Exposing hidden dangers in dictary supplements p. 780

Limiting the dark side FO. 70G, 640, &-852

Diverse opinions on bioweapons p. 792

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SPECIAL ISSUE

FOREST HEALTH

THREATS AND RESILIENCE



By Andrew Sugden, Julia Fahrenkamp-Uppenbrink,
David Malakoff, and Sacha Vignieri

orests and woodlands cover about 20% of Earth's land surface, spanning all but the highest latitudes. In the millennia since humans dispersed across all forested continents, we have transformed large areas of natural forest. Historically, our greatest impacts were made in temperate regions, but they now extend to forests in the tropics and the boreal zone. Only a fraction of the forests present centuries ago have escaped human influence; in many regions the forest is gone, has regrown as secondary forest, or consists of managed and plantation forests. Humans have also introduced new species, including pests and pathogens of trees. Other influences—such as climate warming that causes tree species to shift geographically and anthropogenic drought that causes forest dieback—take effect more slowly and may occur far from their source.

Even though modern forests are generally much altered from their natural state, their "health" still matters. It will dictate whether forests persist and function into the future, sustaining wildlife, producing timber, sequestering carbon, and performing other services.

Yet forest health is difficult to define. Forests experience plenty of natural disturbances: fire, weather variations, competition between plant species, and attacks by insect pests and pathogens. They also experience longer-term successional change. When we speak of threats to forest health, we tend to imply the impacts of humans. However, it may not always be obvious whether human activity or a forest's natural dynamics are at play in, for example, the dieback of a stand or the outbreak of an insect herbivore.

Recognizing the signs of ill forest health and teasing apart the causes are important both for sustaining the services that humans rely on and for the effective conservation of forest biomes. Understanding how we influence forest health and function is a key challenge for the future, as we increasingly realize the importance of forests to the maintenance of a healthy planet.

INSIDE

NEWS

Battling a giant killer p.802

The new North p. 806

Second act p. 810

REVIEWS

Forest health and global change p. 814

Boreal forest health and global change n. 819

Temperate forest health in an era of emerging megadisturbance p. 823

Increasing human dominance of tropical forests p. 827

Planted forest health: The need for a global strategy p. 832

RELATED ITEMS

- ► EDITORIAL P. 771
- ▶ PERSPECTIVE P. 794
- ▶ VIDEO
- http://scim.ag/6250_ForestVid
- ► SLIDESHOW

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Mountain pine beetle infections are becoming more intense as weather warms in coniferous forests, like this one in central British Columbia. Infected trees die slowly, resulting in a forest full of various levels of colorful dieback.

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REVIEW

Planted forest health: The need for a global strategy

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Several key tree genera are used in planted forests worldwide, and these represent valuable global resources. Planted forests are increasingly threatened by insects and microbial pathogens, which are introduced accidentally and/or have adapted to new host trees. Globalization has hastened tree pest emergence, despite a growing awareness of the problem, improved understanding of the costs, and an increased focus on the importance of quarantine. To protect the value and potential of planted forests, innovative solutions and a better-coordinated global approach are needed. Mitigation strategies that are effective only in wealthy countries fail to contain invasions elsewhere in the world, ultimately leading to global impacts. Solutions to forest pest problems in the future should mainly focus on integrating management approaches globally, rather than single-country strategies. A global strategy to manage pest issues is vitally important and urgently needed.

orests and woodland ecosystems are a hugely important natural resource, easily overlooked and often undervalued (1-3). Globally, one in six people is estimated to rely on forests for food (3), and many more depend on forests for other critical ecosystem services, such as climate regulation, carbon storage, human health, and the genetic resources that underpin important wood and wood products-based industries. However, the health of forests, both natural and managed, is more heavily threatened at present than ever before (4-6). The most rapidly changing of these threats arise from direct and indirect anthropogenic influences on fungal pathogens and insect pests (hereafter referred to as pests), especially their distribution and patterns of interactions.

Here we focus on the importance of pests of planted forests, which are particularly vulnerable to invasive organisms yet are of growing importance as an economic resource and for various ecosystem services. Planted forests are typically of a single species. In plantations in the tropics and Southern Hemisphere, they are usually of nonnative species, such as species of Pinus, Eucalyptus, and Acacia. Northern Hemisphere plantations often comprise species of Pinus, Picea, Populus, Eucalyptus, and other genera, often in native areas or with closely related native species. These intensively managed tree farms cover huge areas [currently 7% and potentially 20% of global forests by the end of the century (1)], and they sustain major industries producing wood and pulp products. These tree genera have become natural resources of global importance, much like major agricultural crops, and are unlikely to be easily replaced.

Planted forests face various serious health threats from pests (Fig. 1). Non-native trees in plantations are in part successful because they

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have been separated from their natural enemies. However, when plantation trees are reunited with their coevolved pests, which may be introduced accidentally, or when they encounter novel pests to which they have no resistance, substantial damage or loss can ensue (7). The longer these non-native trees are planted in an area, the more threatened they become by native pests. Where the trees are of native species, they can be vulnerable to introduced pests. But the relative species uniformity of monoculture stands in intensively managed native plantation forests can make them especially susceptible to the many native pests occurring in the surrounding natural forests (8-10).

There are many opportunities to mitigate potential losses caused by pests in planted forests through exclusion (e.g., pre-export treatments and quarantine), eradication of newly established pests, and avoidance of disease through pest containment and management. Yet the lack of investment and capacity, especially in poorer countries, as well as the limited coordination of efforts at a global level, means that the impact of these tools to stem the global problem is limited. Unless this is addressed, pest problems will continue to grow and will threaten the long-term sustainability of forests and forestry worldwide. It should be recognized that the sustainable use of these tree "crops" will require the same global focus and investment to manage pest threat as that of agricultural crops.

Prevention is important but remains porous

Biological invasions of alien pests have been shown to be growing at constant or even increasing ratesand not only for those affecting trees (4-6, 11). Few pests are ever eradicated or completely suppressed, leading to an an ever-changing and increasing number of management programs to juggle. Phytosanitary measures are the major line of defense available to limit the global movement of pests, and various international policies seek to promote them [such as the International Standards For Phytosanitary Measures No. 15 (ISPM 15) (12, 13) that regulates the treatment of wood pallets to avoid bark beetle and wood borer invasions (14)].

There is evidence that strictly applied phytosanitary measures can reduce the rate of pest introductions into new environments (12, 14), and this is the most cost-effective way to deal with the challenge. Some wealthy and biogeographically isolated countries in particular, such as New Zealand and Australia, have tackled this quite successfully (15). But there are limitations to what can be achieved realistically through phytosanitary measures at a global scale. For example, it is unlikely that poorer countries can afford to institute biosecurity actions to achieve effective exclusion to the same extent, and even where the best possible phytosanitary measures have been applied, serious new pest problems continue to occur. The accidental introduction of myrtle rust caused by Puccinia psidii into Australia, despite considerable knowledge of this pathogen and significant efforts to exclude it, is an apt example of the limitations of quarantine (13). This pathogen has now become established on many native Australian Myrtaceae, some of which are now threatened with extinction.

Traditionally, quarantine regulations have been underpinned by a listing process, in which pests threatening to a particularly country are listed after risk analyses. However, many of the most damaging forest pests introduced into new environments were unknown in their areas of origin before their introductions. For example, no listing process would have included *Phytophthora pinifolia*, which has devastated some *Pinus radiata* plantations in Chile (16), before its arrival. Its origin remains unknown. For this reason, contemporary thinking on phytosanitary measures has begun to focus on introduction pathways rather than on particular pests (e.g., the ISPM 15 measures discussed above) (6, 12, 17). In this regard, there is a growing realization that trade in live plants poses a particular threat that is inadequately regulated in most countries (6, 17).

Quarantine can be only as effective as the proverbial weakest link in the chain. A large proportion of countries appear to have no effective quarantine in place for plants or plant products. Even where regulations are in place, the capacity to implement these effectively is often lacking. Therefore, invasive pest problems appear in these countries relatively frequently. Once a pest has become a successful invader in one region, it can serve as a source of new invasions elsewhere: a process that has been referred to as the bridgehead effect (18) (Fig. 2). A correlation is expected between the level of connectivity (e.g., the volume

of trade) of a country and its vulnerability to invasion and potential to serve as a hub for the spread of invasive pests, but other factors also play a role in this regard (5–7).

Opportunities for mitigation

Despite the obstacles, there is reason to be optimistic about the power of established and emerging opportunities to mitigate the impact of pests. Intensive plantation forestry provides some vivid examples of how established pest problems can be confronted. To deal with the global scale and increasing intensity of the problem, however, greater global coordination and alignment of the use of the most effective tools are required.

Intensive management of forests increasingly involves planting tree species that have been selected for particular environments and traits, including resistance to certain pests. From a species base (taxa and provenance trails), it has been possible to breed and select for increasingly better properties.

One of the best examples of modern intensive tree farming is the global *Eucalyptus* forestry industry. Plantations of these trees now cover some 20 million ha, mostly in the tropics and Southern Hemisphere (19) (Fig. 1). *Eucalyptus* is mostly native to Australia, where more than 700 species are

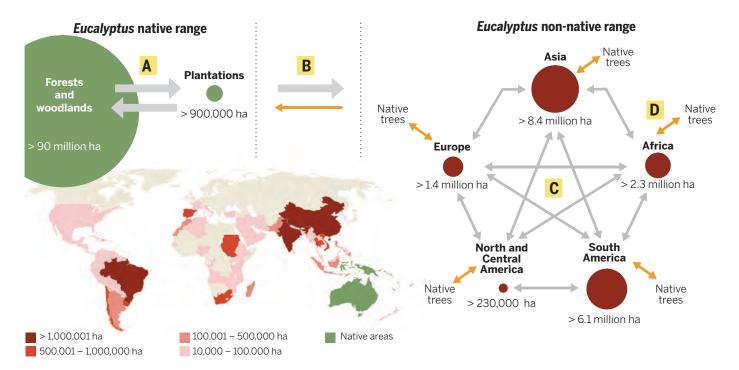


Fig. 1. Eucalyptus as a model to illustrate the origin and spread of planted forest pests. Plantations of Eucalyptus have increased from <1 million ha by 1950 to around 20 million ha today; the map shows the current distribution. These plantations experienced a steady increase of pest problems that has been accelerating during the past two decades. The origin of these pests can include the following: (A) Uninterrupted bidirectional spread of pests between natural and plantation areas of Eucalyptus in its native region. Increasing populations in plantations, and association with trade and human movement (e.g., from urban areas), increase changes in transport to other parts of the world. (B) Fairly large numbers of pests and pathogens spread

from the native area to one or more non-native environments. Few pests spread via non-native plantations back to native *Eucalyptus* areas, but these can have devastating consequences [see, for example, the discussion on *Puccinia psidii* in the text (13)]. (**C**) As population numbers build up in some of the non-native environments, further movement around the world is enhanced through a bridgehead effect. The rate of this spread appears to be increasing because of the confluence of a number of processes linked to globalization (18, 22) (Fig. 2). (**D**) Fairly large numbers of native pests and pathogens adapt to feed on or infect *Eucalyptus* in its non-native range. Some eventually spread to other areas of the world and can threaten *Eucalyptus* in its native range (B).

found in a wide range of environments, of which more than 10 and their hybrids are commonly planted commercially around the world today. This diversity of genetic background has provided opportunities to capture traits for fast growth in many different environments, favorable wood properties, and resistance to many different fungal and insect pests.

Vegetative propagation has underpinned the rapid growth of the Eucalyptus forestry industryand similarly for poplars, pines, and acacias. Mastering vegetative propagation has made it possible to produce and intensively propagate hybrids between tree species, leading to a paradigm shift for the global forest plantation industry. It has also provided one of the most important opportunities to avoid pest problems.A classic example is the case of the stem disease known as Cryphonectria canker, now recognized to be caused by a suite of cryptic species in the fungal genus Chrysoporthe (20). In the early 1980s, Cryphonectria canker was a major threat to the sustainability of Eucalyptus propagation in Brazil and later South Africa. Yet the selection of clones and particularly clonal hybrids with resistance made it possible to avoid the disease to the point where it is hardly considered important today (10).

An approach that is increasingly contemplated is to promote resistance to pest threats by increasing diversity through mixed plantings of species rather than monocultures (9, 21). From a managed forest perspective, this approach can be useful, but it is typically at odds with the needs of commercial forestry when done at a stand level. Nevertheless, introducing this form of resistance could be considered at a landscape level-for example, using clones in uniform but smaller blocks and including a diversity of genes rather than a diversity of species or even genotypes. Exploring the use of tree species and genera other than those currently used could offer further opportunities for mitigating the impact of pests and contribute to the resilience of the industry.

For introduced insect pests, biological control has provided superb solutions. Early examples of biological control in forestry date back to the early 1900s, using two introduced predators against the scale insect *Eriococcus coriaceus* on *Eucalyptus* in New Zealand and an egg parasitoid against the *Eucalyptus* snout beetle, known then as *Gonipterus scutellatus* (22). There have been many subsequent examples in planted forests, such as, for example, the widely applied *Sirex* woodwasp biological control using the parasitic nematode *Deladenus*

siricidicola (23). Dealing with native insect pests is somewhat more complex, and in the absence of resistant planting stock, the application of biocides such as formulations of the insect pathogenic bacterium *Bacillus thuringiensis* and insect pathogens (e.g., *Beauwaria bassiana*) and behavioraltering semiochemical-based strategies provide opportunities (24, 25). But there also remains a strong dependence on synthetic chemical insecticides that may be harmful to the environment and inconsistent with environmental certification (see http://pesticides.fsc.org).

Invest in research and innovation

Our capacity to deal with tree pest problems far outstrips the level of investment in exploring and applying these opportunities. At the outset of dealing with pest problems, we are challenged by our ability to accurately identify the pest in question. There are many examples where new pests appear that are misidentified or unknown elsewhere in the world. This is largely the result of poor or unequal levels of investment in global surveys and in our knowledge of global biodiversity. Hundreds of known pests and pathogens remain undetected, especially in poorer countries, and this problem is significantly more severe in forestry (26).

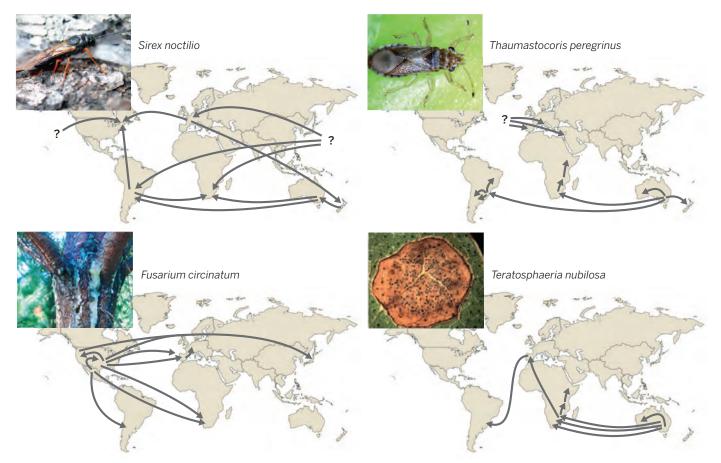
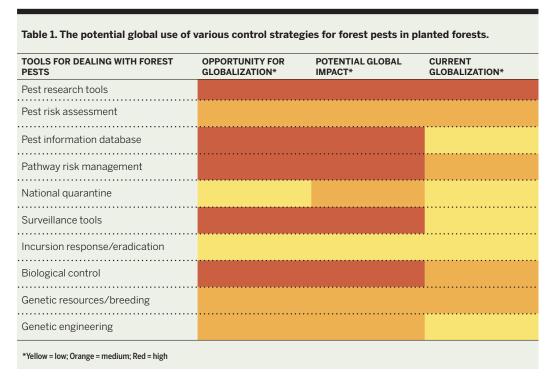


Fig. 2. Examples of invasion routes of pests of planted forests that illustrate an apparently common pattern of complex pathways of spread to new environments, including repeated introductions and with either native or invasive populations serving as source populations (18). Invasion routes of the pine pitch canker pathogen Fusarium circinatum (origin in Central America) (39), eucalypt leaf pathogen Teratosphaeria nubilosa (origin in southeast Australia) (40), the pine woodwasp Sirex noctilio (origin in Eurasia) (23), and the eucalypt bug Thaumastocoris peregrinus (origin in southeast Australia) (41) were determined through historical and genetic data. [Photo credits: (top left) Brett Hurley; (top right) Samantha Bush; (bottom left) Jolanda Roux; (bottom right) Guillermo Perez]

834 21 AUGUST 2015 • VOL 349 ISSUE 6250 sciencemag.org SCIENCE



Research on the identification and taxonomy of forest pests, and novel ways to speed up biodiversity discovery and description (27), should be promoted if we hope to deal with pest problems in the future. Ideally, such efforts will be integrated with the similar needs for agricultural pests, and even for human disease.

The application of DNA-based technologies to identify forest pests has shown that these organisms often represent cryptic species that are different from those originally thought to be present. For example, the Cryphonectria canker pathogen of Eucalyptus in South Africa was originally treated as being in the same genus as the fungus responsible for the devastating chestnut blight disease, Cryphonectria parasitica. DNA-based technologies, however, very clearly showed that the fungus on Eucalyptus is only distantly related to C. parasitica, and the disease is caused by at least four different species of Chrysoporthe (20). Their correct identification is essential for the selection of resistant Eucalyptus clones described earlier. We easily recognize that the accurate identification of pathogens is crucial to human health and well-being, and it is equally true for the health of forests and forestry. The barcoding and typing technologies that are already available allow for much greater levels of accuracy in disease diagnosis than is currently the case.

Research in molecular genetics, including the development of tools for accelerated breeding (including marker-aided selection and genetic engineering), is already well advanced, and the genomes of the most widely planted forest tree species either have been or are in the process of being sequenced (28, 29). The recent approval of the release of a genetically engineered *Eucalyptus* is an important step toward this end (30). The

application of this technology still faces significant regulatory and technical challenges but seems set to play a major role in the industry soon. In parallel, there are also growing numbers of genome sequences available or being determined for the most important pests of these trees (31). The availability of these genome sequences, as well as the rapid growth of associated phenotypic and other "-omics" data, will make it possible to better understand the biology and diversity of the pests, as well as their interactions with their host trees. The continuous emergence of previously unknown pests complicates these processes and highlights the need for identification of general mechanisms of resistance, as well as the continuing nature of this research.

Semiochemicals, which are naturally occurring chemicals that influence insect behavior, can be powerfully used for the surveillance and suppression of insect pests. This tool is underused in forestry in general, and in planted forests in particular (25), because of a lack of capacity to study the behaviorally active compounds of pest insects and a lack of investment in this promising field. Examining the genomics of forest pests could increase the speed of discovering promising alternatives through reverse chemical ecology (32).

There are many positive examples of biological control of invasive alien insect pests. However, many biological control programs for forest pests have been established on flimsy foundations. Although care is often taken today to avoid nontarget effects, biological control agents are often selected with little insight into possible ecological and evolutionary determinants of their success (23, 33). They can also pose significant risks to native ecosystems through nontarget effects, a fact that is broadly recognized and typically tested for

today. Admittedly, the tools to understand, for example, the genetic diversity of biological control agents were not previously readily available. But these and other tools are widely available today and should become standard practice for the development of biological control programs.

A category of pests that is emerging as important is that arising from adaptation after host shifts, symbiont shifts, or hybridization (4, 5, 8, 34). Pathogens such as Ceratocystis spp. that have become adapted to infect forest trees, and the cossid moths Coruphodema tristis and Chilicomadia valdiviana that have emerged as serious pests of eucalypts in South Africa and Chile, are examples of emerging novel tree pests (34, 35). Earlier we described the diseases caused by P. psidii and Chrysophorthe spp., which also resulted from host jumps from native plants to Eucalyptus. It is particularly important to understand the mechanisms and drivers of these changes, in

light of the threat that these and other similar pests pose to native forests (Fig. 1).

Global versus local solutions

Forest pest problems, not only those relevant to planted forests, inevitably affect most or all areas where a particular tree species occurs. Yet these problems are typically being dealt with in an ad hoc and localized manner in response to local damage (Table 1). There are only a few examples where groups of forest scientists have been assembled to tackle particularly important problems at large scales. The European Union has launched a number of impressive programs in this regard, such as the COST Actions [www.cost. eu/COST_Actions/fps/Actions; see Santini et al. (5) for one of the outcomes related to invasive forest pathogens], to develop the networks necessary for a more coordinated approach to key problems.

The only means by which we can realistically deal with tree pests will be through the establishment of global networks of collaboration and to share locally available knowledge [see (22), on biological control). The structures for such networks exist in the International Union of Forest Research Organizations (www.iufro.org), for example, but funding instruments to enable a truly global approach are nonexistent for tree pests. Thus, the time is right to raise the issue of forest pest problems to the level of the United Nations—for instance, via the United Nations Forum on Forests (UNFF; www.un.org/esa/forests/)—and thus to seek intergovernmental support for a serious problem of global relevance.

Although most forest researchers would agree readily that global research collaborations hold the key to improving a clearly inadequate

capacity to deal with tree pest problems (not exclusive to managed and planted forests), answering the "who pays" question is much more challenging (36). Various models are in operation, but the answer most likely lies in collaborations between governments and the commercial sector. They would need to jointly take responsibility for preparedness and for the consequences of incursions, such as in the Government Industry Agreement for Biosecurity Readiness and Response in New Zealand (www.gia.org.nz/) or the Tree Protection Cooperative Program that has been jointly funded by the South African commercial sector, government, and university system for over 25 years. At present, however, it is clear that tree pest problems are made worse by the lack of clear global objectives, priorities, funding, and collaboration. This needs to be addressed, and externally supported where necessary, in developed and lessdeveloped countries, because the overall goal will depend on a more uniform participation.

Outlook

The future of planted forests will be influenced by our ability to respond to damaging pests and the threat of biological invasions. The trends are clear, with at best a constant suite of emerging pests and sometimes a dramatically increasing rate of pest impacts. Increasing numbers of damaging hybrid genotypes and abiotic influences linked to global changes in the environment are further increasing the impact of these pests (4). It would be naïve to believe that local solutions such as quarantine at national borders can present a complete barrier to the global impact of pests on forests. For this reason, much greater focus will need to be placed on global strategies aimed at reducing pest movement and improving pest surveillance and incursion response, as well as optimizing the use of the most powerful tools to mitigate damage.

Genetics offers many outstanding opportunities to mitigate damage from pests, either alien invasive or native and that have undergone some form of adaptation. For managed forests and especially plantation forestry, traditional selection and breeding of species, provenances, clones, and clonal hybrids will increase in importance even further. Beyond this point, genetic engineering with genes conferring resistance to pests will be a valuable additional tool. Such genetic modification is already well advanced for Eucalyptus and poplar. They will also need to be managed with care, as has been true in agriculture, so as to avoid the development of resistance. The rapid decrease in the cost of generating relevant -omics data for nonmodel species, as well as inexpensive tools for gene editing such as CRISPR, will make these technologies available for more plant species sooner than previously anticipated (37). There are, however, valid concerns beyond the management of resistance that will require efficient platforms where the research community and various other societal interest groups can discuss the use of these technologies and collectively inform their regulation.

Pest problems in forests are well recognized and of considerable concern in many parts of

the world, but this is not balanced with the investment that would be required to make a significant difference. This is a situation that should change, but funding and coordinated efforts from across a variety of disciplines and institutions would be needed to make this possible. For example, all the tools and much of the knowledge exist to develop an international database on the diversity of insects and fungi associated with trees used in plantations [there are various unlinked databases on pests and diseases, and with various levels of accessibility, that could be linked via a central database such as, for example, QBOL: Quarantine organisms Barcode Of Life (www.qbol.org)]. Such a database could be powerfully linked to metadata related to host use, natural enemies, climate, surveillance tools and information, and more.

It is not possible to predict which tree pest problems are likely to be most important and damaging in the future. The so-called unknown unknowns and black swan diseases will remain a challenge (35). The appearance of new pests can still surprise local industries and governments, and responses are often erratic and inadequate. Through a more coordinated global investment in relevant research, it should be possible to respond more rapidly and mitigate problems more effectively in the future. There are also increasing opportunities to capture the imagination and support of the public, to create awareness, and to expand the capacity for surveillance beyond the limited number of specialists, through the implementation of citizen science and crowdsourcing mechanisms.

Bill Gates recently called for new thinking about global systems to deal with human infectious disease problems in order to avoid a global health disaster (38). Although the situations for tree pests and human disease are not fully comparable, there are many similarities. Tree health specialists as well as funding agencies concerned with global tree health should learn from these. In particular, it should be recognized that although the impact of tree health disasters is experienced locally, the drivers of their emergence are global. This makes uncoordinated local efforts to slow the overall emergence all but futile. Our capacity to deal with serious tree pest problems will remain minimal unless we can find the support and vision to launch a more global and holistic approach to study these problems and to implement mitigation strategies.

A global strategy for dealing with pests in planted forests is urgently needed and should include:

- A clearly identified body with the mandate to coordinate and raise funds for global responses to key pests and to monitor compliance with regulations.
- · A central database on pests and diseases of key forest plantation species.
- · Shared information on tools for and information from the surveillance of pests and pathogens in planted forests.
- · Identification of measures with potentially high global impact for pest mitigation, and support for the development and sharing of capacity.

- · More-structured systems for facilitating biological control, including global sharing of knowledge, best practices, and the selection of agents (organisms).
- · Protection of the genetic resources of the key forest plantation genera.

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