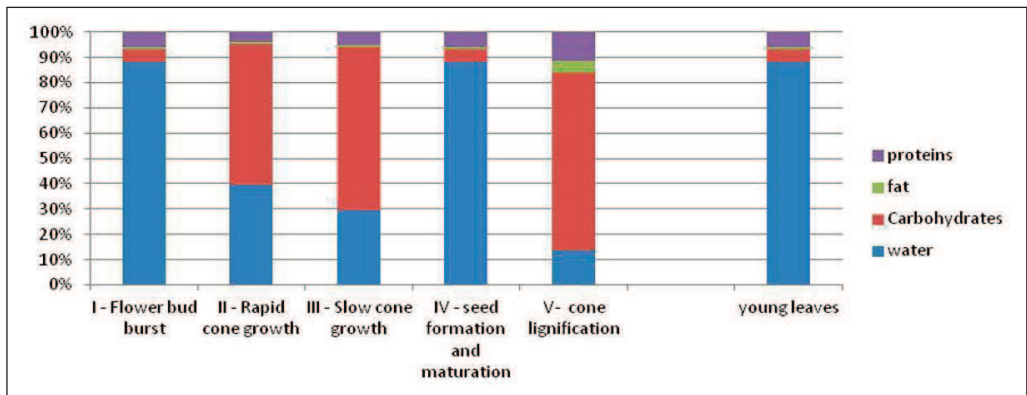


Fig. 6. Differences on *Pinus sylvestris* cone composition during its development (adapted from Jordano 2000).

Larval stages of species belonging to the Coleoptera (*P. validirostris*) and Lepidoptera (*D. mendacella*) feed only on cones (Merlo *et al.*, 2005), while adults and immature nymphs belonging to Hemiptera (*L. occidentalis*) consume individual seeds during the growing season as well as needles, flowers or shoots and twigs (Strong *et al.*, 2001). Insects insert their mouth stylets through the cone tissues directly to the seeds sucking the lipid and protein content (Bates *et al.*, 2001).

E. Biological cycle

In Europe the tree main cone pests (*P. validirostris*, *D. mendacella* and *L. occidentalis*) show different particularities in their biological cycles, which differ by geographic areas. *P. validirostris* completes all the immature stages inside the cones and is univoltine in most of its distribution range, although in Finland the life-cycle takes 2 years (Annala, 1975). In the case of *D. mendacella*, the larvae leave the cone to pupate in the soil, and this insect has 1.5 or two generations per year in the Mediterranean basin.

L. occidentalis is univoltine in Northern California (Koerber, 1963), whereas two to three generations per year are observed in Mexico (Cibrián Tovar *et al.*, 1995). In Europe, recent studies conducted in Italy (Bernardinelli *et al.*, 2006) and Spain (Más *et al.*, 2013) have shown the existence of up to three generations per year (threshold temperature of development: 15°C. Integral thermal 513.72 degree days).

P. validirostris mating and oviposition takes place on cones during April-May when the cone moisture content peaks (Dormont and Roques, 2001). The female lays a variable number of eggs per cone. In *P. pinea* there may be up to 40 eggs in one cone. The eggs hatch in 10-15 days (Romanyk and Bachiller, 1965). Larvae occur in spring and summer, with 4 instars recognised (Roques, 1976). Several larvae can coexist in the same cone implying a higher degree of intraspecific larval competition (Annala, 1975). Pupation occurs within the cones in August and adults emerge in late summer, through a circular exit orifice. Adults can survive for at least 2 years (Annala, 1975) overwintering in the litter and bark crevices, and emerging in the following spring (April-May) (threshold of 12°C and a mass occurrence for more than 15 °C) (Bachiller, 1966, Cuevas and Bachiller, 1970). The adults need a short period of maturation feeding on the pine leader shoots before they are able to lay eggs on cones (Roques, 1976).

Adults of *D. mendacella* emerge in spring/early summer for the 1st generation and in the late summer/very early autumn for the 2nd. Oviposition inside cones and the development of the 1st generation takes around four months, while nine months are required for the 2nd.

One to six larvae can occur in the same cone (Pajares, 2015). Larvae can move from one cone to another. Larvae (5 stages) construct irregular galleries during June to September in the 1st generation and from November to April in the 2nd. Insects overwinter in the larval stage inside the cones. Pupation occurs in the soil, protected by a weak silken cocoon (1 month in summer or 2 to 3 months in winter). *D. mendacella* can be found associated with *P. validirostris* in the same cone (Cuevas and Bachiller, 1969).

L. occidentalis adults mate repeatedly from spring to fall (Koerber, 1963). The female lays eggs (73-80) on the underside of needles (series of 3 to 20). Eggs hatch 10-15 days after laying (Bates and Borden, 2005). Five nymphal stages occur, with a high young nymphal mortality (> 80%) (Koerber, 1963). There is high mobility from one cone to another. The presence of the other pests does not seem to affect *L. occidentalis* (Lesieur, 2014). This insect overwinters in refuge sites, including human-made structures such as wood piles, containers, sheds or houses with an aggregation behavior, grouping up to thousands of individuals (Tamburini *et al.*, 2012), regulated by a pheromone produced by the males (Blatt and Borden, 1996). During the winter they survive using the lipid reserves accumulated in the fall.

F. Dispersal capacity

The dispersal capacities of an invasive population may be a decisive factor to access new and more adequate environments (Travis and Dytham, 2002; Wilson *et al.*, 2009). The dispersal can take different forms, it can be active, involving specific capabilities of each organism (walking or flying, for example). It can also be passive, with insects being transported with their host material.

The history of the European invasion by *L. occidentalis* is complex because it occurred over the past ten years. Recent studies using polymorphic microsatellite markers characterized the invasion scenario by this insect (Lesieur, 2014). It was concluded that the current geographic distribution of *L. occidentalis* in Europe is possibly the result of several independent introductions (Lesieur, 2014), highlighting at least two independent introductions, although additional introductions in Spain, France and Austria are also suggested.

This dispersal can be explained by different mechanisms related to human activity and the specific characteristics of the species. Different means of propagation could underlie its very fast in-

vasion. In this respect, the introduction pathway could be related to timber shipments (e.g. timber logs or wood panels) from the USA (Dusoulier *et al.*, 2007; Malumphy *et al.*, 2008) and the habits of the bug to aggregate inside man-made structures in the fall to seek shelter for overwintering. Moreover, individuals (eggs, nymphs or adults) may also have been brought from established populations via their host plants with for instance the commercial Christmas tree trade or translocations of ornamental trees (Gall, 1992; Gapon, 2012).

During insect outbreaks, the flight behavior and flight capabilities of invasive species are important for understanding the dynamics of the invasion and progression of the front. Important flight capabilities of *L. occidentalis* could facilitate the spread in European territory. For example, the maximum flight distance of breeding insects in laboratory conditions using flight mills is about 15.5 km for males and 12.5 km for females, with values of around 21.5 km and 22.5 km for insects collected under natural conditions (Lesieur, 2014) (Fig. 7). In the autumn, young insects showed good flight capabilities but the flight abilities in early April (with insects exiting hibernation), suggest that the insects can also actively disperse during spring. Such events can lead to a homogenization of genetic diversity in Europe (Koerber, 1963; Malumphy *et al.*, 2008).

For the endemic species, although pine cone weevils are capable of flying, a study on the dispersal of marked adults within a pine stand showed that a high proportion remained on or near the tree where they hibernate, and only a few adults travelled more than 10 m (Annala, 1975). However, all the pine trees in this report contained cones and nothing is known about the weevil's dispersal behaviour when cones are absent in a stand.

For *Dioryctria* spp, recognition and selection of suitable feeding and breeding sites involve both the adult female and its progeny when larvae are capable of moving and finding resources.

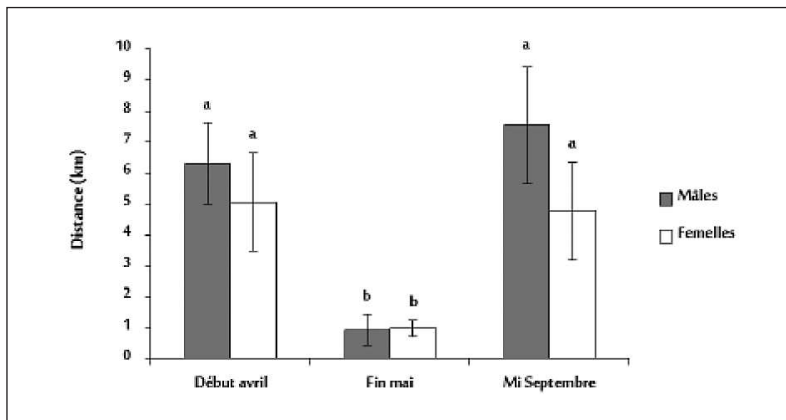


Fig. 7. Evolution of the total flight distance (DP) by individuals of *Leptoglossus occidentalis* depending on the season (from Lesieur, 2014).

3. Associated damage

The demographic and evolutionary consequences of the feeding activities of insects on fruiting structures are likely to differ from most forms of herbivory which only partially remove tissues from individual plants (Hulme, 1998). However until the 1980s this had received little attention because their predominantly cryptic way of life makes them difficult to detect with simple external fruit examination, and because their economic and ecological impact on seed crops was barely quantifiable. However, improvement in tree multiplication and planting programs relying on both certified

seed collections and seed orchards progressively created the need for research on the ecology and impact of insects on seeds (Roques, 1983).

Additionally, insect attacks can facilitate introduction of pathogens, such as the transmission of the fungus *Diplodia sapinea* by the sap-sucking insect *L. occidentalis* (Luchi *et al.*, 2012).

P. validirostris was also considered a vector of the highly virulent fungus, *Fusarium circinatum*, (pitch canker) an important pathogen of *Pinus* seedlings recently introduced in Europe (Romon *et al.*, 2007). However, more recent work done in South Africa showed that the weevils did not transmit the fungus, although damage caused during feeding facilitated the ingress of the fungus into the host plant (Lennox *et al.*, 2009).

The insect's cone and seed consumption have to be looked at in relation to ecological and economic consequences, although damage to cones is not only associated with biotic agents. Schowalter and Sexton (1989) indicated that the major factor in seed losses of Douglas-fir in western Oregon was unexplained developmental failure. In the French Alps during the first year of *P. cembra* conelet development, 66% disappeared mainly because of abiotic factors (85% of the losses) (Dormont *et al.*, 1996).

A. Ecological impact

Insects feeding on plant reproductive structures potentially affect abundance, distribution and dynamics of tree populations (Boivin and Auger-Rozenberg, 2016). When they differentially decrease seed production among individuals that vary in some heritable traits, genetic variability can be reduced (Kolb *et al.*, 2007). In this way, by directly affecting tree reproductive success, impacts on seed quality and supply for regeneration, reforestation, and conservation purposes can be very important.

These aspects can be very critical for attacks of adult and nymph *L. occidentalis* that feed on cones from a wide range of conifer species (Lesieur *et al.*, 2014). In Europe, ecological consequences of its introduction could be significant and its damage is as a serious threat for natural regeneration (Tamburini *et al.*, 2012). Roversi and colleagues (2011) estimated that in Italy, the production of edible seeds of *P. pinea* has sharply decreased over the years, and cone crop production collapsed in 2009.

B. Economic impact

In addition to their impact on host ecology and evolution, the economic consequences of insect feeding activity on fruiting structures are diverse, and essentially depend on the developmental stage or tissues that insects target (Roques, 1983). Insect damages on early developmental stages, e.g. flowers or young cones generally inhibit their growth and accelerate their lignification and dehydration, which leads to a premature drop of the fruiting structure. Insect damages on later developmental stages have a weaker influence on cone growth, but they generally lead to intense resin flow that sticks together cone scales, which prevents the release of the unaffected and viable seeds (e.g. the pine cone weevil *P. validirostris*).

P. validirostris and *D. mendacella* have long been known as important agents that damage cones and seeds in several European countries across the Mediterranean basin. After the detection of *L. occidentalis* in Mediterranean countries, a significant decrease in production and productivity of pine cones was reported although attacked mature cones do not show any symptoms of external damage unlike those attacked by many other cone pests. In Portugal this pattern was also seen, and in the last few years a decrease in the yield of pine cone nuts was observed. Data from two major manufacturing industries (Preparadora de Pinhões Ld^a and António Pais Ld^a) showed stability in pine nut yield during the last 18 years, varying between 3 and 4%. However, in the 2011-2012 season (and subsequent years) the yield dropped to below 2.5%, which had not previously been observed.

However, characterizing the status of empty seeds remained a problem because radiographic interpretations do not allow a clear differentiation between seeds sustaining severe bug damage and empty seeds which have naturally aborted because of a lack of pollination, fertilization problems or any other reasons not linked to insects (Schowalter and Sexton, 1990).

Indeed, overall economic damages due to seed production losses associated with cone pests have not been estimated. Some of the data available from the literature is summarised in Table 1.

Table 1. Examples of cone pests economic damages (*P. validirostris*, *D. mendacella* and *L. occidentalis*)

<i>P. validirostris</i>	<i>D. mendacella</i>	<i>L. occidentalis</i>
Spain (Valladolid) - Damages on <i>P. pinea</i> between 20% and 56% (Gordo Alonso <i>et al.</i> , 1997)		EUA - damages of 70% on <i>Pseudotsuga menziesii</i> . Estimation of a loss of 310 seeds /insect (Bates <i>et al.</i> , 2000)
France - Over 80% of the annual production of cones (Roques <i>et al.</i> , 2004); due to L3 and L4 stages (Roques 1976)	Italy - About 80% of cones of <i>P. pinea</i> (Innocenti and Tiberi 2002)	Abortion 75% of conelets, with a reduction of 47% of the content in seeds of <i>P. monticola</i> (Bates <i>et al.</i> , 2002)
Finland – About 20 % of cones of <i>P. sylvestris</i> and 75% in <i>P. contorta</i> (Annala 1975)		Mexico - 30% of cones on <i>P. cembroides</i> (Cibrian Tovar <i>et al.</i> , 1995).
		France - 70% of the seed yield in both <i>P. nigra</i> and <i>P. sylvestris</i> (Lesieur <i>et al.</i> , 2014)
		Italy - Production on <i>P. pinea</i> sharply on <i>P. pinea</i> sharply decreased since its introduction (Roversi <i>et al.</i> , 2011)
		DNA-based diagnostic protocols can be used to quantify damages even when insect excrements or saliva are the only biological traces available (Bracalini <i>et al.</i> , 2015)

4. Strategies for the integrated management of cone pests

Protection of tree reproductive structures from pest insects is generally a complex process, partly due to the cryptic internal feeding habits of many pest species that makes them difficult to detect and control, and to the spatial heterogeneity of fruiting structures at both tree and stand levels. This is particularly true for insects that spend most of their lives hidden and protected inside pine cones (*P. validirostris* and *D. mendacella*).

If the biology and behavior of pest insects are sufficiently well known, damage can often be controlled by silvicultural, mechanical, biological and genetic measures, without using homologated insecticides.

Repeated spraying or dusting of the trees with chemicals can gradually lead to accumulation of pesticide residues in the seed orchards, upsetting the balance between the pest insects and their enemies. There is also a risk that insects may become resistant to insecticides if chemical control is repeatedly used in seed orchards. Some insecticides may also have phytotoxic effects on seeds, reducing the quality of the seed crop (Annala, 1973).

In Spain, chemical control methods with contact insecticides (deltamethrin) for *P. validirostris* may only be used when adults are in crowns during spring when they leave wintering and fall before wintering. There are no registered insecticides against these pests in Portugal or France. Alternative or complementary methods are being developed and consist mainly of changing the tree species composition in the stand in order to increase ecosystem resistance, and to encourage natural enemies by providing them with both alternative hosts and shelters. Other methods such as seeding

or inundating releases of natural enemies (several species are known – *Coeloides melanostigma*, *Eubadizon atriconis*, *Scambus brevicornis*, *Eubazus robustus* and *Eurytoma annilai*, *Exeristes ruficollis*, *Scambus sagax*, *Scambus sudeticus*, *Coeloides sordidator*, *Spathius rubidus*) and mating disruption have been attempted but with limited success (Kenis *et al.*, 2004).

As *D. mendacella* larvae are inside the cone at time of collection (autumn/winter), observation of attacked cones and their destruction can be an effective way to decrease populations. Destruction of unharvested cones or fruit left on the soil surface is a complementary measure that serves to reduce overwintering populations of many pest species.

Adult trapping techniques with sex pheromones is expected to be used more frequently in the short term in order to assess emergence and flight periods. *D. mendacella* has been the subject of recent research, having given rise to the knowledge of its pheromonal complex, which will be published in the near future. It is likely that attractive lures will become available within a year or two. These studies show that cone moth females produce (Z,E)-9,11-tetradecadienyl acetate (ZE9,11-14:Ac) and (Z,Z,Z,Z,Z)-3,6,9,12,15-pentacosapentaene (ZZZZZ3,6,9,12,15-25:H). The former elicits a strong EAG response from males while no response could be recorded for the latter. In field trapping tests, both compounds were individually unattractive to males, but blends of the two compounds were highly attractive (Pajares, 2016).

Control methods against *L. occidentalis* seemed easier at the onset because the populations are always outside the host. Population control in the area of origin mainly comes from the use of broad-spectrum insecticides (Strong *et al.*, 2001). The results are variable but chemical control is the only means of effectively controlling the population (Strong, 2006). Luring using the attractiveness of infrared radiation for adults has recently been achieved experimentally (Takács *et al.*, 2009). However, no effective trapping technique exists currently.

Only a few studies have dealt with the parasitic spectrum against *L. occidentalis* (*Gryon pennsylvanicum*, *Anastatus pearsalli* and *Ooencyrtus johnsoni* are the most important natural enemies), which appears limited to its area of origin (Bates and Borden, 2004; Maltese *et al.*, 2012). It was shown that the rate of egg parasitism can reach 30% with *G. pennsylvanicum* as the dominant species. This species is the subject of recent studies to determine the effectiveness and relevance of a possible European introduction for biological control (Peverieri *et al.*, 2012; Roversi *et al.*, 2014).

Although parasitoids native to Europe, such as *Anastatus bifasciatus* and *Ooencyrtus pityocampae*, were found parasitizing some egg masses in Italy, it seems that native parasites and parasitoids have yet not adapted to this invasive species (Binazzi *et al.*, 2013).

The use of insect pathogenic fungi, *Beauveria bassiana* and *Isaria fumosorosea*, was recently tested in Italy and the Czech Republic, providing encouraging results (Rumine and Barzanti, 2008; Barta, 2010).

5. Regarding the future

Recent decades represent a major turning point for the movement of species and especially the introduction of organisms beyond their areas of origin. For example (Fig. 8), the number of terrestrial arthropod species introduced by year has increased exponentially since the sixteenth century (Roques, 2010) but particularly in recent decades. It can be anticipated that new damaging outcomes of cone pests will occur in the Mediterranean region.

At the same time, in the next decades, Mediterranean forests will be under pressure from climate change and increased demand on ecosystem services related to human expansion in the area (Regato, 2008, Solomon *et al.*, 2007, Petit *et al.*, 2005). Changes in the biology (insect's developmental cycle, survival and reproduction) and distribution of some forest insects in response to on-going

climatic changes is expected and has already been observed during the last 30-50 years (Bale and Hayward, 2010; Menéndez, 2007). Furthermore, the establishment of alien insect species originating from subtropical and tropical climates may increase due to more favorable climatic conditions. In parallel, tree species can also suffer changes in their phenology and vigor, becoming in some cases, more susceptible to native and introduced pests. Additionally, higher temperatures may favor fungi, viruses and nematodes frequently associated with insects. These organisms, which are vectored by the insects, may subsequently weaken host trees, making them more vulnerable to the insect pest attack (Paine *et al.*, 1997).

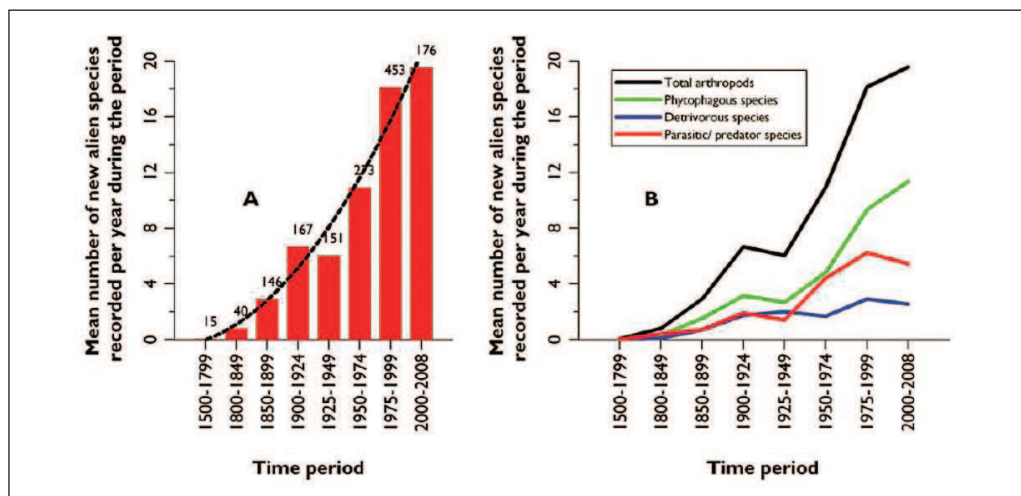


Fig. 8. Temporal changes in the mean number of new records per year of arthropod species alien to Europe from 1500 to 2008. A total arthropods (Best fit: $y = -0.411 - 0.407x + 0.304x^2$; $r^2 = 0.965$); B Detail per feeding regime (from Roques, 2010).

III – Conclusions

Although considerable knowledge has been gathered over the recent years there is strong need for further knowledge, particularly in some countries of the Mediterranean region. The most important identified knowledge gaps relate to the bio-ecology of pests and their interrelationship with host/stand characteristics, impact of forest management techniques, damage assessment and quantification, and development of eco-friendly and sustainable control methods.

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