

## Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations

Angus J. CARNEGIE<sup>a\*</sup>, Mamoru MATSUKI<sup>b</sup>, Dennis A. HAUGEN<sup>c</sup>, Brett P. HURLEY<sup>d</sup>, Rodrigo AHUMADA<sup>e</sup>, Paula KLASMER<sup>f</sup>, Jianguhua SUN<sup>g</sup>, Edson T. IEDE<sup>h</sup>

<sup>a</sup> Forest Resources Research, Department of Primary Industries, PO Box 100, Beecroft, NSW, 2119, Australia

<sup>b</sup> Western Australian Blue Gum Industry Pest Management Group and Co-operative Research Centre for Sustainable Forest Landscapes, c/- Agriculture WA, 444 Albany Hwy, Albany, WA 6330, Australia

<sup>c</sup> USDA Forest Service, 1992 Folwell Avenue, St. Paul, MN 55109, USA

<sup>d</sup> Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria 0002, South Africa

<sup>e</sup> Bioforest S.A., PO Box 70-C, Concepcion, Chile

<sup>f</sup> INTA EEA Bariloche, Campo Forestal, Gral. San Martín, CC 26, 8430 El Bolsón, Argentina

<sup>g</sup> Institute of Zoology, Chinese Academy of Sciences, Beijing 100080, China

<sup>h</sup> Centro Nacional de Pesquisa de Florestas/Embrapa, Colombo – PR, Brazil

(Received 3 January 2005; accepted 18 August 2005)

**Abstract** – The potential distribution of sirex wood wasp (*Sirex noctilio*) in Australia, South America and Africa (where the insect is known to occur and is spreading) and North America and China (where sirex has not established) was assessed from a study of the insect's current distribution and host range. *Sirex noctilio* has a wide host range, mainly in *Pinus*, including many important commercial species planted as exotics in the Southern Hemisphere as well as native stands in North America. Using the climate-matching program CLIMEX the potential distribution range of *S. noctilio* was predicted across the globe based on climatic conditions in Eurasia and northern Africa, where the insect is endemic. *Sirex noctilio* is predicted to establish in the majority of commercial *Pinus* plantations in Australia. Many countries with commercial *Pinus* plantations in South America (Uruguay, Brazil, Argentina, Chile and Paraguay) as well as South Africa are predicted to be colonised by *S. noctilio* by natural migration. Countries that are a long distance from *S. noctilio*-infested areas, such as Ecuador, Colombia, Venezuela, Zimbabwe, Tanzania, Uganda, Ethiopia and plantations in southern Chile, western Australia and north-western Brazil, are only likely to be colonised by *S. noctilio* via human-assisted transport of infested wood. *Sirex noctilio* was predicted to be able to persist in many areas in North America. In China, *S. noctilio* is predicted to be able to persist in many areas where large-scale afforestation of susceptible hosts has occurred and is planned. However, *S. noctilio* is endemic in neighbouring countries of China, indicating that something other than climate and host is restricting *S. noctilio* establishing in China, or that it has not been detected yet. The Sirex Management Strategy will help reduce the spread and impact of *S. noctilio*.

**sirex wood wasp / climate matching / CLIMEX / invasion / risk assessment / biosecurity / species' distribution range**

**Résumé** – Prédiction de la distribution potentielle de *Sirex noctilio* (Hymenoptera : Siricidae), ravageur exotique des plantations de *Pinus*. La distribution potentielle du *Sirex* (*Sirex noctilio*) en Australie, en Amérique du Sud et en Afrique (où l'on sait que l'insecte intervient et s'étend), et en Amérique du Nord et en Chine (où il n'a pas été introduit) a été estimée à partir d'une étude de la distribution actuelle de l'insecte et de sa gamme d'hôtes. *S. noctilio* a un large spectre d'hôtes, principalement chez les pins, y compris chez des espèces importantes d'un point de vue commercial, introduites en plantations dans l'Hémisphère Sud ainsi qu'indigènes en Amérique du Nord. En utilisant le programme d'assortiment climatique CLIMEX, la distribution potentielle de *S. noctilio* a été prédite à l'échelle du globe en se basant sur les conditions climatiques d'Eurasie et d'Afrique du Nord où l'insecte est endémique. On prédit que *S. noctilio* devrait s'établir dans la majorité des plantations commerciales australiennes de *Pinus*. Beaucoup de pays possédant des plantations commerciales de *Pinus* en Amérique du Sud (Uruguay, Brésil, Argentine, Chili et Paraguay) et en Afrique du Sud devraient être colonisés par migration naturelle. Les pays très éloignés des zones infestées par *S. noctilio*, tels que l'Équateur, la Colombie, le Vénézuéla, le Zimbabwe, la Tanzanie, l'Ouganda, l'Éthiopie, le sud du Chili, l'Australie Occidentale et le nord-ouest du Brésil, sont susceptibles d'être colonisés par *S. noctilio*, seulement via les transports par l'homme de bois infestés. *S. noctilio* est capable de persister dans de nombreuses zones d'Amérique du Nord. En Chine, il peut persister dans de nombreuses régions où des reboisements de grande envergure d'essences sensibles ont déjà eu lieu ou sont prévus. Cependant, *S. noctilio* est endémique dans des pays voisins de la Chine, ce qui indique que d'autres facteurs que le climat et l'hôte restreignent son installation en Chine, ou qu'il n'y a pas encore été détecté. La stratégie de gestion de *Sirex* aidera à réduire l'expansion et l'impact de *S. noctilio*.

***Sirex* / assortiment climatique / CLIMEX / invasion / évaluation des risques / biosécurité / gamme de distribution d'espèce**

\* Corresponding author: angusc@sf.nsw.gov.au

## 1. INTRODUCTION

*Sirex noctilio* Fabricius is a siricid wood wasp native to Eurasia and northern Africa [49, 51]. Female *S. noctilio* oviposit eggs into stressed or suppressed trees, along with a phytotoxic mucus and a wood decay fungus (*Amylostereum areolatum*) carried by the wasps [30, 36, 38, 55, 56]. Trees drilled by *S. noctilio* soon die due to the combination of the mucus and fungus. *Sirex noctilio* has a wide host range in *Pinus*, including *P. radiata*, *P. taeda*, *P. ponderosa*, *P. muricata*, *P. pinaster*, *P. elliotii*, *P. caribaea*, *P. patula* and *P. sylvestris* [4, 49, 51]. *Pinus radiata*, *P. taeda* and *P. patula* are particularly susceptible [4, 6, 16, 21, 51, 59].

In its native range *S. noctilio* is not considered an important pest [14, 49]. However, where it has established in the Southern Hemisphere it has become a significant pest of exotic *Pinus* plantations [6, 16, 21, 25, 26, 29, 31, 39, 43, 59]. *Sirex noctilio* was first reported in the Southern Hemisphere in New Zealand in the early 1900s and has since spread throughout that country, mainly in *P. radiata* plantations [43]. In Australia, *S. noctilio* was first detected in 1952 in Tasmania, and over the next 50 years slowly spread north [6, 35]. Between 1987 and 1989 over 5 million trees with a royalty value of A\$10–12 millions were killed in a single area in southern Australia [16]. It is now established in the majority of *Pinus* plantations (mainly *P. radiata*) in south-eastern Australia but has not yet established in north-eastern New South Wales or been detected in Queensland or Western Australia [6]. In response to severe losses in Australia, a *Sirex* Management Strategy was developed [16], which includes biological control (see [3]), forest surveillance, quarantine and silvicultural methods.

In South America, *S. noctilio* was first detected in 1980 in Uruguay, where it spread quickly through the majority of pine plantations in that country [31]. In 1985, *S. noctilio* was detected in north-eastern Argentina [26] most likely entering from Uruguay [44], and is now established in the majority of commercial pine plantations in Argentina [24–26]. In 1988, *S. noctilio* was detected in southern Brazil and spread to nearby plantations by 1996, and it is currently established in approximately 300 000 ha of pine plantation in southern Brazil [20, 21]. More recently *S. noctilio* was detected in central Chile [48], but has not been detected in countries further north.

In South Africa, *S. noctilio* was first detected in 1994 in the Western Cape [57], and spread slowly east [58], being detected in the Eastern Cape by 2002 [12, 59] and more recently in KwaZulu-Natal [59], where it is causing extensive damage in *P. patula* plantations (B. Hurley, 2004, unpublished data). *Sirex noctilio* has not yet been detected in the commercial pine plantations in provinces north of KwaZulu-Natal, nor in countries north of South Africa where *Pinus* is grown commercially.

*Sirex noctilio* has not yet established in North America, although it is commonly intercepted in wood at ports of entry in the United States [18, 49]. North America has extensive natural forests of *Pinus* species [7], many of which are susceptible to *S. noctilio* (e.g., *P. radiata*, *P. taeda*, *P. elliotii* and *P. ponderosa*). Therefore, there is great concern over the potential introduction of *S. noctilio* into Northern America [15, 62].

China has extensive native pine forests (e.g., *P. massoniana* and *P. tabulaformis*) and plantations of exotic pines (e.g.,

*P. sylvestris*, *P. caribaea*, *P. taeda*, *P. elliotii* and *P. radiata*) [13, 27], which are susceptible to *S. noctilio* [4, 49]. *Sirex noctilio* has not been detected in China, although it occurs in neighbouring countries to the north [49]. Assuming that climatic conditions are suitable, there seems no reason why *S. noctilio* should not be established or endemic to China.

Knowledge of the potential distribution and spread of pests or pathogens into new areas enables forest managers to survey for introductions and be prepared with management strategies. Computer programs such as CLIMEX [53, 54] and BIOCLIM [5] enable one to predict the potential distribution of a species and have been used to predict the distribution of insect pests [19, 32, 52, 64], biological control agents [45, 46] and pathogens [2, 9]. In this study we use the CLIMEX program to predict the potential distribution of *S. noctilio* across the globe based on climatic requirements estimated from its current distribution and discuss this in relation to the distribution of susceptible hosts in the Southern Hemisphere, North America and China.

## 2. MATERIALS AND METHODS

### 2.1. Known distribution of *S. noctilio* and susceptible hosts across the globe

The native distribution of *S. noctilio* was determined from published records [17, 49, 51]. The current distribution of *S. noctilio* and its hosts in the Southern Hemisphere was determined from published records from Australia [6, 35, 37, 60], South America [20, 47, 48, 50] and South Africa [12, 51, 59]. For North America, the distribution of susceptible hosts was determined from published records [7].

### 2.2. CLIMEX prediction of distribution of *Sirex noctilio*

The computer program CLIMEX [54] predicts the potential distribution of a species based on climatic parameters. A fundamental assumption of the CLIMEX program is that a species distribution is determined by climate. A CLIMEX model for a species can be developed in two ways. The first method is to obtain parameter values of climatic requirements by carrying out experiments (e.g., [46]) or from literature (e.g., [32]). The second method is to estimate the parameter values using climate data in the species' native range (e.g., [63]). In the second method the parameter values are then adjusted iteratively until the indices for growth and survival at locations within the native range show high values (i.e., persistence), while the indices at locations outside of the native range show low values (i.e., extinction). The first method is preferred over the second method because, due to competition, natural enemies or lack of suitable hosts, a species may be absent from locations climatically suitable for establishment. Model validation is an essential step in developing CLIMEX models, especially when the second method is used.

Several studies have investigated the effects of temperature on the behaviour of *S. noctilio* (see [28, 34]); however, these studies were conducted in areas where *S. noctilio* is an exotic, and where temperature extremes (especially cold) that occur in its native range are not experienced. Therefore, we developed a model in CLIMEX that predicts the distribution of *S. noctilio* within the known native range (the second method above). The precise geographic boundaries of *S. noctilio* are presently not defined; however, surveys of native pine stands in northern Africa, Europe and Turkey [51] and an extensive literature search [17, 49] has provided a detailed list of the distribution records



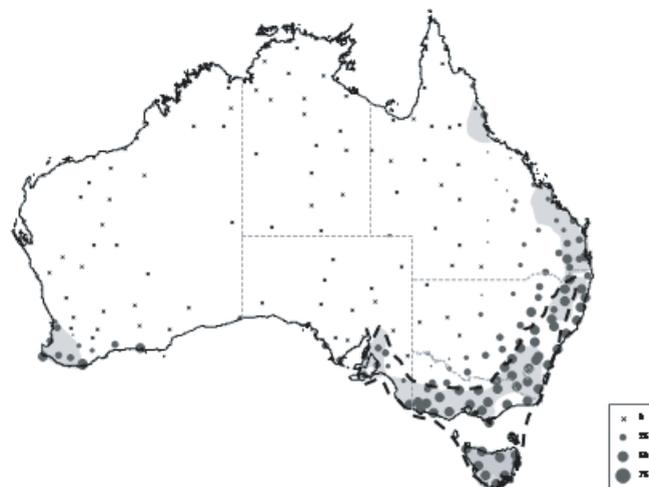
**Figure 1.** CLIMEX model of the distribution of *S. noctilio* (circles) in the Palearctic region. The recorded distribution of *S. noctilio* [17, 49, 51] is bordered by the dashed line. The size of circles indicates likelihood of survival, and crosses indicate climate stations where *S. noctilio* is predicted not to survive.

of *S. noctilio* (Fig. 1). We started with the template parameter values for organisms in temperate regions in CLIMEX (see [54]) and then parameters were iteratively adjusted so that the Ecoclimate Index (EI<sup>1</sup>) values for most locations within the known distribution range of *S. noctilio* in Europe, North Africa and Asia indicate persistence of *S. noctilio* (i.e., EI values greater than 30).

Using the model developed above, distribution of *S. noctilio* in four states in Australia (New South Wales, South Australia, Tasmania and Victoria), where *S. noctilio* is established [6, 35], was predicted. We selected locations with pine plantations in these four states that matched location data in CLIMEX and examined whether *S. noctilio* has been recorded there and whether the EI values are high enough for population persistence (EI greater than 30). We also checked if EI values are greater than 30 for all locations with *S. noctilio* records in Australia. Parameter values were then adjusted so that EI values for locations with a *S. noctilio* record were greater than 30. Using the refined model developed from the Australian data, we predicted the distribution of *S. noctilio* in Uruguay, Argentina and southern Brazil, where *S. noctilio* is established [20, 26]. *Sirex noctilio* has probably reached its maximum distribution in Uruguay and Argentina [20]. Parameter values were again adjusted so that EI values for locations with a *S. noctilio* record were greater than 30. At this stage, we were able to specify values in parameters such as heat stress and high temperature optimum (Tab. I). The resultant CLIMEX model was then used to predict the possible distribution range of *S. noctilio* in (1) areas in Australia where this species has not been recorded, (2) Africa and South America where *S. noctilio* has recently been introduced and spreading, and (3) North America and China where *S. noctilio* is not known to be established, but its host species are widespread.

### 3. RESULTS

The CLIMEX model predicted that *S. noctilio* could colonise eastern Australia (from Queensland through to Tasmania and South Australia) and south-western Australia (Fig. 2). The current distribution of *S. noctilio* in Australia is within the predicted range, from south-eastern South Australia through to Victoria, Tasmania and inland north-eastern New South Wales (Fig. 2). The CLIMEX model predicted that *S. noctilio* could



**Figure 2.** Prediction of distribution of *S. noctilio* (circles) in Australia. The size of circles indicates likelihood of survival. The recorded distribution of *S. noctilio* [6, 35] is bordered by the dashed line. Commercial plantations and amenity plantings of susceptible hosts are located within the shaded area [37, 60].

colonise areas in coastal north-eastern New South Wales, eastern Queensland and south-western Western Australia, where *S. noctilio* has not yet established and where susceptible hosts are planted.

The CLIMEX model predicted that *S. noctilio* could colonise Uruguay, much of Argentina, eastern Brazil, central and southern Chile, Paraguay, Bolivia, Peru, Ecuador, Colombia and Venezuela (Fig. 3). The current distribution of *S. noctilio* in South America is within this predicted range (Fig. 3).

The CLIMEX model predicted that *S. noctilio* could colonise most of the countries along eastern Africa, including South Africa, Zimbabwe, Mozambique, Madagascar, Tanzania, Uganda,

<sup>1</sup> EI = Ecoclimate Index: describes the climate suitability of a location for a species as a single number between 1 and 100; the higher the number the more favourable the location is for permanent occupation of the target species [54].

**Table I.** CLIMEX parameter values for *S. noctilio*<sup>1</sup>.

CLIMEX parameters		Value
	Temperature	
DVO = lower threshold		0 °C
DV1 = lower optimum limit		5 °C
DV2 = upper optimum limit		24 °C
DV3 = upper threshold		30 °C
	Moisture	
SMO = lower soil moisture threshold		0.1
SM1 = lower optimum soil moisture		0.3
SM2 = upper optimum soil moisture		1.0
SM3 = upper soil moisture threshold		2.5
	Cold stress	
TTCS = temperature threshold		0 °C
THCS = stress accumulation rate		0
DTCS = degree-day threshold		0
DHCS = stress accumulation rate		0
	Heat stress	
TTHS = temperature threshold		35 °C
THHS = stress accumulation rate		0.05
DTHS = degree-day threshold		0
DHHS = stress accumulation rate		0
	Dry stress	
SMDS = soil moisture dry stress threshold		0.1
HDS = stress accumulation rate		0.01
	Wet stress	
SMWS = soil moisture wet stress threshold		2.5
HWS = stress accumulation rate		0.002
	Hot-dry stress	
TTHD = hot-dry temperature threshold		23 °C
MTHD = hot-dry moisture threshold		0.1
PHD = hot-dry stress rate		0.1
	Hot-wet stress	
TTHW = hot-wet temperature threshold		32 °C
MTHW = hot-wet moisture threshold		1.5
PHW = hot-wet stress rate		0.5

<sup>1</sup> See Sutherst et al. [54] for further explanation of parameter terms.

Kenya and Ethiopia, as well as countries along the mid-west coast and northern Africa (Fig. 4). The current distribution of *S. noctilio* in South Africa and northern Africa (Morocco and Tunisia) is within the predicted range (Fig. 4).

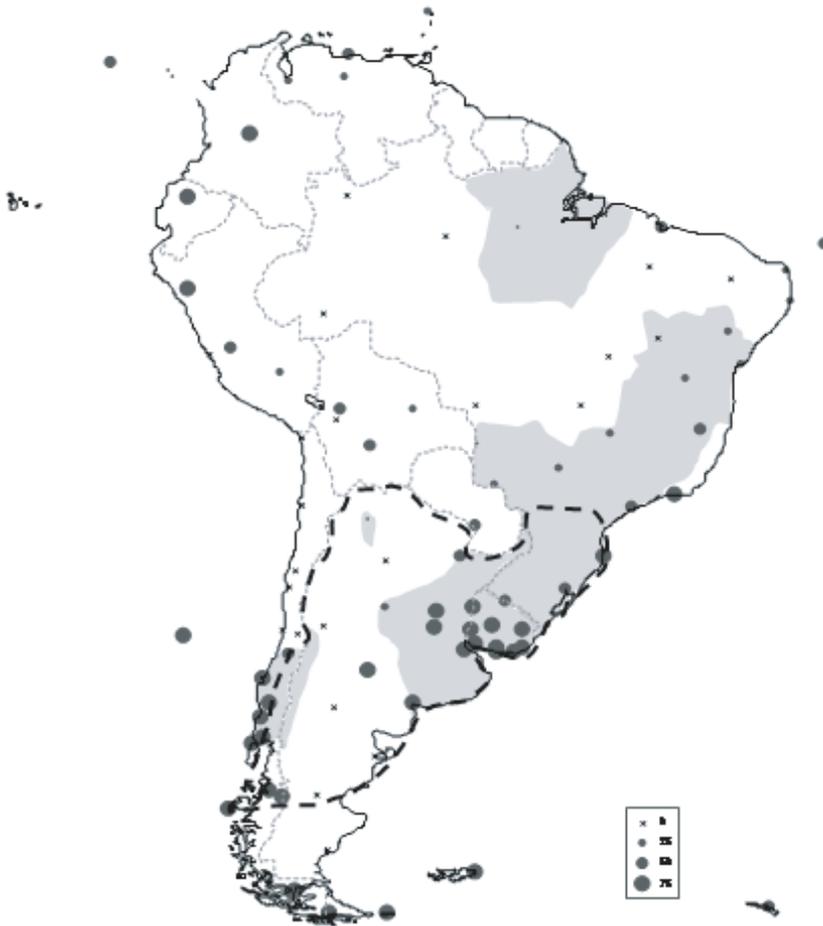
The CLIMEX model predicted that *S. noctilio* could colonise the majority of the United States, Canada and Mexico (Fig. 5). The model also predicted that *S. noctilio* would be able to persist in central Guatemala, Costa Rica and Panama, but not Salvador (see Figs. 3 and 5). There is no climate data for Honduras or Nicaragua in the current version of CLIMEX.

The CLIMEX model predicted that *S. noctilio* could colonise areas from Yunnan Province in south-central China through

to Heilongjiang Province in north-eastern China, with the majority of Provinces between these with high EI values (Fig. 6).

#### 4. DISCUSSION

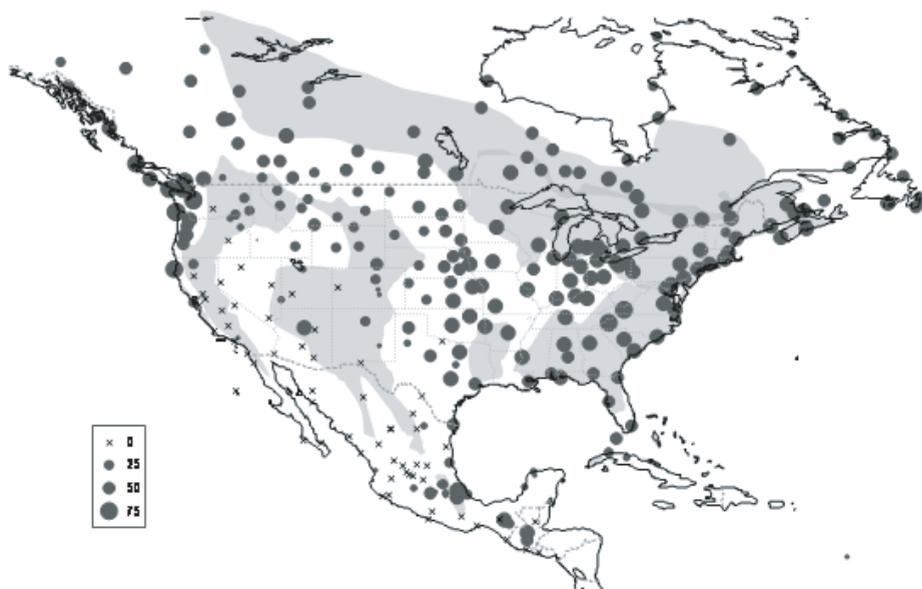
In our CLIMEX model, we estimated parameter values for climatic requirements of *S. noctilio* from the present distribution range of the species, rather than laboratory experiments. Therefore, one needs to be careful about interpreting the predicted distribution range of *S. noctilio*. However, we used all available information and validated the model twice using the data from two different continents where *S. noctilio* had been introduced.



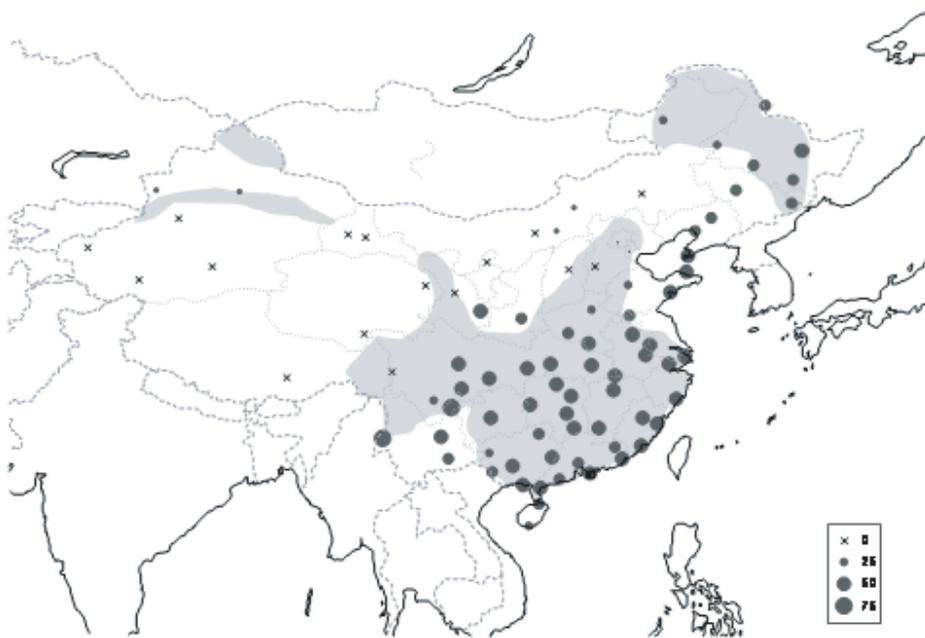
**Figure 3.** Prediction of distribution of *S. noctilio* (circles) in South America. The size of circles indicates likelihood of survival. The recorded distribution of *S. noctilio* ([20, 25], R. Ahumada, 2004, unpublished data) is bordered by the dashed line. Commercial plantations and amenity plantings of susceptible hosts in Uruguay, Argentina, Brazil and Chile are located within the shaded area [47, 48, 50].



**Figure 4.** Prediction of distribution of *S. noctilio* (circles) in Africa. The size of circles indicates likelihood of survival. The recorded distribution of *S. noctilio* ([12, 51, 59], B. Hurley, 2004, unpublished data) is bordered by the dashed line. Commercial plantations and amenity plantings of susceptible hosts in South Africa are located within the shaded area (Mondi Forests, 2004, unpublished data).



**Figure 5.** Prediction of distribution of *S. noctilio* (circles) in North America. The size of circles indicates likelihood of survival. Native forests of susceptible hosts (*Pinus* spp.) are located within the shaded area [7].



**Figure 6.** Prediction of distribution of *S. noctilio* (circles) in China. The size of circles indicates likelihood of survival. Commercial plantations, amenity plantings and native forests of susceptible hosts are located within the shaded area (Jianghua Sun, 2004, unpublished data).

Based on climatic conditions, *S. noctilio* is predicted to be able to persist in the majority of areas where commercial *Pinus* plantations are grown in Australia, Africa and South America. *Sirex noctilio* is already well established on parts of these continents, and based on historic rates of spread within countries where *S. noctilio* is established [6, 10, 20, 39, 59] it is expected that over the next 10–25 years *S. noctilio* will colonise pine plantations currently free of *S. noctilio*. However, there are areas and countries within these continents that are less likely to be colonised by *S. noctilio*.

Based on the historic spread of *S. noctilio* in Australia (30–40 km per year [6, 10, 39]), and distribution of susceptible hosts, plantations in north-eastern New South Wales and south-eastern Queensland are expected to become colonised within the next five years. Currently, quarantine measures restrict the importation of infested pine logs into Queensland, specifically aimed at reducing the chance of *S. noctilio* establishing in that state. Plantations in Western Australia are separated from those in eastern Australia by approximately 2 000 km and thus they are unlikely to become colonised by natural migration of *S. noctilio*.

The most likely means of colonising these plantations is human-assisted transport of infested wood. To prevent this, quarantine restricts the export of infested logs into Western Australia from the eastern states.

*Sirex noctilio* has taken less than 20 years to establish in the majority of *Pinus* plantations in Uruguay, Argentina and southern Brazil [20, 25]. All commercial pine plantations in Uruguay were quickly colonised by *S. noctilio* once it was first detected in the country [20, 31]. However, since 'detection' does not necessarily equate to 'introduction', the speed of this colonisation may be overestimated if detection was actually delayed.

In Argentina, *S. noctilio* is established in the majority of commercial pine plantations [20, 25, 26]. The bulk of these plantations are in north-eastern Argentina, with *P. elliottii* and *P. taeda* the main hosts. However, there are areas in Argentina where CLIMEX predicted *S. noctilio* to persist (e.g., the southern Provinces of Santa Cruz, Tierra del Fuego and Islas Malvinas), but *S. noctilio* has not been detected. There are only a few small and isolated plantations in these Provinces, which are a long distance from the main plantations.

In Brazil, the majority of pine plantations (~ 1 060 050 ha) are in the south of the country, where *S. noctilio* has already established [20, 21]. There are also large areas of plantation (~ 583 080 ha) just north of these, where *S. noctilio* has not been detected. The CLIMEX model predicted the pest could establish and persist in these plantations. With the majority of these planted with susceptible hosts (*P. caribaea* var. *hondurensis*, *P. oocarpa*, *P. kesiya*, *P. tecunumani*, *P. taeda* and *P. elliottii* [8]), the probability of *S. noctilio* reaching and impacting these plantations is high. This is recognised by the forestry sector in Brazil, with the National Fund for Woodwasp Control created in 1989 [21], and adoption of the Sirex Management Strategy as well as Quarantine procedures. There were several areas in Brazil, that have moderate areas of *Pinus* plantation (e.g., Mato Grosso do Sul (~ 64 000 ha), Amapá (~ 80 000 ha) and Pará (~ 22 000 ha)), that the model did not predict *S. noctilio* to colonise.

*Sirex noctilio* has only been reported from *P. radiata* in Chile; however, this is the main species for commercial plantations in the country [22]. The Chilean government and forestry companies are currently attempting to eradicate *S. noctilio*. Due to the close proximity of infested stands within Chile and in neighbouring Argentina, and the high susceptibility of *P. radiata*, the chances that *S. noctilio* will establish in the majority of commercial plantations in Chile is high. Chile has implemented the Sirex Management Strategy to reduce the impact and spread of *S. noctilio* in their pine plantations ([1], R. Ahumada, 2004, unpublished report). In southern Chile there are moderate sized plantations of susceptible species [41]. However, there are only a few isolated plantations between these and infested stands to the north, which are a considerable distance from the main commercial plantations, so *S. noctilio* is unlikely to colonise these southern plantations unless via human-assisted transport of infested wood.

*Sirex noctilio* has not been detected in the ~ 5 000 ha of *P. taeda* plantations in Paraguay [20], although there are infested plantations in neighbouring countries (Argentina and Brazil). The CLIMEX model predicts that *S. noctilio* can persist in Paraguay, thus the likelihood of colonisation is high. There are approximately 67 000 ha of *Pinus* species in Ecuador,

78 000 ha in Colombia and 690 000 ha in Venezuela, mostly *P. taeda*, *P. elliottii*, *P. elliottii* × *P. caribaea* [11]. *Sirex noctilio* has not been detected in Venezuela, Colombia or Ecuador (F. Fernandez, 2004, pers. comm.; F. Montenegro, 2004, pers. comm.), although the model predicted that it may establish in these countries. However, these plantations are over 2 000 km from the nearest infested plantations, thus human-assisted transport of infested wood is the most likely pathway for introduction. The Sirex Management Strategy, as well as quarantine procedures, should be adopted by Paraguay, Ecuador, Colombia and Venezuela. The continued use of this strategy will reduce the economic impact, and spread, of *S. noctilio* in South America. There are few *Pinus* plantations in Peru and Bolivia [11], but *S. noctilio* was predicted to be able to survive in these if introduced.

In Africa, large plantations of *Pinus* occur from Cape Town to Northern Province in South Africa, through Zimbabwe, Tanzania, Uganda and Ethiopia [23, 33, 40, 42]. All of these areas are predicted to be climatically suitable for *S. noctilio*. The main species planted in these countries are *P. patula*, *P. taeda*, *P. radiata* and *P. elliottii*, all known to be susceptible to *S. noctilio*. Due to the distance of plantations in Zimbabwe, Tanzania, Uganda and Ethiopia from plantations in South Africa where *S. noctilio* is established, these are likely to be colonised by *S. noctilio* only via transport of infested wood. Effective quarantine restrictions of infested logs within and among countries will reduce the spread of *S. noctilio*.

The dispersal rate of *S. noctilio* in south-western South Africa, of approximately 48 km per year [59], is similar to the 30 to 40 km per year observed in Australia [6, 10, 39]. However, the recent detection of *S. noctilio* over 670 km north-east of the nearest known infestation in South Africa implies that the wasp was accidentally transported there in untreated poles, or may be due to a separate introduction into the country. Alternatively, the spread of *S. noctilio* to new areas may have been detected years after it was present in those areas, due to lack of adequate surveillance, thus giving a false perception of the rate at which *S. noctilio* had spread.

North America is characterised by extensive native forests of *Pinus* species [7], many of which are susceptible to *S. noctilio*, and therefore *S. noctilio* is considered a significant threat to North America [15, 62]. The CLIMEX model predicted that *S. noctilio* would be able to establish in the majority of areas in North America where susceptible hosts are located. The effect of *S. noctilio* on the native pine forests of North America could be significant [15].

The CLIMEX model predicted that *S. noctilio* would be able to persist in several Central American countries, including Guatemala and Costa Rica, which both have moderate sized *Pinus* plantations [11]. These countries could provide a bridge for *S. noctilio* to spread from South America to North America. However, due to limitations of CLIMEX (no data for several Central American countries) we were unable to show a complete bridge that siren could cross from the infested area in South America, through Central America, to North America. Cooperative work already exists between the United States and countries in South America to reduce the risk of introduction of *S. noctilio* into United States forests [61], and cooperation with countries in Central America will enhance this work.

There are large areas of forests of *P. massoniana* in the south-east of China and of *Larix gmelinii* in the north east, and *P. sylvestris*, *P. tabulaeformis* and *Larix* is widely planted as afforestation species in north-eastern China [27]. In southern China large areas of *P. taeda*, *P. elliotii* and *P. radiata* were planted in the late 1970s and early 1980s [13, 27]. All these hosts are susceptible to *S. noctilio* [4, 49, 51], and many of these areas are planted within the *S. noctilio* range predicted by the CLIMEX model. *Sirex noctilio* is native to Siberia and Mongolia on the northern border with China. Thus, it would seem that the likelihood of invasion by this species into China is very high. Indeed, due to the large area of susceptible hosts endemic to the country and its suitable climate, one would expect *S. noctilio* to be native to China. Perhaps a natural barrier is restricting *S. noctilio* from crossing from Mongolia into China: the high elevation Gobi desert with few host trees. Some suspect that *S. noctilio* may already have invaded China, but needs time to build up its population to be detected (Yuan, 2003, pers. comm.). Twelve species of *Sirex* are already present in China [66], and some are major pests at a regional level, such as *S. rufiabdominis* in Zhejiang [65]. The National Forestry Administration is initiating a nationwide survey of exotic forest pests in China from 2004. *Sirex noctilio* will be listed as one of the targeted survey species in north-eastern and south-eastern China.

In eastern Australia, southern South America and southern Africa, where *S. noctilio* is established, the natural spread into the majority of remaining plantations in these regions is inevitable. The continued use of the Sirex Management Strategy [16] will reduce the economic impact of this pest in these countries. For countries in South America and Africa that are adjacent to infested countries, strict control of movement of lumber from infested areas (e.g., South Africa) into non-infested areas (e.g., Zimbabwe north) will need to be implemented to slow the spread, and therefore economic impact, of *S. noctilio*. Similar quarantine restrictions are in place in Australia to reduce the spread of siren into Queensland and Western Australia. In countries where *S. noctilio* is not yet an established pest, effective training of forestry personnel in pest identification, surveillance and management is essential for early detection and implementation of the management strategy. In North America, where *S. noctilio* is likely to have a significant impact both economically and ecologically, preventing entry is the best strategy. Cooperative work among neighbouring countries will assist in reducing the spread of this significant pest of *Pinus*.

#### Note added in proof

As new information reported after this paper had been accepted: *Sirex noctilio* has recently been detected in New York State in eastern USA. Delimiting surveys have been conducted and a management plan is being developed by the United States Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS) and Plant Protection and Quarantine (PPQ) [accessed online at [http://www.aphis.usda.gov/ppq/ep/emerging\\_pests/sirexnoctilio.html](http://www.aphis.usda.gov/ppq/ep/emerging_pests/sirexnoctilio.html)].

**Acknowledgments:** We would like to thank the respective forestry and research agencies for providing information used in this study (including, from Australia, Nick Collett, Stephen Elms, Charlma Phillips, Dick Bashford, Karl Wotherspoon, Janet Farr and Ray Fremlin), and Robert Eldridge and John Scott for reviewing the manuscript.

#### REFERENCES

- [1] Ahumada R., Estrategia de detección y control de *Sirex noctilio* en el patrimonio de las empresas Arauco, Segundo Workshop sobre fitosidad forestal del Mercosur, Eldorado, Misiones, Argentina, 1997.
- [2] Backhouse D., Burgess L.W., Mycogeography of *Fusarium*: climatic analysis of the distribution within Australia of *Fusarium* species in section *Gibbosum*, Mycol. Res. 99 (1995) 1218–1224.
- [3] Bedding R., Biological control of *Sirex noctilio* using the nematode *Deladenus siricicola*, in: Bedding R., Ackhurst R., Kaya H. (Eds.), Nematodes and the biological control of insect pests, CSIRO, Australia, 1993, pp. 11–20.
- [4] Browne F.G., Pests and diseases of forest plantation trees, Clarendon Press, Oxford, 1968.
- [5] Busby J.R., BIOCLIM – a bioclimatic analysis and prediction system, Plant Prot. Quart. 6 (1991) 8–9.
- [6] Carnegie A.J., Eldridge R.H., Waterson D.G., The history and management of siren wood wasp, *Sirex noctilio* (Hymenoptera: Siricidae), in pine plantations in New South Wales, Australia, N. Z. J. For. Sci. 35 (2005) 3–24.
- [7] Chritchfield W.B., Little E.L. Jr., Geographic distribution of the pines of the world, US Department of Agriculture, Miscellaneous Publication 991, 1966.
- [8] Duraflora S.A., Susceptibilidade de toras de pinheiros tropicais ao ataque da vespa-da-madeira, *Sirex noctilio* (Hymenoptera: Siricidae), in: Conferência Regional da Vespa-da-Madeira, *Sirex noctilio*, na América do Sul. EMBRAPA, Colombom PR, Brazil, 1992, pp. 97–109.
- [9] Ekins M.G., Aitken E.A.B., Goulter K.C., Carpogenic germination of *Sclerotinia* minor and potential distribution in Australia, Aust. Plant Pathol. 31 (2002) 259–265.
- [10] Eldridge R.H., Taylor E.E., Siren woodwasp – a pest of pine in N.S.W., Forestry Commission of N.S.W., Forest Protection Series No. 1, 1989, 5 p.
- [11] Food and Agriculture Organization, Global Forest Resources Assessment 2000 – Main Report, Food and Agriculture Organization of the United Nations, Forestry Paper 140, 2000, 479 p.
- [12] Forest and Agricultural Biotechnology Institute, Tracking Siren. Tree Protection News, November 2002, [accessed online] [www.up.ac.za/academic/fabi/tcpc/](http://www.up.ac.za/academic/fabi/tcpc/).
- [13] Ge Q.S., Zhao M.C., Zhang X.Q., Zheng J.Y., Sun H.N., Zhang P.Y., Statistical analysis of the changes of forest resource and precipitation in China over the past 50 years, J. Nat. Res. 16 (2001) 413–419.
- [14] Hall M.J., A survey of siricid attack on radiata pine in Europe, Aust. For. 32 (1968) 155–162.
- [15] Haugen D.A., *Sirex noctilio* Fabricius, Exotic Forest Pest Information System for North America (EXFOR), [accessed online] [www.spfnic.fs.fed.us/exfor/](http://www.spfnic.fs.fed.us/exfor/) (updated 2005).
- [16] Haugen D.A., Bedding R.A., Underdown M.G., Neumann F.G., National strategy for control of *Sirex noctilio* in Australia, Aust. For. Grower 13 (1990) Special Liftout Section No. 13, 8 p.
- [17] Hedicke H. (Ed.), Hymenopterorum Catalogus, Part 6: Siricidae, Dr W. Junk B.V. Publishers, The Hague, Holland, 1938.
- [18] Hoebeke E.R., Haugen D.A., Haack R.A., *Sirex noctilio*: discovery of a Palearctic siricid woodwasp in New York, Newsletter Michigan Entomol. Soc. 50 (2005) 24–25.
- [19] Hughes R.D., Maywald G.F., Forecasting the favourableness of the Australian environment for the Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae), and its potential impact on Australian wheat yields, Bull. Entomol. Res. 80 (1990) 165–175.

- [20] Iede E.T., Klasmer P., Penteado S.R.C., *Sirex noctilio* in South America: distribution, monitoring and control, in: Proceedings XXI International Congress of Entomology, Brazil, August 2000.
- [21] Iede E.T., Penteado S.R.C., Schaitza E.G., *Sirex noctilio* problem in Brazil: detection, evaluation, and control, in: Iede E., Shaitza E., Penteado S., Reardon R., Murphy T. (Eds.), Proceedings of a Conference: Training in the control of *Sirex noctilio* by use of natural enemies, USDA Forest Service (FHTET 98-13), 1998, pp. 45–52.
- [22] INFOR, Estadísticas Forestales 2000, Instituto Forestal, Corporación de Fomento de la Producción, Santiago, Chile, Boletín Estadístico No 84, 2002, 122 p.
- [23] Kiwuso P., Current status of aphids in Uganda: Their impact on forest resources and control operations thus far employed, in: Kenya Forestry Research Institute Proceedings of a workshop on Exotic Aphid Pests of Conifers: A crisis in African Forestry, 3–6 June 1991, Kenya Forestry Research Institute, Muguga, Kenya, 1991, pp. 81–84.
- [24] Klasmer P., Fritz G., Acciones de detección y control de *Sirex noctilio* F. (Hymenoptera: Siricidae) en la región Andino-patagónica argentina, Informe técnico de la temporada 1993–1994, Campo Forestal general San Martín, EEA, INTA Bariloche, Argentina, 1994.
- [25] Klasmer P., Corley J., Botto E., Presencia de la avispa barrenadora de los pinos *Sirex noctilio* F. (Hymenoptera: Siricidae) en la región andino-patagónica de Argentina Estado actual de las investigaciones para su control biológico, in: Proceedings International Forest Insect Workshop, CONAF, Santiago de Chile, Pucón, Chile, 18 al 21 de agosto, sesión No. 2, 1998, pp. 69–79.
- [26] Klasmer P., Fritz G., Corley J., Botto E., Current status of research on *Sirex noctilio* F. in the Andean-Patagonian region in Argentina, in: Iede E., Shaitza E., Penteado S., Reardon R., Murphy T. (Eds.), Proceedings of a Conference: Training in the control of *Sirex noctilio* by use of natural enemies, USDA Forest Service (FHTET 98-13), 1998, pp. 89–90.
- [27] Li W.H., Forest Resources of China, Chinese Forestry Publishing House, Beijing, 430 p., 1996.
- [28] Madden J.L., Oviposition behavior of the woodwasp, *Sirex noctilio* F., Aust. J. Zool. 22 (1974) 341–351.
- [29] Madden J.L., An analysis of an outbreak of the woodwasp *Sirex noctilio* F. (Hymenoptera: Siricidae), in *Pinus radiata*, Bull. Entomol. Res., 65 (1975) 491–500.
- [30] Madden J.L., *Sirex* in Australasia, in: Berryman A.A. (Ed.), Dynamics of forest insect populations, Plenum Publishing, NY, 1988, pp. 407–429.
- [31] Maderni J.F.P., *Sirex noctilio* F.: present status in Uruguay, in: Iede E., Shaitza E., Penteado S., Reardon R., Murphy T. (Eds.), Proceedings of a Conference: Training in the control of *Sirex noctilio* by use of natural enemies, USDA Forest Service (FHTET 98-13), 1998, pp. 81–82.
- [32] Matsuki M., Kay M., Serin J., Floyd R., Scott J.K., Potential risks of accidental introduction of Asian gypsy moth (*Lymantria dispar*) to Australia and New Zealand: effects of climatic conditions and suitability of native plants, Agric. For. Entomol. 3 (2002) 303–320.
- [33] Mbwana S.B., Tree species for industrial forestry in Tanzania. Experiences and future recommendations, in: Proceedings of a workshop on priority species for tree planting and afforestation in Tanzania. Morogoro, 14–18 May, 1990, Ministry of Tourism, Natural Resources and Environment, Dar es Salaam, 1991, pp. 99–104.
- [34] Morgan F.D., Bionomics of Siricidae, Annu. Rev. Entomol. 13 (1968) 239–256.
- [35] Morgan F.D., Forty years of *Sirex noctilio* and *Ips grandicollis* in Australia, N. Z. J. For. Sci. 19 (1989) 198–209.
- [36] Morgan F.D., Stewart N.C., The biology and behaviour of the woodwasp *Sirex noctilio* (F.) in New Zealand, Trans. Roy. Soc. N. Z. 7 (1966) 195–204.
- [37] National Forest Inventory, Australia's State of the Forest Report 2003, Bureau of Rural Sciences, Canberra, Australia, 2003.
- [38] Neumann F.G., Minko G., The sirex wood wasp in Australian radiata pine plantations, Aust. For. 44 (1981) 46–63.
- [39] Neumann F.G., Morey J.L., McKimm R.J., The sirex wasp in Victoria. Department of Conservation, Forests and Lands, Victoria, Bull. No. 29, 1987, 44 p.
- [40] Odera J., Pernicious exotic pests affecting forests and forest products in eastern, central and southern Africa, in: Proceedings of a workshop on Exotic Aphid Pests of Conifers: A crisis in African Forestry, 3–6 June 1991, Kenya Forestry Research Institute, Muguga, Kenya, 1991, pp. 99–105.
- [41] Oficina de Estudios y Políticas Agrarias, Estadística Forestal Regional, Ministerio de Agricultura, [accessed online 2004] [www.odepa.gob.cl/base-datos](http://www.odepa.gob.cl/base-datos).
- [42] Owen D.L., van der Zel D.W., Trees, forests and plantations in Southern Africa, in: Owen D.L. (Ed.), South African Forestry Handbook, 4th ed., South African Institute of Forestry, South Africa, 2000, pp. 3–8.
- [43] Rawlings G.B., Wilson N.M., *Sirex noctilio* as a beneficial and destructive pest to *Pinus radiata* forests, N. Z. J. For. 6 (1949) 1–11.
- [44] Rebuffo S., La avispa de la madera *Sirex noctilio* F. en el Uruguay, Montevideo, Ministerio de Ganadería Agricultura y Pesca, 17 p., 1988.
- [45] Scott J.K., Biology and climatic requirements of *Perapion antiquum* (Coleoptera: Apionidae) in southern Africa: implications for the biological control of *Emex* spp. in Australia, Bull. Entomol. Res. 82 (1992) 399–406.
- [46] Scott J.K., Yeoh P.B., Bionomics and the predicted distribution of the aphid *Brachycaudus rumexicolens* (Hemiptera: Aphididae), Bull. Entomol. Res. 89 (1999) 97–106.
- [47] Secretaría de Agricultura Ganadería Pesca y Alimentos, Inventario de plantaciones, Buenos Aires, Argentina, 2001.
- [48] Servicio Agrícola y Ganadero (SAG), Plan de contingencia para la detección y control de la avispa de la madera del Pino – *Sirex noctilio* Fabricius, Gobierno de Chile, 2001.
- [49] Smith D.R., Hymenoptera Catalogus (nova edition), Pars 14, van der Vecht J., Schenefelt R.D. (Eds.), Dr W. Junk B.V Publishers, The Hague, Holland, 1978.
- [50] Sociedade Brasileira de Silvicultura, Área plantada com *Pinus* e *Eucalyptus* no Brasil – 2001, [accessed online] [www.sbs.org.br/estatisticas.htm](http://www.sbs.org.br/estatisticas.htm).
- [51] Spradbery J.P., Kirk A.A., Aspects of the ecology of siricid woodwasp (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia, Bull. Entomol. Res. 68 (1978) 341–359.
- [52] Spradbery J.P., Maywald G.F., The distribution of the European or German wasp, *Vespa germanica* (F.) (Hymenoptera: Vespidae), in Australia: past, present and future, Aust. J. Zool. 40 (1992) 495–510.
- [53] Sutherst R.W., Maywald G.F., A computerised system for matching climates in ecology, Agric. Ecosyst. Environ. 13 (1985) 281–299.
- [54] Sutherst R.W., Maywald G.F., Yonow T., Stevens P.M., CLIMEX: predicting the effects of climate on plants and animals, CSIRO Publishing, Australia, 1999.
- [55] Taylor K.L., Evaluation of the insect parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania, Oecologia 32 (1978) 1–10.
- [56] Taylor K.L., The sirex woodwasp: ecology and control of an introduced forest insect, in: Kitching R.L., Jones R.E. (Eds.), The Ecology of Pests, CSIRO, Australia, 1981, pp. 231–248.
- [57] Tribe G.D., The woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), a pest of *Pinus* species, now established in South Africa, Afr. Entomol. 3 (1995) 216–217.

- [58] Tribe G.D., Sirex woodwasp expands its range, *Plant Prot. News* 49 (1997) 9–10.
- [59] Tribe G.D., Cillié J.J., The spread of *Sirex noctilio* Fabricus (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents, *Afr. Entomol.* 12 (2004) 9–17.
- [60] Turvey N.D., Ryan P.J., Smith J.E.N., Suitability and availability of land for expansion of plantations, in: Dargavel J., Semple N. (Eds.), *Prospects for Australian forest plantations*, Australian National University, Canberra, Australia, 1990, pp. 229–354.
- [61] USDA Forest Service, Forest Health Technology Enterprise Team Update: Fall/Winter 2000, [accessed online] [www.fs.fed.us/foresthealth/technology/](http://www.fs.fed.us/foresthealth/technology/).
- [62] USDA Forest Service, Pest risk assessment of importation of *Pinus radiata* and Douglas-fir logs from New Zealand, Miscellaneous Publication 1508, Washington, DC, 1992.
- [63] Wharton T.N., Kriticos D.J., The fundamental and realized niche of the Monterey Pine Aphid, *Essigella californica* (Essig) (Hemiptera: Aphididae): implications for managing softwood plantations in Australia, *Divers. Distrib.* 10 (2004) 253–262.
- [64] Worner S.P., Ecoclimatic assessment of potential establishment of exotic pests, *J. Econ. Entomol.* 81 (1988) 973–983.
- [65] Xaio G.R., *Forest insects of China*, Forestry Publishing House, Beijing, China (1992).
- [66] Xiao G.R., Wu Jian., A study on Siricidae in China, *For. Sci. Suppl.* (1983) 1–29.