A comparison of control results for the alien invasive woodwasp, *Sirex noctilio*, in the southern hemisphere

- Brett P. Hurley,
- Bernard Slippers and
- Michael J. Wingfield

Department of Genetics, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa

Abstract

1 *Sirex noctilio* has resulted in one of the most damaging biological invasions of pine forestry in the southern hemisphere.

2 An intensive, integrated control programme has been developed for this pest and is generally considered very successful. However, a critical comparison of *S. noctilio* infestations and control efforts throughout the southern hemisphere reveals that control has not been uniformly effective. Of particular concern is the apparently unexplained variability in establishment and success of biological control agents, including various parasitic wasps and the parasitic nematode *Deladenus siricidicola*.

3 An overlooked aspect in the establishment of the biological control interventions for *S. noctilio* is the potential influence of genetic bottlenecks on the ability of the agents to adapt to different environments and different populations of *S. noctilio*.

4 Despite established biological control agents, stress in forests caused by silvicultural practices or the environment will predispose trees to heavy infestation. Unfortunately, improved silvicultural practices are not always economically feasible and environmental changes are often unavoidable.

5 *Sirex noctilio* continues to pose a serious threat to pine forestry in many areas. Despite extensive earlier research into a single integrated control for *S. noctilio*, it is important to recognize that such a strategy will probably require significant local adaptation in new areas of infestation and over time.

Introduction

Sirex noctilio Fabricius is a woodwasp endemic to Eurasia and northern Africa that infests conifers, mainly species of *Pinus*. Together with its eggs, the female wasp injects toxic mucus and its symbiotic fungus *Amylostereum areolatum* (Chaillet) Boiden into trees (Fig. 1A, B). If the insect becomes successfully established in newly-infested trees, the combination of mucus and fungus kills the trees. The larvae develop inside these trees, feeding on fungus-infested wood (Talbot, 1977; Spradbery and Kirk, 1978; Madden, 1988).

Although it is not considered a major pest in its native range, *S. noctilio* has been accidentally introduced to various southern hemisphere countries where it has had a major economic impact on exotic pine plantations (Fig. 1C). The first of these biological invasions was in New Zealand in about 1900, followed by Australia (1952), Uruguay (1980), Argentina (1985), Brazil (1988), South Africa (1994) and Chile (2000) (Miller and Clarke, 1935; Gilbert and Miller, 1952; Tribe, 1995; Iede *et al.*, 1998; Klasmer *et al.*, 1998; Maderni, 1998; Ahumada, 2002; Slippers *et al.*, 2003) (Fig. 2). In 2005, an established population of *S. noctilio* was confirmed in the United States of America (Hoebeke *et al.*, 2005).

Slippers *et al.* (2001, 2002) used vegetative compatability groups, DNA sequences and restriction fragment length polymorphism data of *A. areolatum* to consider the origin and movement of *S. noctilio* in the southern hemisphere. These studies showed that, after its introduction to the southern hemisphere, *S. noctilio* probably spread between the southern hemisphere countries, rather than by new introductions from its native range. It was further shown that *S. noctilio* in Brazil and South Africa share the same origin.

Subsequent to its detection in the southern hemisphere, much work has been done in an effort to control populations of *S. noctilio*. For example, in Australia, the main strategy for the control of *S. noctilio* after its introduction was to locate and destroy infested trees (Neumann *et al.*, 1987; Haugen *et al.*, 1990). However, due to the substantial costs associated with this strategy and the realization that *S. noctilio* could not be eradicated from Australia, greater attention was given to biological control (Taylor, 1967; Neumann *et al.*, 1987). This approach has subsequently been followed for new *S. noctilio* invasions in other southern hemisphere countries, where biological control has been the main control strategy.

Sirex noctilio primarily attacks stressed trees (Madden, 1968). Thus, plantation health plays a crucial role in managing *S. noctilio* populations. Various silvicultural practices have been recommended to minimize the impact of *S. noctilio*. These include pruning trees outside the flight season of *S. noctilio* to avoid stress during this period, timely thinning to reduce competition and the removal of infested trees to eliminate the source for the next season's infestation (Neumann *et al.*, 1987). The degree to which these practices have been implemented varies amongst regions and is typically strongly influenced by local economics.

Plantation health is also significantly affected by local environmental conditions. Drought followed by heavy rainfall for a short period can place trees under stress, resulting in their being more prone to attack by *S. noctilio* (Madden, 1988). Other conditions that may place trees under stress include fire, winds and excessive dry heat (Madden, 1988). Such conditions are generally unpredictable and unavoidable. Thus, control measures have focused on biological control and silvicultural practices.

Control measures for *S. noctilio* invasions have been effective in many regions of the southern hemisphere, but this has not been consistently true. Levels of infestation in South Africa remain variable despite the release of biological control agents. In the Western Cape province, populations of *S. noctilio* remain low but, in parts of the Eastern Cape and KwaZulu-Natal provinces, populations are increasing rapidly, as is the associated tree mortality. Similar variability is also observed between and within other southern hemisphere countries where *S. noctilio* has been introduced (V. Klasmer, personal communication).

There have been various reviews of *S. noctilio* and its control in specific regions of the southern hemisphere (Neumann *et al.,* 1987; Iede *et al.*, 1998; Tribe and Cillié, 2004; Carnegie *et al.*, 2005). However, a review of control strategies for this important invasive pest, comparing the situation between these regions, has not been made. The present study considers the spread of *S. noctilio* in southern hemisphere countries and compares the success of efforts to control it. Based on this comparison, hypotheses are presented for possible factors responsible for the variability of control achieved in the various regions. Furthermore, suggestions are made to improve future control of *S. noctilio* where it has invaded pine plantations and forests outside its native range.

Detection, spread and damage of *S.noctilio* in the southern hemisphere

Australasia. *Sirex noctilio* was first reported in the southern hemisphere from standing trees in New Zealand around 1900 (Miller and Clarke, 1935). It subsequently spread throughout the country, mainly in *Pinus radiata* plantations. The pest did not cause serious losses in New Zealand until the drought of 1946. From 1946 to 1951, it was responsible for the devastation of many stands of *P. radiata*, killing approximately 20–30% of intermediate age *P. radiata* in 120 000 ha of unthinned plantations (Rawlings, 1955). However, apart from this outbreak, New Zealand has escaped further serious outbreaks of *S. noctilio* (Gilmour, 1965; Zondag, 1969). This is believed to be due to climatic conditions favourable for tree growth, major reforms in silvicultural practices to reduce stress and well-established populations of biological control agents (Zondag, 1969).

In Australia, *S. noctilio* was first detected in Tasmania in 1952 (Gilbert and Miller, 1952) and on the mainland of the country in 1961 (Neumann *et al.*, 1987). The wasp is presumed to have been accidentally introduced from New Zealand. *Sirex noctilio* is established in Tasmania, Victoria, South Australia, Australian Capital Territory and most of New South Wales, mainly in *P. radiata* plantations (Carnegie *et al.*, 2005). It is not yet established in north-eastern New South Wales and has not been detected in Queensland or Western Australia.

Despite considerable investment in research, the steady spread and occasional serious outbreaks of *S. noctilio* were not completely curtailed in Australia (Neumann *et al.*, 1987; Madden, 1988; Haugen, 1990). The ever present, but moderate damage in Australia was frequently interspersed with serious to very severe outbreaks. The latest of these occurred in the Green Triangle (south-eastern South Australia and south-western Victoria) between 1987 and 1990, despite an established control programme (Haugen, 1990). This was primarily due to the absence of monitoring of the *S. noctilio* population, a neglected biological control programme, and overstocked stands (Haugen, 1990). This outbreak resulted in the death of approximately 4.8 million trees before 1990 (Haugen and Underdown, 1990b; Bedding and Iede, 2005). Subsequently, there have been no serious outbreaks reported from Australia. The majority of infestations in New South Wales from 1996 to 2005 were below 3%, although mortality has been over 20% in some areas. The majority of this mortality resulted from unthinned plantations and suppressed trees (Carnegie *et al.*, 2005).

South America. In South America, *S. noctilio* was first detected in Uruguay in 1980 (Maderni, 1998), Argentina in 1985 (Klasmer *et al.*, 1998), Brazil in 1988 (Iede *et al.*, 1998) and Chile in 2000 (Ahumada, 2002). It has not yet been detected in other South American countries. Infestations are mainly in *Pinus taeda* and *Pinus elliottii* plantations in Brazil, northern Argentina and Uruguay, *Pinus elliottii ponderosa*, *P. radiata* and *Pinus elliottii contorta* var. *latifolia* in southern Argentina, and *P. radiata* plantations in Chile (Maderni, 1998; Ahumada, 2002; Carnegie *et al.*, 2006; V. Klasmer, personal communication).

Over the 20 years after its introduction into South America, *S. noctilio* damage has varied from very minimal to devastating in some areas. This is despite widespread awareness of its potential impact and attempts to control it. Tree mortality has been over 60% in some stands in Argentina (V. Klasmer, personal communication) and as high as 70% in some stands in Uruguay (Maderni, 1998). In Brazil, 350 000 ha of pine plantations are infested and an estimated US$ 6.6 million would be lost each year if an integrated pest management programme were not in place (Bedding and Iede, 2005). Large areas of *P. radiata* in Chile are susceptible to infestation, but populations of *S. noctilio* are currently low in that area and they are not widespread (R. Ahumada, personal communication).

Africa. *Sirex noctilio* was first reported in imported wood in South Africa at a timber yard in Port Elizabeth in 1962 (Taylor, 1962). At that time, the wasp apparently did not escape to become established in the pine plantations of South Africa. In April 1994, *S. noctilio* was reported in Cape Town from *P. radiata* plantations (Tribe, 1995). During the first three seasons after its initial discovery, the wasp spread in a 90-km arc through pine plantations of this region (Tribe and Cillié, 2004). In 2002, *S. noctilio* was detected in the Eastern Cape and KwaZulu-Natal provinces (B.P. Hurley, unpublished data). A variety of

Pinus species were infested, but mostly *P. radiata* in the Western Cape and *Pinus patula* in the Eastern Cape and KwaZulu-Natal. Of the remaining provinces, Mpumalanga and the North Province, which contain approximately 50% of pine plantations in South Africa (Anonymous, 2005), are the most seriously threatened by *S. noctilio*.

Sirex noctilio infestation levels in the Western Cape province of South Africa have generally been low. The main exception was an infestation in George in 2002, where tree mortality was an average of 10% in 100 ha of 12–13-year-old *P. radiata* (M. Strydom, personal communication). These trees were overstocked and the infestation subsided during the course of the next year. Infestation levels in the north-eastern Cape and KwaZulu-Natal were substantially higher than those reported in the Western Cape, with a number of compartments having over 10% infestation, and some higher than 35% (P. Croft, personal communication). Currently, it is estimated that approximately 35 000 ha of pine in the Eastern Cape and KwaZulu-Natal are infested to a mean level of 6%, with a total estimated value of damage being R300 million per annum (M. J. Wingfield, unpublished data).

Biological control in the southern hemisphere

Parasitic wasps

Australasia. From 1928 to 1968, 11 species of parasitic wasps were received from the U.S.A., Europe and Asia for rearing in New Zealand (Nuttall, 1989). Of these, only five species were eventually released in that country (Table 1). The first of these was *Rhyssa persuasoria persuasoria* (L.), collected in England, and introduced into New Zealand from 1928 (Hanson, 1939; Nuttall, 1989). This represented the first attempt to control *S. noctilio* as an alien invasive pest using a biological control agent. Shortly after this, attempts were made to establish the European parasitic wasp *Ibalia leucospoides leucospoides* (Hockenwarth). Initial attempts were unsuccessful, but by 1954 numerous releases of *I. l. leucospoides* had been made in New Zealand and it was reported to be well established by 1957 (Zondag, 1969). The other parasitic wasps released in New Zealand were *Megarhyssa nortoni nortoni* (Cresson) from the U.S.A., *Rhyssa persuasoria himalayensis* Wilkinson from Pakistan and India, and *Ibalia leucospoides ensiger* Norton, originally from the U.S.A. but reared and released from Tasmania

(Taylor, 1967; Nuttall, 1989). Of these five parasitic wasps released in New Zealand, all but *R. p. himalayensis* became well established (Table 1). Parasitism by *I. l. leucospoides* was recorded between 25% and 35% on average, but sometimes as high as 55%, whereas the combined parasitism of *I. l. leucospoides* and the rhyssines was over 70% in some areas (Nuttall, 1989). Interbreeding is known to occur between *I. l. leucospoides* and *I. l. ensiger* and between *R. p. persuasoria* and *R. p. himalayensis*, with the hybrids being indistinguishable from *I. l. leucospoides* and *R. p. persuasoria*, respectively (Nuttall, 1989). Thus, it is probable that releases of *I. l. leucospoides* and *R. p. persuasoria* in New Zealand and the rest of the southern hemisphere have also included these hybrids.

Nine species of parasitic wasps were released into Australia as biological control agents from the late 1950s (Table 1). Of these, *I. leucospoides*, *M. nortoni* and *R. persuasoria* have been the most successful. Taylor (1978) showed that *M. nortoni* and *R. persuasoria* were responsible for reducing *S. noctilio* populations in Tasmania between 1965 and 1974. *Ibalia leucospoides* was considered the most effective parasitic wasp in Victoria and New South Wales, attaining up to 40% parasitism in some areas of Victoria (Neumann *et al.*, 1987; Carnegie *et al.*, 2005). In combination, these species usually do not kill more than 40% of a *S. noctilio* population and are therefore not considered sufficient to control *S. noctilio* on their own.

South America. The parasitic wasp *I. leucospoides* was first recorded in Uruguay in 1984, where it had apparently been introduced naturally with its host *S. noctilio* or another siricid, *Urocerus gigas*. It has subsequently spread with the pest complex throughout Uruguay, Argentina, Brazil and Chile (Eskiviski *et al.*, 2004; R. Ahumada, personal communication). The natural migration, and occasional human assisted introductions, of *I. leucospoides* in South America has resulted in considerable, although variable, parasitism. Iede *et al.* (2000) reported parasitism rates of *I. leucospoides* in Brazil to be as high as 39%, and 25% on average, similar to the parasitism rates obtained in Australasia. Similarly, parasitism in the Andean Patagonian region of Argentina was in the range 20–40% (Klasmer *et al.*, 1998). Greater variation in three sites in Misiones, Argentina (0%, 2.4% and 35%) (Eskiviski *et al.*, 2004) may have been due to tree age but limited information is, however, available on the first appearance or releases of *I.*

leucospoides at these various sites, which makes direct comparisons between these reported parasitism rates difficult.

Rhyssa persuasoria and *M. nortoni* were imported and released in many affected areas of South America. The first introduction of *M. nortoni* was with wasps sent from Tasmania to Brazil in 1996 (Iede *et al.*, 2000). Fifty females and 27 males were used to start a rearing colony. The first release was in 1997 with only 18 females, but 136 males and 97 females were released the next year. *Rhyssa persuasoria* was first introduced in Brazil in 1997 (Iede *et al.*, 2000). Only nine females were used to start a rearing colony, resulting in the release of only two males and ten females the next year. Information on the establishment and further releases of *I. leucospoides, R. persuasoria* and *M. nortoni* within South America is not available.

Africa. Of the various parasitic wasps used to control *S. noctilio*, only *I. leucospoides* and *M. nortoni* have been released in South Africa. Of these, only *I. leucospoides* is known to have become established (Table 1). Eighteen females and 19 males of *I. leucospoides* were imported from Uruguay and reared in captivity for subsequent releases (Tribe and Cillié, 2004). Despite these limited releases (Table 1), establishment of this parasitic wasp has been confirmed in some plantations of the Western Cape. Sirex-infested logs collected in that area from 2001 to 2005 reveal that *I. leucospoides* has become established in some areas, but not in others (B.P. Hurley, unpublished data). It is unknown whether the establishment of 176 *I. leucospoides* collected from the Western Cape in 2006 and released the same year in the Eastern Cape and KwaZulu-Natal, have become established. Forty-four mated females and ten males of *M. nortoni* were brought from Tasmania to South Africa in 1998 and reared in captivity (Tribe and Cillié, 2004). A very small number of *M. nortoni* were released the next year in an isolated pine stand (Table 1). *Megarhyssa nortoni* were not found in Sirex-infested logs collected from the original release stand in 2003, nor has *M. nortoni* been recovered from the field in nearby plantations during surveys from 2001 to 2003.

Factors influencing successful establishment of parasitic wasps

It is clear that parasitic wasps play an important, albeit not primary, role in the control of *S. noctilio* in the southern hemisphere. *Ibalia leucospoides*, *M. nortoni* and *R.*

persuasoria are generally considered to be the most important parasitic wasps of *S. noctilio*, and in combination they can achieve significant levels of parasitism. Data pertaining to the release and establishment of these parasitic wasps in the southern hemisphere is incomplete, but it is evident that great variation in establishment exists between regions. In South Africa in particular, no parasitic wasps are currently well established. The establishment of *I. leucospoides*, *M. nortoni* and *R. persuasoria* is especially needed in KwaZulu-Natal, where *S. noctilio* is currently in an epidemic phase. The population variation of the parasitic wasps within and between different regions is not well understood. Releases of *Rhyssa* spp. in Tasmania and New South Wales, releases of *R. persuasoria* and *M. nortoni* in parts of South America, and releases of *I. leucospoides* in South Africa, have been from very small numbers of wasps (Table 1). Such small releases of biological control agents have been known to result in genetic bottlenecks (Hufbauer *et al.*, 2004; Lloyd *et al.*, 2005). Although the exact influence of genetic bottlenecks on the success of biological control agents is unclear, low genetic diversity could decrease the ability of the biological control organism to adapt to new environments and host types (Baker *et al.*, 2003; Roderick and Navajas, 2003; Lloyd *et al.*, 2005).

Villacide and Corley (2003) showed a good match between the climate of Argentina and the species characteristics of *I. leucospoides* using the CLIMEX model (http://www.hearne.com.au/climex/). However, the species characteristics used are from its native environment, where genetic diversity is expected to be high, and does not necessarily reflect introduced populations of *I. leucospoides*, where genetic diversity is low. Thus, research is needed to determine the adaptability of parasitic wasp populations to new environments as influenced by their genetic diversity. Other important factors that could influence the establishment of these parasitic wasps include the population density of *S. noctilio* when the parasitic wasps are released, the ratio of female to male wasps released, and the synchrony between the parasitic wasps and *S. noctilio* life cycles, as *I. leucospoides* only parasitizes eggs and first-instar larvae of *S. noctilio*.

Parasitic nematodes

Australasia. In 1962, the nematode *Deladenus* (*Beddingia*) *siricidicola* Bedding was found infecting *S. noctilio* in New Zealand, on *P. patula* logs in the North Island (Zondag, 1969). These nematodes entered New Zealand together with *S. noctilio* and were not intentionally introduced from Eurasia, where the wasp is native. Subsequent surveys showed that the nematode was present in most Sirex-infested plantations on the North Island, with some plantations having infection levels of *S. noctilio* as high as 90% (Zondag, 1969, 1979). No nematodes were found on the South Island. In 1967, Zondag (1971) tested various methods to artificially introduce the nematode from the North Island to the South Island. This resulted in nematodes being introduced into the South Island by means of moistened wood shavings from 1969 to 1970 (Zondag, 1979). From 1971 onwards, the gelatin-based method (Bedding and Akhurst, 1974) was used. Approximately 200 trees in the South Island were inoculated with the nematode from 1967 to 1974. By 1975, infections of *S. noctilio* of over 75% were recorded from some areas of the South Island from uninoculated trees (naturally introduced nematodes) (Zondag, 1979). No further active releases of the nematode were made after the 1970s (J. Bain, personal communication).

Hundreds of isolates of seven species of *Deladenus* that were found parasitizing siricids in their native range were collected and screened for selectivity and high parasitism (Bedding and Akhurst, 1978; Bedding and Iede, 2005). This resulted in the selection of a strain of *D. siricidicola* from Sopron, Hungary, known as the Sopron strain. Infections by this *D. siricidicola* strain were raised to levels of almost 100% in inoculated trees in Australia (Bedding and Akhurst, 1974). From the first experimental liberation of *D. siricidicola* (Sopron strain) in 1970 in northern Tasmania, 92% of Sirex-infested trees from a 12-ha compartment contained nematodes in just two years, where an estimated 50 parasitized *S. noctilio* wasps emerged from inoculated logs (Bedding and Akhurst, 1974). A loss of virulence of *D. siricidicola* was first detected during the Green Triangle outbreak in 1987–90 (Haugen and Underdown, 1993). This loss in virulence resulted from rearing the nematode in laboratory cultures for over 20 years without allowing it to go through a parasitic cycle (Bedding and Iede, 2005). To establish new cultures for laboratory breeding, nematodes were recollected during 1991 from the Kamona forest in

Tasmania (the site of the first nematode liberations in Australia during 1970). This 'Kamona' strain was subsequently reared and released to replace the Sopron strain throughout Australia.

South America. The depth of experience on the biological control of *S. noctilio* from Australasia, contributed to the establishment of biological control programmes in South America soon after the detection of the pest in this region. The Sopron strain of *D. siricidicola* was imported into Brazil from Australia in 1989, with the first inoculations in Brazil occurring that same year (Iede *et al.*, 2000). The Kamona strain was imported in 1995 (Bedding and Iede, 2005). Nematodes were isolated from infected insects in Encruzilhada do Sol, Brazil, in 1995, and these were used to establish a laboratory colony in Misiones, Argentina (Eskiviski *et al.*, 2003). Likewise, Uruguay and Chile have also imported the nematode from Brazil for direct inoculations or to establish a laboratory colony (R. Ahumada, personal communication).

Establishment of *D. siricidicola* in South America has been variable across different areas. Parasitism from uninoculated trees was up to 70–80% parasitism in a 12000-ha *P. taeda* plantation in the Rio Grande do Sul state in Brazil (Iede *et al.*, 1998), and 85% from the Andean Patagonian region of Argentina (V. Klasmer, personal communication). Despite these successful cases, parasitism from inoculated trees has often been very low. In the Santa Cantarina state of Brazil, only 18.84% parasitism was obtained from directly inoculated logs (n = 1810 wasps) (Fenili *et al.*, 2000). Fenili *et al.* (2000) suggested loss of nematode viability or virulence, inoculation technique, nematode migration ability and climatic conditions as possible reasons for the low level of parasitism. In Argentina, Eskiviski *et al.* (2003) compared parasitism rates between nematodes originally obtained from Brazil and reared for 3 years and nematodes obtained from infected wasps caught in Misiones and reared for 1 year. From the two sites tested, parasitism from inoculated logs was 2% and 35% (n = 60 wasps) for the 3-year and 1-year source, respectively, at the one site, and 10.3% and 15.5% (n = 201 wasps) for the 3-year and 1-year source, respectively, at the other site tested. Similarly, Becerra *et al.* (2000) reported parasitism below 5% from trees inoculated in some areas of Misiones. Data are unavailable on whether the nematode has managed to establish in these areas despite the low inoculation success, but the difference in inoculation success in these areas, compared with the almost 100% obtained in Australia (Bedding and Akhurst, 1974), is reason for concern.

Africa. South Africa has also benefited considerably from experience regarding the biological control of *S. noctilio* in Australasia. It was thus possible to introduce biological control agents soon after the detection of *S. noctilio* in the Western Cape. The Kamona strain of *D. siricidicola* was the first biological control agent introduced into South Africa. During 1995 and 1996, 50 and 20 million nematodes, respectively, were used to inoculate 400 trees in a 90-km arc around Cape Town. Parasitism rates in uninoculated trees were assessed in one of the plantations inoculated in 2005 and found to be 22.6% in 1996 (*n* = 402 wasps), 54% in 1997 (*n* = 89 wasps) and 96.1% in 1998 (*n* = 77 wasps) (Tribe and Cillié, 2004). These sample sizes are small and might not have represented the population as a whole. Logs collected in 2001 and 2002 from six of the plantations inoculated in 1995/6 showed variable parasitism in the range 0–64%, with an average of 20% (*n* = 191 wasps). Logs collected in this period from six plantations in the Western Cape that were not inoculated in 1995/6 showed no parasitism (*n* = 162 wasps) (B.P. Hurley, unpublished data). For logs collected in 2005 from previously inoculated plantations, percentage parasitism was in the range 0–30% (*n* = 168 wasps) (authors unpublished). Although these results are from a very limited sample, they do show variable parasitism in the Western Cape, even for areas that had previously been inoculated with the nematode. It is not known if the variation in parasitism is a consequence of the low abundance of *S. noctilio* in this region or due to the failure of the nematode to establish.

Between 1996 and 2003, no further nematodes were released for the biological control of *S. noctilio* in South Africa. Shortly after the serious new invasion of this pest in 2003, 180 million nematodes were used to inoculate approximately 1800 trees in 2004. These inoculations were mainly in the Eastern Cape and KwaZulu-Natal, where infestations of *S. noctilio* were highest. This inoculation programme was increased in 2005, with approximately 480 million nematodes used to inoculate about 4400 trees. These nematodes were of the Kamona strain imported from Australia, but reared in South Africa. Both these inoculations gave poor results, with less than 5% parasitism obtained from trees inoculated in 2004 (*n* = 2472 wasps) and less than 10% parasitism obtained from trees inoculated in 2005 (n = 13999 wasps) (authors unpublished). These disappointing results were despite considerable efforts to streamline rearing, transport and inoculation methods for the nematodes used in the 2005 inoculations. Parasitism in naturally infested trees has yet to be determined in these areas.

Factors influencing successful establishment of *D. siricidicola*

Although *D. siricidicola* inoculations have been a success in most areas where they have been applied, it is clear this is not true for all areas. Even within countries, parasitism in inoculated trees has been variable, in the range 0% to almost 100%. Various factors could influence the inoculation success and therefore the efficacy of *D. siricidicola* as a biological control agent. Possible factors include the inoculation technique, moisture content of the wood, loss of virulence in the nematode, incompatibility among the specific populations of *S. noctilio, A. areolatum* and *D. siricidicola* in that area, and pine species.

Innoculation technique. One of the important factors that can influence the efficacy of *D. siricidicola* as a biological control agent is the technique used to inoculate trees with the nematode. Bedding and Iede (2005) described the inoculation technique in detail (Fig. 1D–G). Inappropriate application of this technique, including the use of blunt inoculation hammers, is known to result in a drastic reduction in inoculation success (Bedding and Akhurst, 1974; Bedding and Iede, 2005). After the poor parasitism results obtained in South Africa for the 2004 inoculations, special attention was paid to inoculation techniques. Despite these refinements, parasitism results for the next year remained low. Similarly, in Argentina, the same inoculation technique was applied in Misiones and the Andean Patagonian regions and yet parasitism is high in the Andean Patagonian region and low in Misiones (V. Klasmer, personal communication). Thus, although the inoculation technique can influence the success obtained with the nematode, it can be easily addressed and is not believed to be the primary factor explaining low success in South Africa and parts of South America.

Moisture content. Moisture content of the wood during the period for nematode infection of *S. noctilio* larvae can be a key factor explaining the variation in inoculation success. Bedding and Akhurst (1974) indicated that *D. siricidicola* prefers moisture content of the wood to be 50% and higher for successful establishment. By contrast, Haugen and Underdown (1993) concluded that moisture content was not a major factor causing low levels of parasitism in *P. radiata* logs inoculated in Australia. The moisture content of these logs was in the range 33–72%, with a mean of approximately 45%. However, preliminary studies in KwaZulu-Natal indicate that moisture content is as low as 15% in the top section of trees during inoculation, far lower than recommended by Bedding and Akhurst (1974) or tested by Haugen and Underdown (1993). Inoculations in KwaZulu-Natal are carried out from March to July, and wasps begin to emerge in October. As KwaZulu-Natal is a summer rainfall area, the nematodes are in the wood during the dry season. This is in contrast to the Western Cape, where most inoculations are carried out from June to July, and wasps begin to emerge in November. The Western Cape is a winter rainfall area, thus the nematodes are in the wood during the wet season. Areas of New Zealand and Australia where *S. noctilio* occurs and *D. siricidicola* is successfully applied are also mainly winter or all year rainfall areas. Details of the rainfall and moisture content of trees in Sirex-infested areas of South America are not currently available.

Further studies are underway to consider the influence of moisture content on nematode establishment and survival in the KwaZulu-Natal province of South Africa. In this regard, it will be particularly valuable to have a comparison of parasitism in this area, and the Western Cape province, where moisture content in the trees could differ due to the different pine species planted and the different climates. If the influence of climate on moisture content is a serious barrier to nematode movement and survival in certain areas, the technique to release *D. siricidicola*, and possibly the feasibility of using this agent in these areas at all, will need to be re-examined.

Parasitism with *D. siricidicola* is still relatively low in the Western Cape province of South Africa. This is despite the fact that the area has a climate similar to that of New Zealand and Sirex-infested areas of Australia. The variable parasitism rates in the Western Cape may not be a result of the nematode’s inability to establish in these areas, as observed by the initial inoculations in this area, where high parasitism was obtained (Tribe and Cillie, 2004). Rather, the limited initial inoculations in the Western Cape and the small *S. noctilio* population may be the cause of the current low parasitism.

Loss of virulence. The loss of virulence in *D. siricidicola* can be an important factor influencing the success of this biological control agent. *Deladenus siricidicola* could loose its ability to change to the parasitic form when reared in the laboratory for long periods, as was the case in the Green Triangle (Haugen and Underdown, 1993; Bedding and Iede, 2005). To overcome this potential obstacle, nematodes are stored in liquid nitrogen and only reared for a short period in culture before release in the field. In the Western Cape province of South Africa, nematodes stored in liquid nitrogen cultures in Australia were directly inoculated into trees. In KwaZulu-Natal, nematodes were imported from Australia and then further reared in South Africa before release. Nematodes were reared for 3 months after arrival from Australia, before they were released in the field for the 2004 inoculations in KwaZulu-Natal. In the case of 2005 inoculations, they were reared for approximately 15 months before release, although they were also stored at 5 °C for brief periods during this time. It is possible that nematodes released in 2005 may have had reduced virulence but this could not have been the case for those released in 2004. However, the results from both years' inoculations were low. In Argentina, the nematodes released in Misiones where parasitism is low, and in the Andean Patagonian region where parasitism is high, are both produced in the same facility in Misiones (V. Klasmer, personal communication). Thus, differences in virulence would not be expected. At least in some cases, a loss of virulence is unlikely to be responsible for the low parasitism achieved.

Incompatibility between populations. Incompatibility between specific nematode and wasp strains can be a significant barrier to the use of *D. siricidicola*. Bedding (1972) showed that different populations of *S. noctilio* were differently affected by the same nematode strain. In certain strains of *S. noctilio*, the nematodes are released too late to penetrate the wasp eggs because the egg shells have already formed (Bedding and Iede, 2005). Despite its importance, the presence of different strains of *S. noctilio* within and between southern hemisphere countries has not been examined.

All strains of *D. siricidicola* are not equally compatible with all strains of *A. areolatum*. Certain isolates from the field in Australia were found to be better for rearing the nematode than others (R. A. Bedding, personal communication in Slippers *et al.*, 2001). Similarly, in South Africa, preliminary observations reveal that nematodes imported from

Australia are more easily reared using the fungus imported with the nematodes than using the fungus isolated from the field in KwaZulu-Natal and Western Cape. Incompatibility between the nematode and fungus would influence the feeding and reproduction of the nematode on the fungus. This in turn would affect the survival and spread of the nematode in the tree and its potential to parasitize *S. noctilio* larvae.

A serious shortcoming in our understanding of the biological control of *S. noctilio* is the complete absence of any information regarding population variation and structure of *D. siricidicola* in the southern hemisphere. The majority of *D. siricidicola* releases in the southern hemisphere have been with the Kamona strain. Thus, the genetic and phenotypic diversity of *D. siricidicola* in the southern hemisphere and its ability to adapt to different conditions could be limited. Given specific interactions of this nematode with *S. noctilio*, *A. areolatum* and, possibly, the environment, this area of research requires urgent attention.

Pine species. Pine species differ across the different regions affected by *S. noctilio*, and include *P. radiata*, *P. patula*, *P. taeda*, *Pinus carribea*, *P. pondersae*, *P. elliottii*, *P. contorta* var. *latifolia*, and others. Differences between these species, such as resin composition, tracheid structure, moisture content and other factors, could influence nematode establishment. The influence of these factors is currently unknown.

Silvicultural control in the southern hemisphere

Poor silviculture and environmental events, leading to stress on trees, have been a key factor in most major outbreaks in Australia and New Zealand (Madden, 1988). That stressed trees are more susceptible to attack by *S. noctilio* is well known (e.g. Madden, 1968; Talbot, 1977; Neumann and Minko, 1981). *Sirex noctilio* females test the vigour of trees with their ovipositors, thus determining the osmotic pressure. High osmotic pressure is found in trees with high levels of vigour, and these trees are generally rejected by female wasps, whereas trees with low osmotic pressure are generally more susceptible to attack (Madden, 1968). Stress in trees may result from (i) suppression (e.g. in overstocked stands where competition is high); (ii) physical damage, including damage that occurs during pruning; (iii) attack by insect or disease; and (iv) unfavourable environmental conditions; and other factors.

Silvicultural practices, as described by Haugen *et al.* (1990) and Neumann *et al.* (1987), have been used to control *S. noctilio* in Australia and New Zealand. After the outbreak of *S. noctilio* in New Zealand between 1946 and 1951, improvements in silviculture, together with the introduction of parasites, kept *S. noctilio* populations low (Neumann and Minko, 1981). The importance of silviculture for control in Australia was emphasized by Neumann *et al.* (1987) who stated that outbreaks were largely a management problem that could be prevented by routine surveillance of plantations and the application of silviculture measures. Neumann *et al.* (1987) further stated that biological control measures were not necessary for some well-managed plantations. Likewise, the majority of recent mortality in New South Wales and Tasmania above 3% was associated with unthinned stands, stands with suppressed trees or summer pruning (Carnegie *et al.*, 2005).

Silvicultural practices differ between and within southern hemisphere countries (Table 2). There is no great difference in initial stand density of *Pinus* species within the southern hemisphere. KwaZulu-Natal, South Africa, is the only region where no thinning occurs before harvest. As a result, stand density may be as high as 1250 stands/Ha at time of harvest. By contrast, stand density at time of harvest generally does not exceed 500 stands/Ha in other Sirex-infested regions of the southern hemisphere. Although stand density is also high in other regions before the first thinnings, the trees are generally too small at this stage to be favourable to *S. noctilio* infestation. High stand density is known to increase the stress on trees, which predisposes them to attack by *S. noctilio* (Neumann *et al.*, 1987). *Pinus* plantations in KwaZulu-Natal provide an abundance of stressed trees, and together with a lack of established biological control agents, *S. noctilio* is currently causing substantial damage in this region.

Despite the importance of silvicultural measures, market demands and difficult terrain can result in situations, such as delayed thinning, which favour a build-up of *S. noctilio* populations (Carnegie *et al.*, 2005). In areas where the main market for timber is pulp, and the objective is to obtain as much wood volume as possible at time of harvest, stand density is typically very high. Many Sirex-infested areas of the southern hemisphere represent plantations where sawn-timber is the main product. Thus, individual tree size and timber quality is important and sites are thinned to reduce competition. To change the management styles of a pulp regime (e.g. to include thinning) could seriously affect profitability of plantations and in some cases this may not be economically viable.

Other control methods in the southern hemisphere

Other important management considerations include eradication and quarantine. Eradication is not a feasible option where *S. noctilio* has become established, but destruction of infested logs can be important in maintaining low abundance of *S. noctilio* in newly-infested areas. In the Western Cape province of South Africa, all infested trees that could be found were removed and burned immediately after detection of *S. noctilio*, and older (> 40 years) infested compartments were clear felled (Tribe and Cillié, 2004). These measures probably had a significant impact on lowering the initial populations and slowing the population build-up of *S. noctilio*. In KwaZulu-Natal, harvesting of severely-infested compartments and the processing and burning of this timber began in 2005. Thus, the opportunity to impair the spread and population build-up of *S. noctilio* was probably not achieved.

Quarantine measures that prevent the movement of timber from infested areas to noninfested areas are essential. In Australia, quarantine measures restrict the movement of Sirex-infested pine into the states of Queensland and Western Australia (Carnegie *et al.*, 2006). In South Africa, established populations of *S. noctilio* have only been detected in the Western Cape, Eastern Cape and KwaZulu-Natal provinces. These populations are greater than 200 km from the closest pine plantations in the Mpumalanga province. It would thus take an estimated 5 years for *S. noctilio* to arrive in this uninfested area, assuming a movement of 40 km per year (Eldridge and Taylor, 1989). It is therefore essential to establish strict quarantine on the movement of infested timber so that *S. noctilio* does not move more rapidly into uninfested areas. Likewise, quarantine is also needed in South America to prevent the movement of *S. noctilio* to countries where pines are widely grown and where *S. noctilio* has not yet appeared (e.g. Equador, Colombia and Venezuela). Quarantine should also aim to limit further international movement of *S. noctilio*, which could result in the introduction of different genotypes of *S. noctilio* and/or *A. areolatum*.

Discussion

Subsequent to the first arrival of *S. noctilio* in the southern hemisphere, this alien invasive pest has resulted in severe losses to pine forestry in every country where it has become established. In all of these countries, control programmes have been established to counter increasing *S. noctilio* populations. The success of these control programmes, including both silvicultural control measures and biological control, has been variable. In New Zealand, *S. noctilio* is no longer considered a major threat and an active control programme is not considered necessary. In Australia, infestations are mostly below 1%, although an active control programme remains in place. *Sirex noctilio* is still considered a major threat in South America, where biological control has been very successful in some areas, but less so in others. In South Africa, infestations remain low in the Western Cape, but are above 30% in some areas of KwaZulu-Natal and the Eastern Cape, and they are increasing in these provinces.

The nematode *D. siricidicola* and various parasitic wasp species have been introduced as biological control agents in all southern hemisphere countries where *S. noctilio* has been introduced. Amongst these agents, *D. siricidicola* has been considered the primary biological control tool, and it has been particularly successful in Australia. However, inoculation success with this nematode has been variable in South America and South Africa, ranging from very poor to good. Preliminary evidence from current assessments also suggests that this low introduction success translates into poorer establishment and spread of *D. siricidicola* than is seen in areas with high initial introduction success. The long-term influence of low inoculation success in these environments needs to be determined. It is also crucial that the causal factors resulting in low inoculation success and parasitism are discovered and resolved. These causal factors might be unavoidable (e,g, low moisture content of the wood or incompatibility between strain of nematode and wasp or nematode and fungus). In such cases, the feasibility of using *D. siricidicola* will need to be re-examined and further species or strains of *Deladenus* might need to be evaluated to match specific conditions.

In addition to variation in the establishment of *D. siricidicola*, the establishment of parasitic wasps is also not consistent throughout the southern hemisphere. This is particularly true for South Africa, where only *I. leucospoides* is established in parts of the

Western Cape. Further introductions of *I. leucospoides* and introductions of *M. nortoni* and *R. persuasoria* are needed in these areas. These introductions should entail large numbers of wasps to avoid possible genetic bottlenecks associated with releases of small numbers (Roderick and Navajas (2003).

The common denominator for outbreaks of *S. noctilio* in the southern hemisphere has been an abundant supply of stressed trees. This has primarily been due to environmental stress and/or associated silvicultural practices, particularly heavily stocked stands. In places where such adverse conditions are perpetuated, such as parts of Australia and South America and the Eastern Cape and KwaZulu-Natal province of South Africa, *S. noctilio* remains a substantial threat where high infestations of the wasp can occur, even in the presence of an active biological control programme. The importance of silviculture is evident, notably in South Africa, where differences in the planting regimes in the Western Cape and the north-eastern Cape/KwaZulu-Natal areas is probably important in causing the difference in infestation. Without silvicultural adjustments in these areas, high infestations are likely to continue, even in the presence of an established biological control programme.

A selective reading of the literature pertaining to this pest, could easily promote the view that *S. noctilio* is a serious pest, but one that is easily controlled. Although extensive research has been undertaken to develop a control strategy that is effective in many areas, it is important to recognize that this strategy might require significant local adaptation. This is especially regarding the application of biological control agents. The interactions between *S. noctilio*, its fungal symbiont *A. areolatum*, biological control agents and the environment are still poorly understood. This hinders local adaptations to control programmes in areas where these are seriously needed. Great opportunities exist to study the interactions among these organisms using modern ecological and molecular tools. Such studies are likely to significantly advance our knowledge of the very complex interactions that typify *S. noctilio* infestations in introduced environments.

References

Ahumada, R. (2002) Diseases in commercial *Eucalyptus* plantations in Chile, with special reference to *Mycosphaerella* and *Botryosphaeria* species. MSc Thesis, Faculty of Natural and Agricultural Science, University of Pretoria.

Anonymous (2005) *Abstract of South African forestry facts for the year 2003/2004*. Forestry South Africa, South Africa.

Baker, D.A., Loxdale, H.D. & Edwards, O.R. (2003) Genetic variation and founder effects in the parasitoid wasp, *Diaeretiella rapae* (M'intosh) (Hymenoptera: Braconidae: Aphidiidae), affecting its potential as a biological control agent. *Molecular Ecology*, **12**, 3303–3311.

Becerra, C., Bennesch, M., Faraldo, G., de Coll, O., Eskiviski, E. & Figueredo, I. (2000) Establishment and efficiency of the nematode *Deladenus siricidicola* B. to control *Sirex noctilio* F. in *Pinus taeda* plantations of Misiones and NE of Corrientes. *Proyecto Forestal de Dessarrollo. Final report PIA 12A/96*. INTA, Argentina.

Bedding, R.A. (1972) Biology of *Deladenus siricidicola* (Neotylenchidae) an entomophagous-mycetophagous nematode parasitic in siricid woodwasps. *Nematologica*, **18**, 482–493.

Bedding, R.A. & Akhurst, R.J. (1974) Use of the nematode *Deladenus siricidicola* in the biological control of *Sirex noctilio* in Australia. *Journal of the Australian Entomological Society*, **13**, 129–135.

Bedding, R.A. & Akhurst, R.J. (1978) Geographical distribution and host preferences of *Deladenus* species (Nematoda: Neotylenchidae) parasitic in siricid woodwasps and associated hymenopterous parasitoids. *Nematologica*, **24**, 286–294.

Bedding, R.A. & Iede, E.T. (2005) Application of *Beddingia siricidicola* for Sirex woodwasp control. *Nematodes as Biocontrol Agents* (ed. by P. S. Grewal, R. Ehlers and D. I. Shapiro-Ilan), pp. 385–400. CAB International, U.K.

Carnegie, A.J., Elderidge, R.H. & Waterson, D.G. (2005) History and management of Sirex wood wasp in pine plantations in New South Wales, Australia. *New Zealand Journal of Forestry Science*, **35**, 3–24.

Carnegie, A.J., Matsuki, M., Haugen, D.A. *et al*. (2006) Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. *Annals of Forest Science*, **63**, 119–128.

Eldridge, R.H. & Taylor, E.E. (1989) *Sirex Woodwasp – A Pest of Pine in N.S.W*. Forest Protection Series no. 1. Forestry Commision of New South Wales, Australia.

Eskiviski, E., de Coll, O., Faraldo, G.S. & Bennesch, M.A. (2003) Efficiency of new isolations of Deladenus siricidicola *B. in the biological control of* Sirex noctilio. *Jornadas Tecnicas Forestales y Ambientales – FCF, UnaM – EEA Monetecarlo*, INTA, Argentina.

Eskiviski, E., Nuñez Cresto, M., Olmedo, D., de Coll, O. & R. (2004) *Biological aspects of* Sirex noctilio *F. &* Ibalia leucospoides *H. parasitism in forest plantations of* Pinus sp. in Santo Tome, Corrientes. *Jornadas Tecnicas Forestales y Ambientales – FCF, UnaM – EEA Monetecarlo*, INTA, Argentina.

Fenili, R., Mendes, C.J., Miquelluti, D.J. *et al*. (2000) *Deladenus siricidicola*, Bedding (Neotylenchidae) parasitism evaluation in adult *Sirex noctilio*, Fabricius, 1793 (Hymenoptera: Siricidae). *Revista Brasileira de Biologia*, **60**, 683–687.

Gilbert, J.M. & Miller, L.W. (1952) An outbreak of *Sirex noctilio*. *Tasmania. Australian Journal of Biological Sciences*, **22**, 905–914.

Gilmour, J.W. (1965) The life cycle of the fungal symbiont of *Sirex noctilio*. *New Zealand Journal of Forestry*, **10**, 80–89.

Hanson, H.S. (1939) Ecological notes on the Sirex wood wasps and their parasites. *Bulletin of Entomological Research*, **30**, 27–65.

Haugen, D.A. (1990) Control procedures for *Sirex noctilio* in the Green Triangle: review from detection to severe outbreak (1977–87). *Australian Forestry*, **53**, 24–32.

Haugen, D.A., Bedding, R.A., Underdown, M.G. & Neumann, F.G. (1990) National strategy for control of *Sirex noctilio* in Australia. *Australian Forest Grower*, No. 13, 8 pp (special liftout section)

Haugen, D.A. & Underdown, M.G. (1990a) Release of parasitoids for *Sirex noctilio* control by transporting infested logs. *Australian Forestry*, **53**, 266–270.

Haugen, D.A. & Underdown, M.G. (1990b) *Sirex noctilio* control programme in response to the 1987 Green Triangle outbreak. *Australian Forestry*, **53**, 33–40.

Haugen, D.A. & Underdown, M.G. (1993) Reduced parasitism of *Sirex noctilio* in radiata pines inoculated with the nematode *Beddingia siricidicola* during 1974–89. *Australian Forestry*, **56**, 45–48.

Hoebeke, E.R., Haugen, D.A. & Haack, R.A. (2005) *Sirex noctilio*: discovery of a Palearctic siricid woodwasp in New York. *Newsletter of the Michigan Entomological Society*, **50**, 24–25.

Hufbauer, R.A., Bogdanowicz, S.M. & Harrison, R.G. (2004) The population genetics of a biological control introduction: mitochondrial DNA and microsatellie variation in native and introduced populations of *Aphidus ervi*, a parasitoid wasp. *Molecular Ecology*, **13**, 337–348.

Iede, E.T., Penteado, S.R.C., Filho, W.R. & Schaitza, E.G. (2000) Updated situation of *Sirex noctilio* integrated management program in Brazil. *Serie Tecnica IPEF*, **13**, 11–20.

Iede, E.T., Penteado, S.R.C. & Schaitza, E.G. (1998) *Sirex noctilio* problem in Brazil – detection, evaluation and control. Proceedings of a Conference: Training in the Control of Sirex noctilio *by Use of Natural Enemies* (ed. by E. Iede, E. Shaitza, S. Penteado, R. Reardon and T. Murphy), pp. 45–52. FHTET 98-13. USDA Forest Service, Morgantown, MV.

Klasmer, P., Fritz, G., Corley, J. & Botto, E. (1998) Current status of research on *Sirex noctilio* F. in the Andean-Patagonian region in Argentina. *Proceedings of a Conference: Training in the Control of Sirex noctilio by Use of Natural Enemies* (ed. by E. Iede, E. Shaitza, S. Penteado, R. Reardon and T. Murphy), pp. 89–90. FHTET 98-13. USDA Forest Service, Morgantown, MV.

Lloyd, C.J., Hufbauer, R.A., Jackson, A., Nissen, S.J. & Norton, A.P. (2005) Pre- and post-introduction patterns in neutral genetic diversity in the leafy spurge gall midge, *Spurgia capitigena* (Bremi) (Diptera: Cecidomyiidae). *Biological Control*, **33**, 153–164.

Madden, J.L. (1968) Physiological aspects of host tree favourability for the woodwasp, *Sirex noctilio* F. *Proceedings of the Ecological Society of Australia,* **3**, 147–149.

Madden, J.L. (1988) *Sirex in Australasia Dynamics of Forest Insect Populations Patterns, Causes, Implications* (ed. by A. A. Berryman), pp. 407–429. Plenum Press, New York, New York.

Maderni, J.F.P. (1998) *Sirex noctilio* F. present status in Uruguay. *Proceedings of a Conference: Training in the Control of Sirex noctilio by Use of Natural Enemies* (ed. by E. Iede, E. Shaitza, S. Penteado, R. Reardon and T. Murphy), pp. 81–82. FHTET 98-13. USDA Forest Service, Morgantown, MV.

Miller, D. & Clarke, A.F. (1935) *Sirex noctilio* (Hym.) and its parasites in New Zealand. *Bulletin of Entomological Research*, **26**, 149–154.

Neumann, F.G. & Minko, G. (1981) The sirex woodwasp in Australian radiata pine plantations. *Australian Forestry*, **44**, 46–63.

Neumann, F.G., Morey, J.L. & McKimm, R.J. (1987) The Sirex Woodwasp in Victoria. Bulletin no. 29. Department of Conservation, Forest and Lands, Australia.

Nuttall, M.J. (1989) *Sirex noctilio* F., sirex wood wasp (Hymenoptera: Siricidae). Review of Biological Control of Invertebrate Pests and Weeds in New Zealand From 1874 to 1986 (ed. by P. J. Cameron, R. L. Hill, J. Bain and W. P. Thomas), pp. 299–306. *Technical Communication No. 10. CAB International Institute of Biological Control, U.K.*

Rawlings, G.B. (1955) Epidemics in *Pinus radiata* forests in New Zealand. *New Zealand Journal of Forestry*, **7**, 53–58.

Roderick, G.K. & Navajas, M. (2003) Genes in new environments: genetics and evolution in biological control. *Nature Reviews Genetics*, **4**, 889–899.

Slippers, B., Coutinho, T.A., Wingfield, B.D. & Wingfield, M.J. (2003) The genus *Amylostereum* and its association with woodwasps: a contempary review. *South African Journal of Science*, **99**, 70–74.

Slippers, B., Wingfield, M.J., Coutinho, T.A. & Wingfield, B.D. (2001) Population structure and possible origin of *Amylostereum areolatum* in South Africa. *Plant Pathology*, **50**, 206–210.

Slippers, B., Wingfield, B.D., Coutinho, T.A. & Wingfield, M.J. (2002) DNA sequence and RFLP data reflect geographical spread and relationships of *Amylostereum areolatum and* its insect vectors. *Molecular Ecology*, **11**, 1845–1854.

Spradbery, J.P. & Kirk, A.A. (1978) Aspects of the ecology of siricid woodwasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research*, **68**, 341–359.

Talbot, P.H.B. (1977) The *Sirex–Amylostereum–Pinus* association. *Annual Review of Phytopathology*, **15**, 41–54.

Taylor, J.S. (1962) *Sirex noctilio* F., a recent introduction in South Africa. *Entomologist's Record*, **74**, 273–274.

Taylor, K.L. (1967) *The Introduction, Culture, Liberation, and Recovery of Parasites of Sirex noctilio in Tasmania, 1962–67*, pp. 1–19. Technical Paper 8. CSIRO Division of Entomology, Australia.

Taylor, K.L. (1978) Evaluation of the insect parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. *Oecologia*, **32**, 1–10.

Tribe, G.D. (1995) The woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), a pest of *Pinus* species, now established in South Africa. *African Entomology*, **3**, 215–217.

Tribe, G.D. & Cillié, J.J. (2004) The spread of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents. *African Entomology*, **12**, 9–17.

Villacide, J.M. & Corley, J.C. (2003) The potential distribution of the parasitoid *Ibalia leucospoides* (Hymenoptera: Ibaliidae) in Argentina. *Revista de Ciences Forestals – Quebracho*, **10**, 7–13.

Zondag, R. (1969) A nematode infection of *Sirex noctilio* (F.) in New Zealand. *New Zealand Journal of Science*, **12**, 732–747.

Zondag, R. (1971) Control of *Sirex noctilio* (F.) with *Deladenus siricidicola* Bedding. Part I – 1967 Field trial. *New Zealand Journal of Forestry Science*, **1**, 5–14.

Zondag, R. (1979) Control of *Sirex noctilio* (F.) with *Deladenus siricidicola* Bedding. Part II. Introductions and establishments in the South Island 1968–75. *New Zealand Journal of Forestry Science*, **9**, 68–76.

Figures and Tables

Figure 1 *Sirex noctilio*, its damage and the biological control programme used in the southern hemisphere. (A) Female *S. noctilio* wasp ovipositing in a *Pinus* tree. (B) A typical siricid larva and larval tunnels with tightly packed frass. (C) Mortality in a *Pinus patula* compartment in KwaZulu-Natal, South Africa, after heavy attack by *S. noctilio*. (D) The mycetophagous stage of the parasitic nematode *Deladenus siricidicola*, used as a biological control agent for *S. noctilio*. (E) Mass rearing of *D. siricidicola* for release in the field. (F) The nematodes suspended in a gel mixture, inoculated into *Sirex*-infested trees. (G) The parasitic stage of *D. siricidicola* inside the eggs of *S. noctilio*.

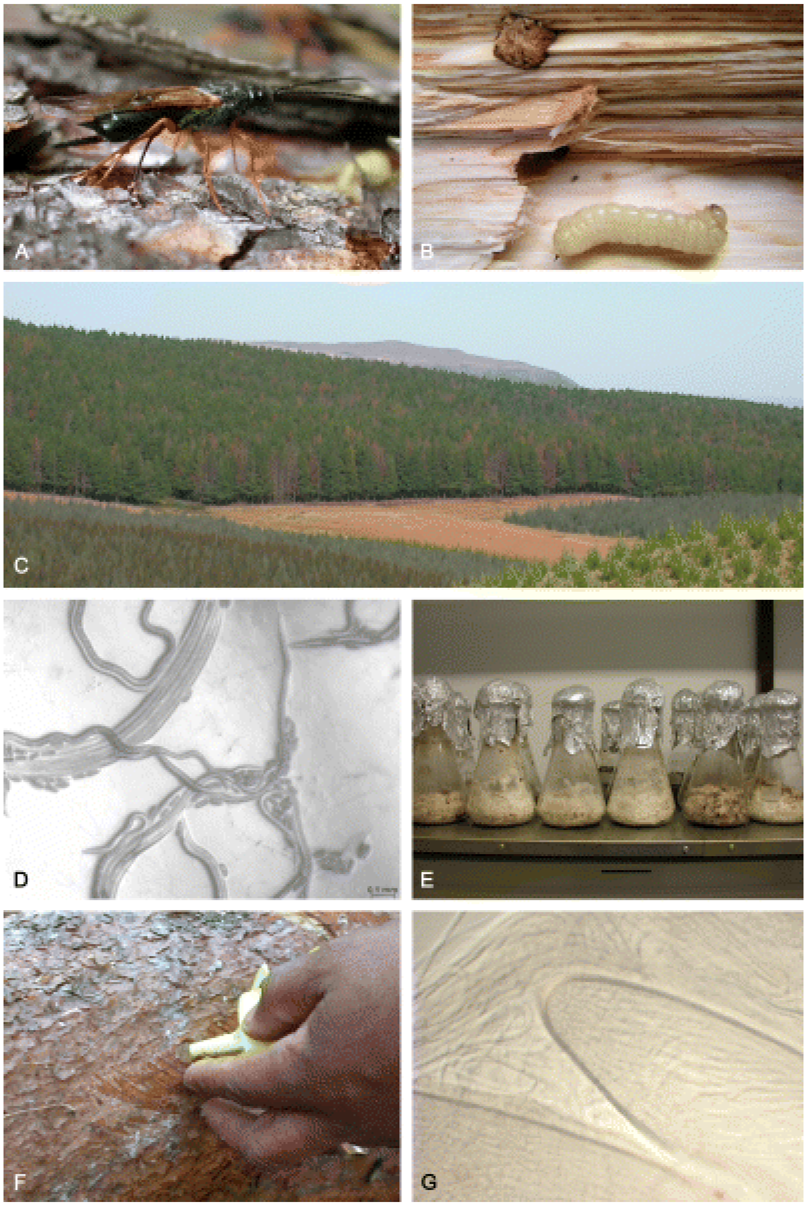

Figure 2 Detection of *Sirex noctilio* in the southern hemisphere. Countries are indicated as: Ar, Argentina; Au, Australia; Br, Brazil; Ch, Chile; NZ, New Zealand; SA, South Africa; Ur, Uruguay. The number after the letters indicates the date that *S. noctilio* was first detected in those countries. (Map source: http://www.eduplace.com/ss/maps/pdf/s_hemis.pdf; Copyright © Houghton Mifflin Company. Reprinted by permission of Houghton Mifflin Company. All rights reserved. Any further duplication is strictly prohibited unless written permission is obtained from Houghton Mifflin Company.)

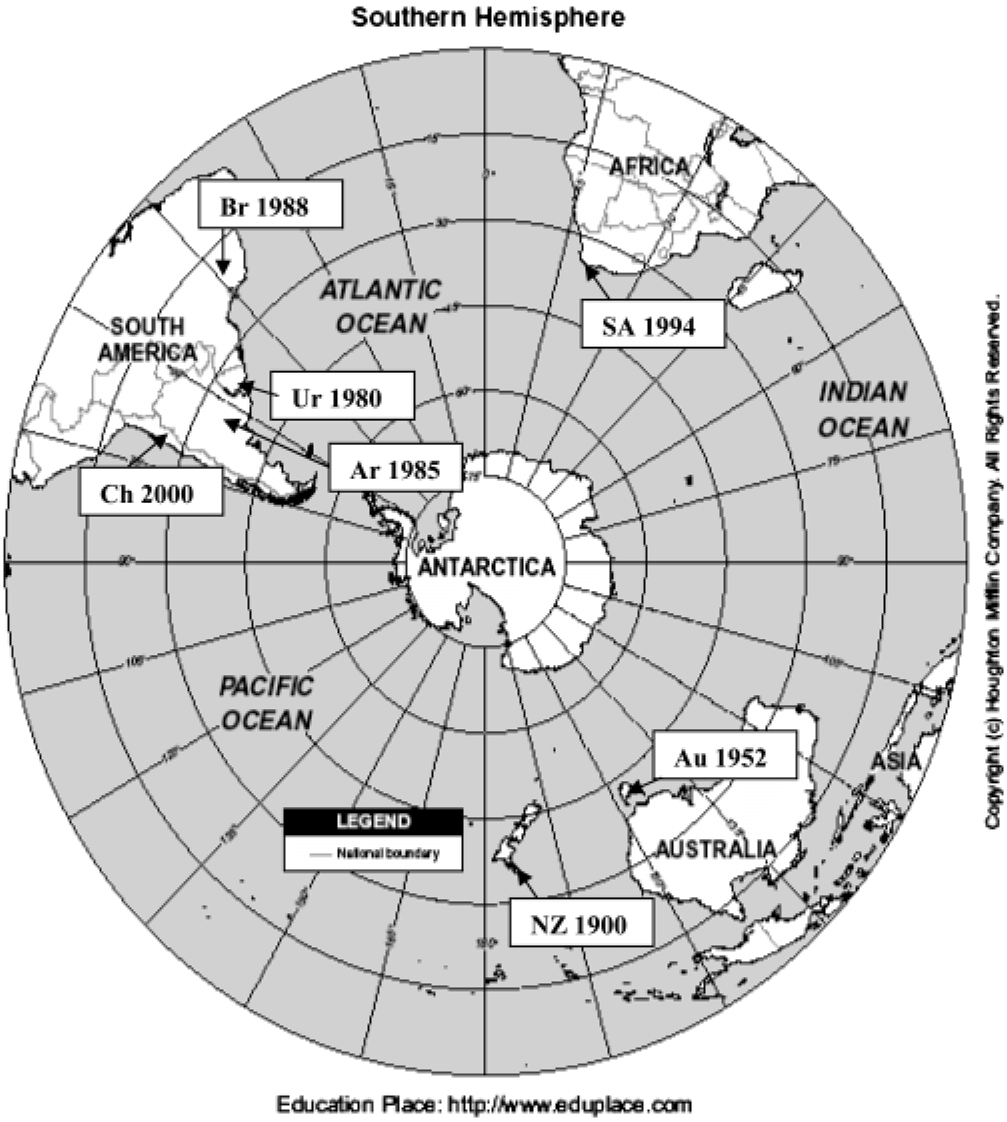

Table 1 Parasitoid wasps of *Sirex noctilio* released in the southern hemisphere[a]

	Rhyssa persuasoria persuasoria				***Rhyssa persausoria himalayensis***				***Rhyssa hoferi***				***Rhyssa lineolata***			
	Years liberated	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**
New Zealand	1929–1950	52[b]	3500	1936	1964–1970	89	198	Not recovered	–	–	–	–	–	–	–	–
Australia – Tasmania[c]	1957–1965	0	56	1959	1964	111	128	Not recovered	–	–	–	–	1962–1965	452	53	1963
Australia – Victoria	1970–1985	2852	3685	1988	–	–	–	–	1980–1982	Not known	32	1988	–	–	–	1988
Australia – New South Wales	1980–1983	256[d]		Not recovered	–	–	–	–	1982–1984	78[d]		1988/1989	–	–	–	–
South Africa – Western Cape	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
South Africa – KwaZulu-Natal	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

	Ibalia leucospoides leucospoides				*Ibalia leucospoides ensiger*				*Schletterius cinctipes*				*Megarhyssa nortoni nortoni*			
	Years liberated	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**
New Zealand	1954–1978	8537	8096	1957	1966–1971	1883	1729	1968	–	–	–	–	1964–1984	1258	1863	1968
Australia – Tasmania[c]	1959–1966	2015	2005	1960	1965–1966	297	236	1966	Not known			1973	1965–1966	138	301	1966
Australia – Victoria	1967?–1985[e]	89 033+	79 084+	1969?	[e]	[e]	[e]	[e]	1970–1985	317	1095	1988	1970–85[f]	10 903	12 494	1972
Australia – New South Wales	1980–1989	19 331[d]		1991/1992	–	–	–	–	1981–1983	297[d]		Early 1980s	1980–1989	4087[d]		1991/1992
South Africa – Western Cape	1998–2001	456[d]		2002	–	–	–	–	–	–	–	–	1999	41	38	Not recovered
South Africa – KwaZulu-Natal and Eastern Cape	2006	176[d]		Not yet attempted	–	–	–	–	–	–	–	–	–	–	–	–

	Ibalia leucospoides leucospoides				***Ibalia leucospoides ensiger***				***Schletterius cinctipes***				***Megarhyssa nortoni nortoni***			
	Years liberated	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**	**Years liberated**	**Male**	**Female**	**First recovered from field**

[a] Data from Taylor (1967), Taylor (1978), Neumann and Minko (1981), Neumann *et al.* (1987), Nuttall (1989), Haugen and Underdown (1990a), Tribe and Cillie (2004), Carnegie *et al.* (2005), and B.P. Hurley, unpublished data.

[b] Male numbers for 1929–32 only.

[c] Male and female numbers for 1962–67 only.

[d] Total male and female wasps.

[e] Releases contained both *I. l. leucospoides* and *I. l. ensiger*.

[f] Releases contained both *M. n. nortoni* and *M. n. quebecensis*.

Table 2 Comparison of silvicultural practices used in *Pinus* plantations in the southern hemisphere[a,b]

	Initial stand density (spha)	Thinning	Final stand density (spha)	Pruning	Harvest age (years)	Main market for timber
KwaZulu-Natal (South Africa)	1111–1667	None	Approx. 800–1250	For access only	15–20	Pulp
Western Cape (South Africa)	1111	8 years, to 650 spha (optional); 13 years, to 400 spha; 18 years, to 250 spha	250	3–4 prunes, last prune to 7.0 m	27–35	Sawn timber
Chile	1100–1330	9 years, to 800 spha; 11/12 years, to 400–500 spha	400–500	2–3 prunes, last prune to 5.2 m	18–22	Pulp and sawn timber
Brazil	1600	8 years, to1040 spha; 12 years, to 580 spha; 16 years, to 350 spha	350	3 prunes, last prune to 7.0 m	20	Pulp and sawn timber
Uruguay	1250	4 years, to 800 spha; 9 years to 450 spha	450	3 prunes, last prune to 5.5 m	20	Sawn timber
Argentina	1400–1450	7 years, to 700–800 spha; 10–12 years, to 450 spha	450	Varies, but often none	22	Pulp and sawn timber
Australia (New South Wales)	1100	15 years, to 450 spha; 23 years, to 200–250 spha	200–250	Rare, but sometimes 3 prunes at age 7, 8 and 9	32–35	Sawn timber

[a] Silvicultural practices differ between land owners within the same country. Although these figures therefore do not represent all the silvicultural practices in each country, they do indicate general trends.

[b] Information obtained from R. Ahumada and V. Klasmer for South America, A. Carnegie for Australia, and P. Croft, G. Boreham and D. Carstens for South Africa (personal communication).spha, Stands/Ha.