

This article was downloaded by: [University of Pretoria]

On: 12 August 2012, At: 03:37

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



International Journal of Pest Management

Publication details, including instructions for authors and subscription information:
<http://www.tandfonline.com/loi/ttprm20>

Biological control of forest plantation pests in an interconnected world requires greater international focus

Jeffrey R. Garnas^{a b}, Brett P. Hurley^{a b}, Bernard Slippers^{b c} & Michael J. Wingfield^{a b}

^a Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa

^b Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, 0002, South Africa

^c Department of Genetics, University of Pretoria, Pretoria, 0002, South Africa

Version of record first published: 09 Aug 2012

To cite this article: Jeffrey R. Garnas, Brett P. Hurley, Bernard Slippers & Michael J. Wingfield (2012): Biological control of forest plantation pests in an interconnected world requires greater international focus, *International Journal of Pest Management*, 58:3, 211-223

To link to this article: <http://dx.doi.org/10.1080/09670874.2012.698764>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Biological control of forest plantation pests in an interconnected world requires greater international focus

Jeffrey R. Garnas^{a,b*}, Brett P. Hurley^{a,b}, Bernard Slippers^{b,c} and Michael J. Wingfield^{a,b}

^aDepartment of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa; ^bForestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria 0002, South Africa; ^cDepartment of Genetics, University of Pretoria, Pretoria 0002, South Africa

(Received 23 January 2012; final version received 28 May 2012)

The worldwide homogenization of genetic resources used in plantation forestry (primarily *Pinus*, *Eucalyptus*, *Populus* and *Acacia* spp.) together with accelerating rates of human-aided dispersal of exotic pests, is resulting in plantation pests becoming broadly distributed extremely quickly, sometimes reaching a global distribution within a decade. This unprecedented rate of establishment and spread means that the risk associated with new and emerging pests is shared globally. Biological control represents a major component of the strategy to mitigate such risk, but the current efforts and scope for developing such controls are woefully inadequate for dealing with the increasing rates of pest spread. Given the global nature of the problem, biological control would benefit enormously from an international, collaborative focus. Though inherent difficulties and potential pitfalls exist, opportunities for cost-sharing, growth and maintenance of resources and capacity, and more comprehensive research programmes are critical to the long-term success of biological control. Governments and industries will need to increase their strategic investment in structures specifically designed to promote such focus if they are to successfully protect their forest resources.

Keywords: *Acacia*; biotic homogenization; *Eucalyptus*; global transfer; invasive species; *Pinus*; *Populus*

1. Introduction

The rapidly increasing rates of introduction and establishment of non-native insects worldwide has become a part of the central canon of invasion biology and forest health protection (Liebhold et al. 1995; McCullough et al. 2006; Wingfield et al. 2008b). As a result of greatly increasing rates of global movement and trade, the number of truly isolated places in the world is dwindling. Serious pests that became established outside of their native range are increasingly likely to become established on suitable hosts elsewhere in the world. In a plantation forestry context, the impact of this breakdown of historically important dispersal barriers is greatly compounded by growing genetic uniformity at a global scale arising from widespread dominance of a small number of fast-growing species – largely pines, eucalypts, acacias and poplars (Lockwood and McKinney 2001; Sands 2005; FAO 2009, 2010). Not surprisingly, major threats to forest and plantation health are increasingly shared among countries and continents that only a few decades ago were considerably more isolated (Lockwood and McKinney 2001; FAO 2009). This new and changing landscape, where risk is global but increasingly homogeneous, presents novel challenges and opportunities that demand new models of forest health

protection that transcend regional, national and international boundaries.

Widespread recognition exists among scientists and forest managers that the risks posed by forest pests are shared among neighbours, and further, that organized control and management efforts, even among land-owners with competing interests, carry mutual benefits. This fundamental need for cooperation has not changed with globalization. What *has* changed is that the neighbourhoods in question have grown much larger, now spanning countries and even continents. Perhaps the most dramatic example of an emerging global threat to plantation health is *Leptocybe invasa*, a highly damaging eulophid gall wasp which was unknown to science prior its first report in Israel in 2000 (Mendel et al. 2004; see Figure 2a). Within approximately a decade, *L. invasa* has expanded its range from native source populations in Australia to a minimum of 25 countries on all continents except Antarctica, threatening the continued cultivation of numerous *Eucalyptus* species and hybrids worldwide (Mendel et al. 2004; Table 1). Clearly, the expansion in scope of forest health problems has far outpaced the development of appropriate networks for dealing with chronic and emerging threats at an appropriate spatial scale (Waage et al. 1988). In this paper we argue that a

*Corresponding author. Email: jeff.garnas@fabi.up.ac.za

Table 1. Top-ranking insect pests of *Eucalyptus* and pine plantations worldwide where biocontrol agents have been successfully introduced.

Pest name (host) ¹	Insect pest			Biological control agent		
	Established range: continents ²	Year (country) 1st detected	Year global ³	Established biocontrol agents	Established range: continents ⁴	Year 1st introduced (country)
<i>Cinara cronartii</i> /black pine aphid (P)	A	1974 (S. Africa)	–	<i>Pauesia</i> sp.	A	1983 (S. Africa)
<i>Ctenarytaina eucalypti</i> /eucalyptus psyllid (E)	A, As, Au, E, NA, SA	1889 (N. Zealand)	1991	<i>Psyllaephagus pilosus</i>	E, NA, SA	1993 (USA)
<i>Glycaspis brimblecombei</i> /red gum lerp psyllid (E)	A, E, NA, SA	1998 (USA)	–	<i>Psyllaephagus bliteus</i>	SA ⁵ , NA, E ⁵	2000 (USA)
<i>Gonipterus scutellatus</i> /eucalyptus snout beetle (E)	A, As, Au, E, NA, SA	1890 (N. Zealand)	1994	<i>Anaphes nitens</i>	A, E, NA, SA	1916 (S. Africa)
<i>Leptocybe invasa</i> /eucalyptus gall wasp, or blue gum chalcid (E)	A, As, E, NA, SA	2000 (Israel)	2008	<i>Quadrastichus mendelli</i> ; <i>Selitrichodes</i> spp.; <i>Megastigmus</i> spp.	As	2007 (Israel)
<i>Ophelimus maskelli</i> /eucalyptus gall wasp (E)	A, As, E	2000 (Italy)	–	<i>Closterocerus chamaeleon</i>	As, E	2005 (Israel)
<i>Orthotomicus erosus</i> /pine engraver (P)	A, Au, NA, SA	1968 (S. Africa)	2004	<i>Dendrosoter caenopachoides</i>	A	1984 (S. Africa)
<i>Paropsis charybdis</i> /paropsis tortoise beetle (E)	Au	1900s (N. Zealand)	–	<i>Enoggera nassaui</i>	Au	1987 (N. Zealand)
<i>Phorocantha recurva</i> /eucalyptus long-horn beetle (E)	A, E, NA, SA	1906 (S. Africa)	–	<i>Megalyra fasciipennis</i> ; <i>Avetianella longoi</i>	A, NA	1910 (S. Africa)
<i>Phorocantha semipunctata</i> /eucalyptus long-horn beetle (E)	A, Au, E, NA, SA	1870s (N. Zealand)	–	<i>Syngaster lepidus</i> ; <i>Megalyra fasciipennis</i> ; <i>Avetianella longoi</i> ; <i>Syngaster lepidus</i>	A, NA	1910 (S. Africa)

(continued)

Table 1. (Continued).

Pest name (host) ¹	Insect pest		Biological control agent		
	Established range: continents ²	Year (country) 1st detected	Established biocontrol agents	Established range: continents ⁴	Year 1st introduced (country)
<i>Rhyacionia buoliana</i> /pine shoot moth (P)	NA,SA	1914 (USA)	<i>Ogrilus obscurator</i> ; <i>Temelucha interruptor</i> ; <i>T. turionum</i> ; <i>Pimpla turionellae</i> ; <i>Trichogramma nerudai</i>	NA, SA	1928 (USA)
<i>Sirex noctilio</i> /European woodwasp (P)	A, Au, NA, SA	~1900 (N. Zealand)	<i>Deladenus siricidicola</i> ; <i>Ibalia leucospoides</i> ; <i>Megarhyssa</i> spp.; <i>Rhyssa</i> spp.; <i>Schlettererius cinctipes</i>	A, Au, NA, SA	1928 (N. Zealand)
<i>Thaumastocoris peregrinus</i> /bronze bug (E)	A, SA, E	2003 (S. Africa)	<i>Cleruchooides noackae</i>	SA	2010 (Chile)
<i>Trachymela tincticollis</i> /eucalyptus tortoise beetle (E)	A	1982 (S. Africa)	<i>Enoggera reticulata</i>	A	1986 (S. Africa)
<i>Uraba lugens</i> /eucalyptus leaf skeletonizer (E)	Au	1992 (N. Zealand)	<i>Cotesia urabae</i>	Au	2010 (N. Zealand)

¹E: Eucalyptus, P: pine²A: Africa (excluding N. Africa), As: Asia, Au: Australia, NA: N. America, SA: S. America, E: Europe (including N. Africa); continent of origin is included only if the pest is known to have been introduced to countries outside of its historical range limits.³Insect pest is considered global when it reaches all other continents (not necessarily all countries) where its host tree is planted as an exotic.⁴Corresponds to the most widely distributed biocontrol agent.⁵Introduced accidentally.

truly coordinated, international focus on monitoring, management and control of exotic insect pests of plantation forestry is sorely needed but that the required focus and support from governments and international bodies lag seriously behind the problem. We further argue that given the suite of management options available, biological control of plantation forestry insect pests is among the most promising strategies going forward, and that the benefits of adopting a global perspective towards promoting plantation health are particularly tangible in the context of biocontrol (see Table 2).

2. Drivers of global homogenization of plantation pests

Several prominent factors act and interact to influence the homogenization of pests across countries and continents (Figure 1). Together with unprecedented growth in direct and indirect linkages between distant or isolated regions (box c), the global homogenization of hosts (box e) arising from rapidly expanding planting of a small number of exotic genera is arguably the most important factor driving global pest sharing. As the global pool of exotic pests capable of colonizing common plantation species grows, so does the likelihood of subsequent transfer among suitable areas via

secondary transfer from invaded to uninvaded ranges (boxes a and d) in a positive feedback referred to as a “beachhead effect” by Wingfield et al. (2011). The beachhead effect is necessarily a transient feedback, as once a pest becomes globally distributed, the risk of subsequent transfer goes to zero (though translocation of particular strains or ecotypes may still occur, with potentially important consequences – see “Secondary pest transfer” below). The rate of such feedbacks may also be influenced by human behaviour to the degree to which exotic pests, once identified, become easier to stop via quarantine and inspection (“Q/I”). Natural dispersal across borders is also a serious threat as has been seen with *L. invasa*. This threat is especially pronounced in areas where plantation resources are more or less contiguous or where neighbours vary greatly in their capacity or willingness to manage pest density and spread.

Two mitigating factors that could potentially slow the process of pest homogenization include the contribution of indigenous fauna to the plantation forest community (box b), and environmental conditions that may limit the potential distributions of emerging global pests (box h). Colonization of exotic plantations by native insects does occur with some frequency, though the long-term effects of such events

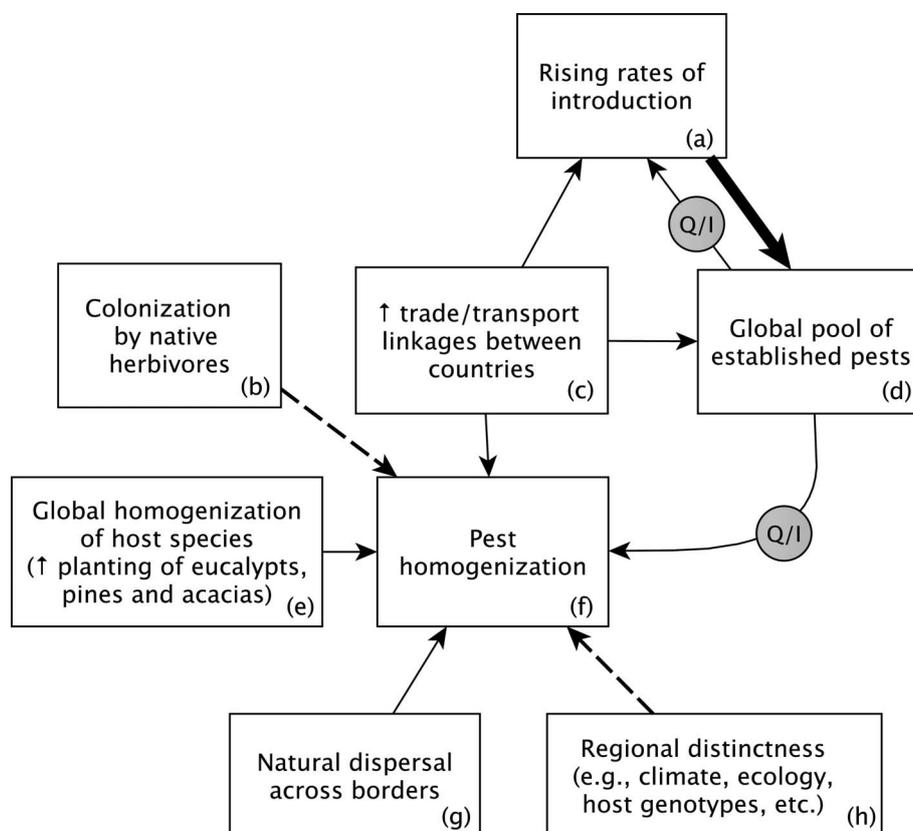


Figure 1. Dominant factors influencing pest homogenization in plantation forestry at a global scale. Q/I refers to quarantine and inspection, which in both cases mitigate the otherwise positive interactions or feedbacks between linked factors (see text for details). Solid and dashed arrows denote positive and negative effects, respectively.

Table 2. Factors influencing the utility of promoting greater focus on international collaboration on biological control projects.

Factor	Opportunities	Challenges
Cost	Upfront and ongoing costs could be shared/estimated across countries (see “Costs of biocontrol” section)	Fair funding models elusive, especially in the context of developed and developing economies with variable invasion risks; legislative and bureaucratic barriers
Capacity	Sharing knowledge and expertise across regions could help alleviate short-term demand and develop future capacity to accommodate future needs	Risk of canalized thinking/approach; suppression of private-sector initiatives
Field testing	Coordinated field testing in areas approved for release far easier and superior to in quarantine	Results may be region-specific, and must be replicated locally
Source material	Reciprocal availability of source material for inoculation/ augmentation with biocontrol agent individuals or genotypes	Over-reliance on one or a few species or genotypes for control of specific pests worldwide
Local adaptation	Divergent control biotypes from one region could be sourced as “pre-adapted” to novel areas (or areas with suboptimal control) matched by climate or ecology	Biocontrol effectiveness may be region-specific
Research opportunities	Opportunities to conduct large-scale, replicated experiments on the ecology/ evolution of introduced biocontrol agents	–

is typically minimal compared with the impacts of exotic invaders. In South Africa, native insects such as the pine emperor moth (*Imbrasia cytherea*), pine brown-tailed moth (*Euproctis terminalis*), and the wood-boring cossid moth (*Coryphodema tristis*), newly associated with *Eucalyptus nitens* (Gebeyehu et al. 2005), constitute localized and/or sporadic pests that can reach economically important levels, and are a target of management and control. Interestingly, all major pests of Australian acacias are native in South Africa (e.g. the wattle mirid [*Lygidolon laevigatum*], and wattle bagworm [*Kotochalia junodi*], perhaps as a consequence of phylogenetic proximity of this group to a diverse native *Acacia* flora present in the country; Wingfield et al. 2011). There are few examples to date of novel associations between native insects and exotic plantation trees, where the insect has later been exported as a global invasive pest. One notable exception is the Asian long-horned beetle (*Anoplophora glabripennis*) which became superabundant on exotic poplar in China prior to being introduced into Europe and North America (Hu et al. 2009). The degree to which native insects form part of local or regional pest assemblages will influence the uniqueness of each community from a global perspective. Distinctness in biotic and abiotic conditions among regions (box h) is likely to limit the geographic distributions of exotic insect pests to a subset of the area where host trees are planted. CLIMEX models for the invasive pine pest *Sirex noctilio* do not predict equal risk for all areas where pine is present as a native or an exotic plantation species (Carnegie et al. 2006). Also, different combinations of plantation tree species and genotypes are planted in different regions. This, along with the

interaction between species/genotype and environment should maintain some degree of regional uniqueness in plantation pest assemblages.

3. Current approaches to managing insect pests: the case for biological control

Strategies for minimizing losses due to invasive insect pests are varied and complex, and can be roughly divided into pre- and post-establishment approaches. Pre-establishment strategies are primarily focused on preventing the introduction and/or establishment of known or potential threats, primarily through modified product treatment or handling, inspection and quarantine. Post-establishment strategies fall under the umbrella of pest management, dominated by the management of tree genetics, adaptive cultural or silvicultural practices or through chemical and biological control. We briefly describe the merits and drawbacks of each.

3.1. Pre-establishment strategies

The majority of internationally traded goods spend days or even weeks in transit and at ports of entry. This offers a window of opportunity to inspect goods for invasive species and to eradicate unwanted organisms by targeted or blanket treatment (e.g. using chemical fumigation, heat treatment, irradiation, bark or soil removal, extended storage, etc.). The major problem facing inspection as an effective tool is the sheer volume of material shipped globally. Rates of inspection are uniformly low, estimated at <2% of shipments entering the United States (Haack 2006) and are

much lower elsewhere in the world (but see Brockerhoff et al. 2006 for an example specific to wood packing material). In short, efforts are woefully underfunded and inadequate, despite considerable effort. The widespread use of wood products as packing material and the ongoing global trade in live plant material means that threats to forests are likely to be equal or greater than to other ecosystems (McCullough et al. 2006).

For recognized pests of limited geographic distribution, quarantine is often the primary strategy adopted by yet uninfested countries or regions. Limiting anthropogenic movement of pests via trade regulation is a difficult task, and the approach suffers from problems of enforcement, capacity, incomplete knowledge (e.g. of true geographic ranges, or of secondary vectors of spread), unauthorized transport, and natural dispersal. Where some countries in a given region are less willing or less able to quickly develop legislation for quarantine policy or to enforce existing rules, “leakage” across borders becomes a significant barrier to success. Quarantine can also cripple local economies in infested regions and can represent an undesirable impediment to global trade (Sumner 2003). That said, strengthening and enforcing targeted legislation – to ban or seriously limit the trade in live plants for planting responsible a high proportion of exotic introductions, for example – is highly desirable (Liebhold et al. 2012; Montesclaro Declaration: <http://www.iufro.org/science/divisions/division-7/70000/publications/montesclaros-declaration>).

Once established outside their native range, forest pests are often both superabundant and closely associated with human production systems, facilitating subsequent transfer and challenging efforts to prevent further range expansion (Wingfield et al. 2011). Tourism and commercial transportation are receiving growing scrutiny as a crucial pathway for the movement of many plant pests, further complicating quarantine efforts (Tatem 2009). While challenging, quarantine efforts remain a key element of national and international forest protection.

3.2. Post-establishment strategies

Once pests have become established, the most commonly employed and effective approaches to control population growth, spread and damage in plantation environments include utilizing tree genetics for host resistance (via tree breeding and site-appropriate species/cultivar selection), cultural/silvicultural management, and chemical and biological control. Advances in tree breeding such as marker-assisted selection have shown great promise as a strategy to combat chronic or emerging pests (Neale and Kremer 2011). Coupled with an improved understanding of the molecular basis of plant–insect and plant–pathogen interactions, breeding will undoubtedly form a cornerstone mitigating losses due to pests and diseases. The

increasing availability of tree genomes (*Populus trichocarpa* and *Eucalyptus grandis* were recently released, and *Pinus taeda* is currently being sequenced) is highly likely to transform our understanding of how to effectively combat biotic and abiotic threats. However, several factors limit the extent to which breeding programmes can be effectively used to manage pests: high costs and considerable time associated with tree breeding; limitation of heritable genetic variation in resistance that does not compromise other desirable traits; intellectual property issues; and negative public perceptions concerning the use of transgenics.

Cultural and silvicultural practices can contribute greatly to managing insect pests, particularly at a local or regional scale. However, plantation management is first and foremost aimed at maximizing timber/fiber quality and yield, and in general is less frequently seen as a risk-mitigation strategy. In fact, management plans are rarely formulated with explicit consideration of more than one or a few damaging pests. On the other hand, site–species matching (or the explicit recognition of the interaction between tree provenance and environment with respect to species selection) has the potential to positively affect plantation health on a broad spatial scale, including perhaps reducing or eliminating the planting of susceptible species. For example, *Eucalyptus viminalis* and *E. globulus* were discontinued as plantation species in South Africa due to damage by the leaf-feeding beetle *Goniapterus scutellatus sensu lato* (Tooke 1955; Figure 2d), although in the latter case the serious leaf pathogen *Teratosphaeria nubilosa* was also involved in the decision (Hunter et al. 2008). At a more local scale, effective monitoring, careful and timely pruning/thinning, removal and proper disposal of infested material, and management for resident natural enemies form the cornerstones of an effective integrated pest management (IPM) programme. However, efforts to directly control pest densities via silvicultural controls are largely ad hoc and are unlikely to represent a viable long-term solution against an increasing number and diverse range of damaging invasive pests.

The use of synthetic insecticides against forest insects is not without precedent, but long-term chemical control is ecologically and economically costly, is minimally effective against cryptic pests (e.g. wood-boring or galling insects), and can disproportionately impact natural enemies present in the system (leading to outbreaks of secondary pest insects; Eveleens et al. 1973). Perhaps equally important, global market pressures are dictating that fewer and fewer chemicals be used to control pests, driven by government regulation, pressure from environmental organizations and elevated consumer scrutiny (often under the umbrella of forest certification authorities). Such constraints have driven many forestry companies worldwide to recognize the absolute necessity of minimizing or eliminating the use of chemicals in their

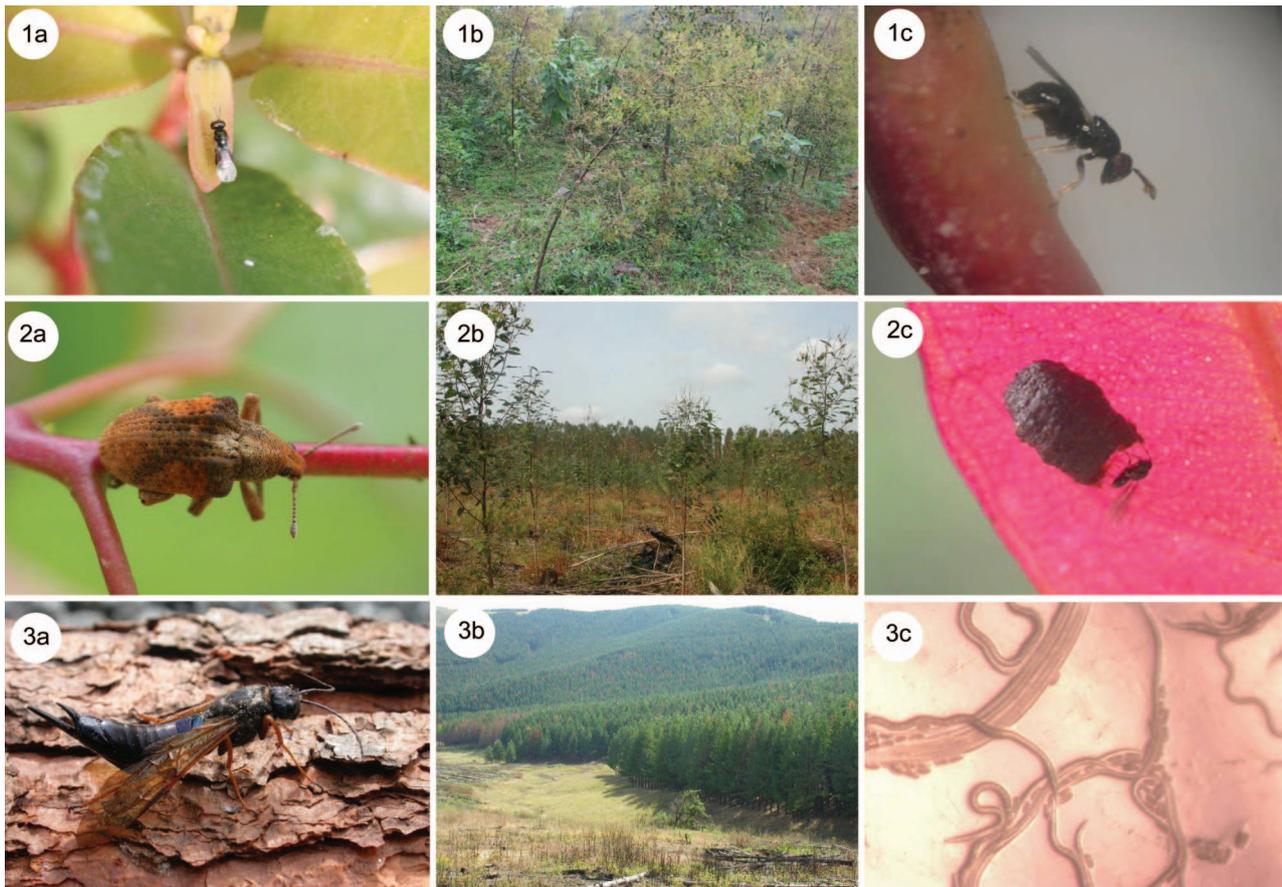


Figure 2. (Colour online) Examples of important pests of plantation species worldwide (column 1), with damage (column 2) and biocontrol agents (column 3). All photos were taken in South African plantations. Subjects are as follows: *Leptocybe invasa* (a), *L. invasa* damage in *Eucalyptus* hybrid (b); *Selitrichodes* spp., currently under testing as a biocontrol agent for *L. invasa* (c); *Gonipterus scutellatus sensu lato* (d); *Gonipterus* damage in *Eucalyptus* (e), *Anaphes nitens* (f); *Sirex noctilio* female (g); *Sirex*-induced mortality *Pinus patula* (h); parasitic nematodes, *Deladenus siricidicola* (i).

plantations (see National Standards for the Forest Stewardship Council, FSC; www.fsc.org).

Biological control (the introduction or augmentation of natural enemies to suppress herbivore populations) has long been relied upon to provide a sustainable, cost-effective, long-term approach to controlling damaging insects in plantation forestry. Often such strategies rely on the introduction of insect predators and parasitoids (typically wasps, flies and beetles), but programmes using mites, entomopathogenic fungi, viruses, or bacterial products (e.g. *Bt*) have shown great promise in both forestry and agriculture (Hajek and Tobin 2010).

There are numerous examples of successful biocontrol programmes in plantation forestry worldwide. When such programmes work, the savings over chemical or other controls can be enormous, often ranging in the tens of millions of dollars (Hajek 2004). For example, classical biological control of *Pineus* aphids (*Pineus pini* and *Pineus boeneri*) by a handful of specialized predators in three distinct orders (Diptera, Coleoptera, and Hemiptera) has been extremely

successful in Chile, Hawaii, and several countries in eastern and southern Africa (Day et al. 2003). Control of the European woodwasp by the parasitic nematode *Deladenus siricidicola* has yielded superb results in Australia where it was originally developed (see Figure 2g–i). Nematode rearing and inoculation technology has since been exported and adopted by a number of Southern Hemisphere countries. Despite variable levels of success, the technology appears to be strongly mitigating damage by *Sirex*. In South Africa, for example, cumulative foregone income due to *S. noctilio* damage was calculated in 2007 to be R780 million (US\$109 million) to growers and processors following severe outbreaks the years before, with the potential to rise to R1900 million (US\$ 266 million) or more if outbreaks of equivalent levels were to occur throughout all the pine-growing regions of the country without control (R. Godsmark, Forestry South Africa, pers. comm.). These outbreaks have been brought under control, at least partly due to the biological control using *D. siricidicola*. The rearing and deployment of *D. siricidicola* in South Africa has an estimated annual

cost of R3.1 million (US\$434,000; P. Croft, ICFR; pers. comm.), minimal compared to costs associated with potential losses.

4. The future of biocontrol in plantation forestry

Biological control clearly represents one of the major ways forward for managing the global problem of exotic pests in plantation environments. Abiotic environments and native communities vary among growing regions, but increasingly the major threats (Table 1) – and by extension, the suite of plausible solutions – are shared across borders or even continents. As both the costs and benefits of biological control are common, it is imperative that we take a more international approach to build, share and synergize existing capacity, maximize efficiency and minimize costs (see Table 2 for a summary of opportunities and challenges influencing this process). It seems evident that the demand to develop and implement biological control for an ever-growing number of important pests far exceeds current capacity. Despite this perspective, it is difficult to make the case to maintain a large team of researchers, given the sporadic nature of the establishment and spread of forest pests. It is thus critical to maximize resources, and to share knowledge, capacity, and resources wherever possible.

4.1. Shared problems call for shared solutions

Increasingly, threats to plantation forestry are the same in many parts of the world. Table 1 lists the major current pest threats to plantation-grown *Eucalyptus* and *Pinus* species and clearly reflects the shared nature of the pest problems across continents. More than two-thirds of the pests occur on two or more continents, many on all continents where their hosts are planted as exotics (e.g. all continents where the pest can plausibly be introduced). It has become evident that the establishment of a pest on one continent greatly increases the chances of introduction into other areas (Wingfield et al. 2011). The extent of this increase will be well worth quantifying in future. The reasons seem obvious, namely that recently established populations tend to reach high population levels due to the absence of biological and other control measures soon after their discoveries. These elevated populations tend to become stepping stones and sources of new introductions to surrounding areas and to trading partners of the invaded area, leading to increased chances of mass dispersal (Lockwood et al. 2005b; Wilson et al. 2009; Wingfield et al. 2011).

Just as the rate of global introductions is increasing, so too is the speed with which pests appear to be capable of expanding their range within and among continents after initial establishment outside of their native range. Pests that established 80–100 years ago

appear to have spread quite slowly for the first part of their tenure as non-natives, followed by rapid recent expansion. For example, the European pine woodwasp, *S. noctilio*, was initially detected in New Zealand in 1900 and putatively remained within Australasia until it was detected in South America (Uruguay) in 1980, South Africa in 1994, and North America (Oswego, New York) in 2004 (Hurley et al. 2007). Similarly, the eucalyptus snout beetle, *Gonipterus scutellatus* (currently regarded as a complex of species; Mapondera et al. 2012, Garnas, unpublished data) was first reported outside of Australia in 1890, in South Africa in the 1920s, and spread to most parts of the world growing *Eucalyptus* over the next 80 years (Tooke 1955). Spread rates among continents have been much faster in recent decades. In stark contrast to the pattern for *S. noctilio* and *G. scutellatus*, *L. invasa* spread globally in less than a decade since it was first detected in Israel in 2000 (FAO 2009). Given the relatively small sample size of highly damaging global pests shown in Table 1, we cannot exclude stochastic effects linked to the particular biology or life histories of the insects in question. However, such patterns are consistent with increasing rates of global movement and trade and apply to many invasive species across many ecosystems, including tree pathogens and insect pests (Lockwood et al. 2005a). It bears mentioning that of the five pests that have attained global status (defined here as being present on all continents outside of the native range, save Antarctica), the three that were introduced before 1950 (*S. noctilio*, *G. scutellatus*, *Ctenarytaina eucalypti*) took 104, 104 and 102 years, respectively, to reach all continents, whereas the two introduced after 1950 (*Orthotomicus erosus*, *L. invasa*), took 36 and 8 years, respectively, to achieve the same status (Table 1).

Based on current trends, the majority of plantation pests would be predicted to arrive on all continents soon after initial detection, in some cases nearly simultaneously. Early signs of rapid spread rates together with large populations of *Thaumastocoris peregrinus* in Africa and South America (together with its recent detection in Europe), *Glycaspis brimblecombei* in North and South America, Europe and North Africa, and *Ophelimus maskelli* in North Africa and Southeast Asia, should lead forest managers all over the world to anticipate the imminent arrival of these pests. Few industries, research organizations or governments in these or other regions have adequate capacity to effectively deal with the pressure from these pests all at once, further highlighting the need for broad networks of collaboration in the area of biological control.

4.2. Costs of biocontrol

Despite clear advantages, developing successful biological control programmes can be slow, and they carry significant upfront costs. By far the most significant

cost related to developing a successful biological control programme is time. In the examples shown in Table 1, the deployment of biocontrol lagged behind pest discovery by between 2 years (*Psyllaephagus bliteus*) and 104 years (*P. pilosus*) (mean \pm SE = 28 ± 8). While little information is available on the actual number of person hours spent on the development of these and other programmes, the identification, development and testing of potential biocontrol agents can be a monumental task. Timber and pulp losses due to pest-related declines in plantation productivity and tree mortality while biological control development and release efforts are underway are sure to far exceed direct costs in researcher salaries and programme running costs.

Not all of the biocontrol projects undertaken actually lead to effective releases. According to Klein (2011), of the 270 non-native weed biocontrol agents (84% phytophagous insects) considered in South Africa since 1913, 75 were established (of the 106 released) while 102 were rejected or shelved and 43 are still under active consideration. Examples specific to plantation forestry include the biological control of *Trachymela tincticollis* in South Africa, where only one of the four potential biological control agents identified and introduced became established (Tribe and Cillie 2004). Likewise, for the biological control of *Rhyacionia buoliana* in North America pre-1960, of the 16 biological control agents introduced in the United States and 13 introduced in Canada, only 4 became established (Invasives Species Compendium (Beta), www.cabi.org). More recent attempts at biological control, having benefited from past research and practice, may have higher rates of success but also face a more difficult regulatory landscape in many countries. However, biological control programmes can extend over long periods, and these numbers demonstrate the stark reality that a large proportion of work does not result in the establishment, or even release of a biocontrol agent (Freckleton 2000).

The use of specialized equipment is relatively minimal in the field of biocontrol, but quarantine facilities, required when working with non-indigenous insects or pathogens, demand significant capital expense and must be maintained with great care. Such facilities require climate-controlled growth rooms and glasshouses, including extensive back-up, alarm and response systems to avoid losses due to inevitable equipment failure. Intensive routine maintenance schedules and inspections are required to comply with strict standards set by regulatory bodies. Thus, continuous investment in infrastructure, equipment and permanent personnel is needed (Fisher and Andres 1999).

4.3. Changing tools for a changing landscape

While the basic infrastructure for mass rearing of plants and insects under quarantine conditions is a key

component of any biological control programme, researchers and practitioners increasingly realize that genetic and genomic tools are essential to fully understand species and population diversity and to ensure the long-term effectiveness of biocontrol (Roderick and Navajas 2003; Hufbauer and Roderick 2005; Garipey et al. 2007; Estoup and Guillemaud 2010). Such tools can help to overcome some of the challenges that have resulted in various failures of biological control, such as species misidentifications, poor understanding of host/parasitoid native phylogeography, incorrect inference of invasion pathways and patterns based on historical data and spatiotemporal patterns in genetic diversity of introduced populations. Molecular tools can also be used to assess population structure and the potential for local adaptation, as well as dispersal patterns, evidence for host–parasite co-evolution, the evolution and spread of resistance, host shifts and range expansions. Application of these technologies is costly, however, and requires its own set of specialized equipment and skills.

4.4. Secondary pest transfer – cryptic invasion

The arrival of an invasive, damaging pest to an area where it was not known to occur is a dramatic event that carries with it important economic consequences. It stands to reason, however, that if rates of initial introductions are rapidly rising, so too is the incidence of multiple introductions of the same species, or even effective gene flow between disparate regions. Such repeated introduction events, often from multiple sources, are common in plants (e.g. summary in Wilson et al. 2009), animals (Kolbe et al. 2004) and fungal pathogens (Burgess et al. 2004; Hunter et al. 2008). In the cases where it has been studied, a similar pattern has been shown for forest insect pests (Cognato et al. 2005; Carter et al. 2010; Hurley et al. 2010; Nadel et al. 2010). Such events are often cryptic and can only be detected with molecular tools but have important implications for accrual of genetic diversity and the spread of resistance to pesticides, biocontrol agents or genetically resistant planting stock.

4.5. Ecological costs of biocontrol

The ecological costs on native ecosystems resulting from introduced biocontrol agents are often thought of as low or non-existent, especially as compared with chemical alternatives. Despite rigorous testing and careful evaluation, however, non-target effects do occur and these are of growing public concern (van Lenteren et al. 2006). According to Hawkins and Marino (1997), 16% of the 313 parasitoids introduced to North America attacking holometabolous insects were also found to attack native species, with variable impacts (though more rigorous standards now exist for the introduction of biocontrol agents). Suppressive

effects of biocontrol agents on populations of native, non-target organisms require careful study to detect, but *Compsilura concinnata*, the generalist tachinid (fly) parasitoid, provides one such example. Introduced into North America multiple times over the past century against 13 pest species, including gypsy moth, *C. coccinata* was later found to be responsible for between 36% and 81% of larval mortality in three native giant silkworm (saturniid) moth species and was shown to parasitize at least 12 other species in the field (Boettner et al. 2000).

Community-level consequences of the introduction of exotic biocontrol agents can also be mediated via competitive exclusion. The predatory ladybird *Harmonia axyridis*, originally introduced to control aphid populations in North America and Europe, is now superabundant in many places (including areas where it was not intentionally released) with detrimental effects on competing native coccinellids (Roy et al. 2012). Still other ecological costs have been incurred due to indirect community-level effects, which are difficult or impossible to anticipate based on laboratory or even controlled field studies (Pearson and Callaway 2003, 2005).

Increasingly strict regulations governing the import and release of biocontrol agents requiring rigorous testing of non-target effects on native species will help to avoid some mistakes. However, researchers, legislators and the public should be cognizant of the inevitability of some spillover and/or unanticipated consequences stemming from biocontrol (Louda et al. 2003). Direct and indirect effects of introduced biocontrol agents are likely to be idiosyncratic by region. More facile information sharing across borders could help to identify unanticipated effects of a particular agent which were not picked up in specificity testing. In this way, other countries would have the opportunity to avoid similar errors or unanticipated problems (Thomas and Willis 1998).

Overall, the costs associated with biological control can be considered minimal when compared to the ongoing ecological/economic costs associated with pesticide use. However, these upfront costs remain high for individual stakeholders to carry, especially when they involve multiple introductions over a short period of time, and the consideration of possible ecological costs is a timely and complex process. International collaborative efforts in biocontrol offer a solution, because upfront costs can be diluted across a larger pool of stakeholders. Careful consideration of societal and stakeholder values is critical to success. For example, biological control in South Africa and elsewhere is actively being developed both to protect exotic plantation trees from insect damage and to control seed production of invasive trees (including some exotic plantation tree species) to limit tree invasion into native ecosystems. Such programmes can exist side by side and may even synergize one

another, but the potential for conflict does exist (e.g. *Pissodes validirostris* was proposed for introduction as a seed predator of pine, but has been shown to positively effect infection by *Fusarium circinatum*, which is devastating to growth and yield; Lennox et al. 2009). In addition, since a degree of overlap in possible ecological costs between regions is expected, sharing of information (e.g. concerning host specificity of introduced agents in field, and/or interactions with the broader community) can assist in streamlining the process required to assess these costs.

5. Potentially useful models of international collaboration for biocontrol

The need to cooperate across borders with regards to biological control development is well recognized within the scientific community. Classical biological control is by definition an international endeavour, as source material necessarily originates outside the invasive range of the pest (typically in its region of origin). A truly international focus, involving long-term institutional collaboration across countries, has as yet been elusive. We recognize that logistical constraints and challenges exist, but argue that the benefits far outweigh the potential challenges (Table 2).

Interestingly, quarantine depends critically on the rapid adoption and implementation of trade legislation and on international cooperation with respect to compliance and enforcement. As such, the philosophy and regulatory infrastructure surrounding quarantine may provide an existing model that could be adapted to foster cooperation with respect to the biological control of established pests.

To date, the majority of cross-border collaboration in the field of biological control has been driven largely by personal relationships and by a relatively small number of international collaborative funding initiatives. Such funding, while important to stimulate and facilitate international cooperative research, typically comprises short-term agreements between specific grant holders in no more than a few participating countries. The value of such relationships and initiatives should not be understated as they have served as the cornerstone for most biological control efforts to date. However, relying on these old models fails to recognize the need for focused change in an increasingly complex world. Concerted effort is also required to ensure that national or international regulations, such as the “International Regime on Access and Benefit-Sharing” proposed by the Convention on Biology Diversity, do not frustrate cooperation going forward. While ensuring each country’s sovereign rights over its biological/genetic resources and equitable benefit-sharing in the case of commercial exploitation is a laudable goal, careful thinking is essential so that bureaucratic hurdles do not emerge

that could seriously threaten classical biological control (Cock et al. 2010).

Government organizations with a mandate to promote tree health (i.e., the USDA Forest Service, the Animal and Plant Health Inspection Service [APHIS], or their equivalents worldwide) have long recognized the need for international focus and continue to forge and maintain many links among countries. The intergovernmental European Plant Protection Organization (EPPO; www.eppo.org) has 50 member countries in the European and Mediterranean region (plus associated satellite organizations in other regions worldwide) that promotes plant health and invasive species management by aggregating and synthesizing information on invasive species distributions and threats, current control methods and quarantine, among other aspects. The International Union of Forest Research Organizations (IUFRO; www.iufro.org) has likewise been integral in bringing researchers and policy makers together from all over the world to discuss current trends and knowledge regarding forest health, productivity and economics.

CABI and IOBC (International Organisation for Biological Control of Noxious Animals and Plants) are organizations that have an international biological control focus. These organizations are involved in promoting biological control projects connecting countries across the globe, and play a crucial role in disseminating information. However, the focus of these organizations is primarily food security and the environment, and plantation forestry – particularly of non-native species – is largely neglected. An international collaborative approach to biological control, with a focus on plantation forestry and where the resource owners are actively involved, is urgently needed.

Collectives of companies with interests in tree growth, health and protection have proven particularly successful and provide a possible way forward in the context of biocontrol. One example is Camcore (Central America and Mexico Coniferous Resources Cooperative, a name which derives from the group's original, narrower focus), which is a non-profit international organization with a mission to conserve genetic material and to domesticate tropical and subtropical trees, primarily those of economic importance (www.camcore.org). In its pursuits, Camcore partners with local landowners around the world who conduct replicated provenance trials with the goal of genetic improvement via selection for desirable phenotypes, including pest and disease resistance. At its core, Camcore is a seed bank cooperative with members from the forest industry and governments worldwide, a model which has proved highly successful. Members pay annual dues to Camcore in support of their broader goals and in turn retain access to genetic material, much of which has been improved as well as matched to particular growing conditions. This service

has proved invaluable as a response to numerous pests and pathogens including, most recently, pitch canker caused by the fungus *Fusarium circinatum* in South Africa (Wingfield et al. 2008a, 2008b).

Numerous examples can be listed of individual international collaborative efforts around biological control. In the past, these have emerged as a result of emerging, serious pest problems. Perhaps one of the best examples is the Australian response to the introduction of *S. noctilio*, a serious pest in Australian pine plantations in the 1960s (see summaries in Hurley et al. 2007, Carnegie and Bashford 2011). Mostly through public funding (Commonwealth and Australian central and state government), research stations were established in both England (Imperial College at Silwood Park) and Tasmania (Hobart). Numerous researchers were employed in both countries, and collections as well as research on parasitoids and parasitic nematodes were launched at a scale which is hard to imagine today. For example, Spradbery and Kirk (1978) report on some of these collections, including approximately 4000 logs from 150 sites in 19 countries across Eurasia and North Africa for emergence at Silwood Park station. Bedding and Akhurst (1978) reported dissections of over 22,000 insects, from 31 hosts and 29 countries, collecting seven species of parasitic *Deladenus* nematodes. The result of these efforts is very evident. Not only were numerous seminal research papers published on this pest and its control, but it has left a legacy of control agents that are used in the field and extensively studied to this day across the world. It is hard to quantify the economic benefit of this work, but based on local estimates, it would amount to hundreds of millions of dollars. This benefit from an investment made from Commonwealth and Australian public funds has not only been beneficial to Australia, but to numerous countries across the Southern Hemisphere (see "Post-establishment strategies" above). Commonwealth funding eventually ceased, but a central funding body remains in Australia with contributions from government and private land owners (through an enforced levy). Such initiatives might well serve as a model for what will be needed in the future. Governments and industries will need to consider how they can collaborate to make such efforts possible. It is unlikely to be affordable in isolation.

6. Conclusions

The long-term persistence and profitability of plantation forestry around the world depends to a large degree on the ways in which forestry companies adapt to and cope with continuously emerging exotic pest invasions. The global forestry industry, research organizations and governments must recognize that demand for biological control as a major component of this response will continue to increase substantially in

future. Forest owners, companies and governments with a vested interest in these resources must have access to the human and technological capacity to deal with the rapidly increasing demand for biological control as a long-term solution for threats to forests and plantations.

Current models of responses to novel pests that rely too heavily on available biocontrol capacity, or that scramble to build capacity after a crisis has emerged, are very likely to fail in future given increasing rates of pest arrival and spread. Investing in structures that promote long-term, international focus rooted in collaborations among researchers worldwide has the potential to cut costs, reduce redundancy, and share and grow capacity, with benefits for all involved. Bridging gaps among biological control organizations worldwide is certain to be challenging but represents a critical step toward building long-term and visionary approaches to understanding and responding to pest problems going forward.

Acknowledgements

Thank you to Phillip Croft and Roger Godsmark for information regarding costs related to Sirex damage and biological control. We also acknowledge funding for research underpinning this review from the members of the Tree Protection Co-operative Programme (TPCP), the THRIP initiative of the Department of Trade and Industry and the National Research Foundation, South Africa.

References

- Bedding R, Akhurst RJ. 1978. Geographical distribution and host preferences of *Deladenus* species (Nematoda: Neotylenchidae) parasitic in siricid woodwasps and associated hymenopterous parasitoids. *Nematologica*. 24: 286–294.
- Boettner GH, Elkinton JS, Boettner CS. 2000. Effects of a biological control introduction on three nontarget native species of saturniid moths. *Conserv Biol*. 14:1798–1806.
- Brockhoff EG, Bain J, Kimberley M, Knížek M. 2006. Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Can J For Res*. 36:289–298.
- Burgess TI, Wingfield MJ, Wingfield BD. 2004. Global distribution of *Diplodia pinea* genotypes revealed using simple sequence repeat (SSR) markers. *Aus Plant Pathol*. 33:513–519.
- Carnegie A, Bashford R. 2011. Sirex woodwasp in Australia: Current management strategies, research and emerging issues. In: Slippers B, de Groot P, Wingfield MJ, editors. *The Sirex woodwasp and its fungal symbiont: Research and management of a worldwide invasive pest*. The Netherlands: Springer. p. 175–201.
- Carnegie AJ, Matsuki M, Haugen DA, Hurley BP, Ahumada R, Klasmer P, Sun J, Iede ET. 2006. Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. *Ann For Sci*. 63:119–128.
- Carter M, Smith M, Harrison R. 2010. Genetic analyses of the Asian longhorned beetle (Coleoptera, Cerambycidae, *Anoplophora glabripennis*), in North America, Europe and Asia. *Biol Invasions*. 12:1165–1182.
- Cock MJW, Lenteren JC, Brodeur J, Barratt B, Bigler F, Bolckmans K, Cónsoli FL, Haas F, Mason PG, Parra JR. 2010. Do new Access and Benefit Sharing procedures under the Convention on Biological Diversity threaten the future of biological control? *BioControl*. 55:199–218.
- Cognato AI, Sun J-H, Anducho-Reyes MA, Owen DR. 2005. Genetic variation and origin of red turpentine beetle (*Dendroctonus valens* LeConte) introduced to the People's Republic of China. *Agric For Entomol*. 7:87–94.
- Day R, Kairo MTK, Abraham YJ, Kfir R, Murphy ST, Mutitu KE, Chilima CZ. 2003. Biological control of homopteran pests of conifers in Africa. In: Neuenschwander P, Borgemeister C, Langewald J, editors. *Biological control in IPM systems in Africa*. Wallingford (UK): CAB International. p. 101–112.
- Estoup A, Guillemaud T. 2010. Reconstructing routes of invasion using genetic data: Why, how and so what? *Mol Ecol*. 19:4113–4130.
- Eveleens KG, van den Bosch R, Ehler LE. 1973. Secondary outbreak induction of beet armyworm by experimental insecticide applications in cotton in California. *Environ Entomol*. 4:497–503.
- FAO [Food and Agriculture Organization]. 2009. Global review of forest pests and diseases. FAO Forestry Paper 156. Rome: FAO.
- FAO [Food and Agriculture Organization]. 2010. Global forest resources assessment. Rome: FAO Forestry Paper 163. Rome: FAO.
- Fisher T, Andres L. 1999. Quarantine: Concepts, facilities and procedures. In: Bellows TS, Fisher TW, editors. *Handbook of biological control: Principles and applications*. San Diego: Academic Press. p. 103–124.
- Freckleton R. 2000. Biological control as a learning process. *Trends Ecol Evol*. 15:263–264.
- Garipey TD, Kuhlmann U, Gillott C, Erlandson M. 2007. Parasitoids, predators and PCR: The use of diagnostic molecular markers in biological control of arthropods. *J Appl Entomol*. 131:225–240.
- Gebeyehu S, Hurley B, Wingfield M. 2005. A new lepidopteran insect pest discovered on commercially grown *Eucalyptus nitens* in South Africa. *S Afr J Sci*. 101:26–28.
- Haack R. 2006. Exotic bark- and wood-boring Coleoptera in the United States: Recent establishments and interceptions. *Can J For Res*. 36:269–288.
- Hajek A. 2004. *Natural enemies: An introduction to biological control*. Cambridge: Cambridge University Press.
- Hajek A, Tobin P. 2010. Micro-managing arthropod invasions: Eradication and control of invasive arthropods with microbes. *Biol Invasions*. 12:2895–2912.
- Hawkins B, Marino P. 1997. The colonization of native phytophagous insects in North America by exotic parasitoids. *Oecologia*. 112:566–571.
- Hu J, Angeli S, Schuetz S, Luo Y, Hajek AE. 2009. Ecology and management of exotic and endemic Asian longhorned beetle *Anoplophora glabripennis*. *Agric For Entomol*. 11:359–375.
- Hufbauer RA, Roderick GK. 2005. Microevolution in biological control: Mechanisms, patterns, and processes. *Biol Control*. 35:227–239.
- Hunter GC, van der Merwe NA, Burgess TI, Carnegie AJ, Wingfield BD, Crous PW, Wingfield MJ. 2008. Global movement and population biology of *Mycosphaerella nubilosa* infecting leaves of cold-tolerant *Eucalyptus globulus* and *E. nitens*. *Plant Pathol*. 57:235–242.
- Hurley B, Slippers B, Wingfield B, Govender P, Smith J, Wingfield M. 2010. Genetic diversity of *Bradysia difformis* (Sciaridae: Diptera) populations reflects movement of an invasive insect between forestry nurseries. *Biol Invasions*. 12:729–733.

- Hurley BP, Slippers B, Wingfield MJ. 2007. A comparison of control results for the alien invasive woodwasp, *Sirex noctilio*, in the southern hemisphere. *Agric For Entomol.* 9:159–171.
- Klein H. 2011. A catalogue of the insects, mites and pathogens that have been used or rejected, or are under consideration, for the biological control of invasive alien plants in South Africa. *Afr Entomol.* 19:515–549.
- Kolbe JJ, Glor RE, Schettino LRG, Lara AC, Larson A, Losos JB. 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature.* 431:177–181.
- Lennox CL, Hoffmann JH, Coutinho TA, Roques A. 2009. A threat of exacerbating the spread of pitch canker precludes further consideration of a cone weevil, *Pissodes validirostris*, for biological control of invasive pines in South Africa. *Biol Control.* 50:179–184.
- Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO. 2012. Live plant imports: The major pathway for forest insect and pathogen invasions of the US. *Front Ecol Environ.* 10(3):135–143.
- Liebhold AM, Macdonald W, Bergdahl D, Maestro V. 1995. Invasion by exotic forest pests – a threat to forest ecosystems. *For Sci.* 41:1–49.
- Lockwood JL, Cassey P, Blackburn T. 2005a. The role of propagule pressure in explaining species invasions. *Trends Ecol Evol.* 20:223–228.
- Lockwood JL, Cassey P, Blackburn T. 2005b. The role of propagule pressure in explaining species invasions. *Trends Ecol Evol.* 20:223–228.
- Lockwood JL, McKinney ML. 2001. *Biotic homogenization*. New York: Kluwer Academic/Plenum Publishers.
- Louda SM, Pemberton RW, Johnson MT, Follett PA. 2003. Nontarget effects: The Achilles heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. *Annu Rev Entomol.* 48:365–396.
- Mapondera TS et al. 2012. Identification and molecular phylogenetics of the cryptic species of the *Gonipterus scutellatus* complex (Coleoptera: Curculionidae: Gonipterini). *Aus J Entomol.* Available from: <http://online.library.wiley.com/doi/10.1111/j.1440-6055.2011.00853.x/abstract>
- McCullough DG, Work TT, Cavey JF, Liebhold AM, Marshall D. 2006. Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. *Biol Invasions.* 8:611–630.
- Mendel Z, Protasov A, Fisher N. 2004. Taxonomy and biology of *Leptocybe invasa* gen. & sp. nov. (Hymenoptera: Eulophidae), an invasive gall inducer on *Eucalyptus*. *Aus J Entomol.* 43:101–113.
- Nadel RL, Slippers B, Scholes MC, Lawson SA, Noack AE, Wilcken CF, Bouvet JP, Wingfield MJ. 2010. DNA barcoding reveals source and patterns of *Thaumastocoris peregrinus* invasions in South Africa and South America. *Biol Invasions.* 12:1067–1077.
- Neale DB, Kremer A. 2011. Forest tree genomics: Growing resources and applications. *Nat Rev Genet.* 12:111–122.
- Pearson DE, Callaway RM. 2003. Indirect effects of host-specific biological control agents. *Trends Ecol Evol.* 18:456–461.
- Pearson DE, Callaway RM. 2005. Indirect nontarget effects of host-specific biological control agents: Implications for biological control. *Biol Control.* 35:288–298.
- Roderick G, Navajas M. 2003. Genes in new environments: Genetics and evolution in biological control. *Nat Rev Genet.* 4:889–899.
- Roy H, Adriaens T, Isaac N, Kenis M, Onkelinx T, Martin G, Brown P, Hautier L, Poland R, Roy DB, Comont R, Eschen R, Frost R, Zindel R, Van Vlaenderen J, Nedvød O, Ravn HP, Grégoire J, de Biseau J, Maes D. 2012. Invasive alien predator causes rapid declines of native European ladybirds. *Diversity and Distributions.* DOI: 10.1111/j.1472-4642.2012.00883.x.
- Sands R. 2005. *Forestry in a global context*. Wallingford (UK)/Cambridge (MA): CABI Publishing.
- Spradbery JP, Kirk AA. 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. *Bull Entomol Res.* 68:341–359.
- Sumner DA. 2003. *Exotic pests and diseases: Biology and economics for biosecurity*. 1st Ed. Ames (IA): Iowa State Press.
- Tatem AJ. 2009. The worldwide airline network and the dispersal of exotic species: 2007–2010. *Ecography.* 32:94–102.
- Thomas MB, Willis AJ. 1998. Biocontrol – risky but necessary? *Trends Ecol Evol.* 13:325–329.
- Tooke F. 1955. The Eucalyptus snout beetle *Gonipterus scutellatus* Gyll.: A study of its ecology and control by biological means. *Entomology Memoirs no. 3*. Pretoria: Department of Agriculture, Union of South Africa. p. 1–282.
- Tribe G, Cillie 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. *Afr Entomol.* 12:9–17.
- Van Lenteren JC, Bale J, Bigler F, Hokkanen HMT, Loomans AJM. 2006. Assessing risks of releasing exotic biological control agents of arthropod pests. *Annu Rev Entomol.* 51:609–634.
- Waage JK, Greathead DJ, Brown R, Paterson RRM, Haskell PT, Cook RJ, Krishnaiah K. 1988. Biological control: Challenges and opportunities [and discussion]. 318:111–128.
- Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM. 2009. Something in the way you move: Dispersal pathways affect invasion success. *Trends Ecol Evol.* 24:136–144.
- Wingfield M, Hammerbacher A, Ganley R, Steenkamp E, Gordon T, Wingfield B, Coutinho T. 2008a. Pitch canker caused by *Fusarium circinatum* – a growing threat to pine plantations and forests worldwide. *Aus Plant Pathol.* 37:319–334.
- Wingfield M, Slippers B, Hurley B, Coutinho T, Wingfield B, Roux J. 2008b. Eucalypt pests and diseases: Growing threats to plantation productivity. *South For.* 70:139–144.
- Wingfield MJ, Roux J, Wingfield BD. 2011. Insect pests and pathogens of Australian acacias grown as non-natives – an experiment in biogeography with far-reaching consequences. *Divers Distrib.* 17:968–977.