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Pest Risk Analysis and Invasion Pathways for Plant Pathogens[†]

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Summary

Examples of the accidental introduction of pathogens are commonplace. When released from hosts and habitats where they have co-evolved over millennia, some pathogens have proved to be highly invasive and extremely damaging to many plant species, including long-lived woody perennials such as trees. Opportunities for such introductions have grown hugely in recent decades with the vast increase in global trade, particularly the trade in living plants and timber products, as well as through the international movement of people. Although most introduced organisms are unlikely to establish when transferred to new regions, the potential for damage is large if they do and the impact on habitats and ecosystems is long term and usually irreversible. Our challenge is to understand and predict the likelihood of invasive behaviour, and to manage the pathways along which these organisms move to prevent their arrival at new destinations.

Management of the risk posed by exotic pathogens is embedded in plant health regulations, which have their basis in the International Plant Protection Convention and the World Trade Organisation Sanitary and Phytosanitary Standards. The tool for assessing risk - the Pest Risk Analysis - is initiated if a pathway is identified as a potential pest hazard, or if phytosanitary policy is revised, but most often when an organism is recognised as a potential threat. Unfortunately this is usually only when a severe disease problem becomes apparent elsewhere, because of a newly escaped or emerging pathogen. Therefore, Pest Risk Analyses tend to be reactive, applied to named taxa, and assume that species are relatively homogeneous and genetically stable. With short generation times, this may be a critical over simplification for pathogens especially as introducing these organisms to new environments and hosts exposes them to episodic selection which drives genetic change and adaptation.

Once an organism is identified as a significant threat, biosecurity measures rely on treatments to destroy it such as kiln drying or pasteurisation, as well as inspection to detect it. Drawbacks in this ‘pest-by-pest’ regulation, with its reliance on inspection to intercept potentially damaging pathogens, are probably greatest with the global trade in live plants. To combat this, the International Union of Forestry Research Organisations Working Party on Alien Invasive Species and International Trade recently suggested focussing regulation and management on pathways rather than on specific individual pests. This entails placing emphasis on detecting pests at the origin of pathways, coupled with better understanding of what potential

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pests and pathogens might already occur there. However, although the global trade in plants and wood undoubtedly presents high risk pathways, other potential routes are often ignored or considered too difficult or sensitive to regulate. Better education about all these risks, plus new approaches to biosecurity, are needed if we are to avoid more destruction of our forests and natural ecosystems as a result of introduced pathogens.

Keywords: systemic induced resistance; systemic acquired resistance; plant defence theory; resistance mechanisms; cross effects.

Introduction

Examples of the accidental introduction of plant pathogens have been documented for well over a 100 years and undoubtedly some of these events have had very serious impacts on the economies of affected regions. One of the earliest and probably best known is the Great Famine in Ireland during the 1840s - a natural catastrophe of extraordinary magnitude which followed after the introduction of *Phytophthora infestans* (Mont.) De Bary, the causal agent of potato blight. Disease caused by this pathogen robbed more than one-third of the population in Ireland of their usual means of subsistence for several years in a row, and resulted in many dying of starvation as well as mass migration. Since then, introductions of plant pathogens around the world affecting other staple food-crop plants such as wheat, rice and maize, have been reported in some detail not least because of the resultant economic and social consequences (Levetin & McMahon, 2002). However, during the twentieth century several pathogens have emerged which have proved to be extremely harmful to wild or naturalised plant species including long-lived woody perennial species such as trees (Despres-Loustau et al., 2007). In these instances, the threat they pose is not just economic but environmental, and the resulting damage is frequently long term and irreversible.

Combating introduced pathogens in natural environments raises particular challenges. The intrinsic heterogeneity embodied in plant communities, be they native woodlands, man-made conifer plantations or urban forests, makes it difficult to detect introductions at an early stage or predict the long term outcome. Only decades later may the full environmental impact develop and become apparent. Some pathogens recognised as highly damaging to trees (mainly in the Northern Hemisphere) are listed in Table 1, and two features emerge from the literature surrounding them. Firstly, most have been serially, and sometimes repeatedly, introduced into new bio-geographical zones following their initial discovery. Secondly, these repeat introductions all too often result from man's activities, moving infested plants, seeds, or some form of timber around the world, consequently bringing non-native pathogens into contact with new hosts and ecosystems.

A well documented example of repeated introductions around the globe is provided by chestnut blight caused by the fungal pathogen, *Cryphonectria parasitica* (Murrill) M.E. Barr. This disease was first detected in New York City in 1904 (Merkel, 1905) and over the next 50 years it spread rapidly throughout the range of the American chestnut (*Castanea dentata* (Marchall) Borkh.) leading to its virtual elimination. The pathogen is now considered to have come from Japan on infected nursery stock of Japanese chestnut trees, and was probably brought into North America in the 1880s (Anagnostakis, 1997; Milgroom & Cortesi, 2004). *Cryphonectria parasitica* was next reported in Italy in the 1930s (Biraghi, 1950), apparently transferred from America on tree breeding stock. A similar story unfolded as it spread rapidly throughout much of the chestnut growing region of Europe, and today it is present in most European countries as well as in parts of north Africa (Smith et al., 1992; Robin & Heiniger, 2001). In 2001, the same pathogen was detected in the Australian Quarantine and Inspection Service (AQIS) Post Entry Quarantine facility in Victoria, Australia, following the development of symptoms on material held in quarantine for more than 16 months (Cunningham & Pascoe, 2003). Although in the latter case introduction was averted, it serves as testament to the difficulty of controlling the movement of even well recognised and controlled quarantine organisms.

Another striking feature of such highly damaging introduced pathogens is that, with few exceptions, their origins remain largely a matter of speculation, although Asia is often cited as a possible source because of the acknowledged plant diversity in this region. Even for pathogens as well known as *Dothistroma septosporum* (Dorog.) M. Morelet (= *Mycosphaerella pini* Rostr., the cause of red band needle blight on pines) or *Ophisotoma ulmi* (Buisman) Nanff./*Ophiostoma novo-ulmi* Brasier (Dutch elm disease), it has not proved possible to identify their origins definitively. This fact serves to emphasise our still often rudimentary understanding about pathways for pathogen movement and our ignorance about the extent of the threats posed by, as yet, unknown pathogens.

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TABLE 1: Examples of damaging pathogen introductions repeated across continents

Disease/pathogen	**Known or likely pathway for introductions**	**Possible geographical origin**	**Earliest Citations**
Cinnamomi root rot *Phytophthora cinnamomi* Rands	Live plants 1800s to 1900s	South west Pacific	Europe: Day, 1938 North America: White, 1937 Australasia: Podger et al., 1965
White pine blister rust *Cronartium ribicola* J.C. Fisch.	Live plants 1900s	Asia	Europe: Fries, 1815 North America: Spaulding, 1909
Chestnut blight *Cryphonectria parasitica* (Murrill) M.E. Barr	Chestnut plants, wood 1880s	Japan, China, Korea	North America: Merkel, 1905 Europe: Biraghi, 1950
Dutch elm disease *Ophiostoma ulmi* (Buisman) Nanff.	Elm logs 1900s to 1940s	Eastern Asia	Europe: Guyot, 1921, North America: May, 1934, Asia: Afsharpour & Adeli, 1974
Port Orford cedar root rot *Phytophthora lateralis* Tucker & Milbrath	Live plants 1920s	Taiwan, China, Japan	North America: Tucker & Milbrath, 1942 Europe: Meffert, 2006
Canker stain *Ceratocystis plantani* (J.M. Walter) Engelbr. & T.C. Harr.	Wood packaging and plants 1940s	North America	North America: Jackson & Sleeth, 1935 Europe: Panconesi, 1972
Red band needle blight, Dothistroma blight *Dothstroma septosporum* (Dorog.) M. Morelet	Live plants 1940s	Himalayas or South America	Europe: Murray & Batko, 1962 Africa: Gibson, 1962, South America: Dubin & Staley, 1966, Australasia: Gilmour, 1967
Dutch elm disease *Ophiostoma novo-ulmi* Brasier	Elm logs 1960s	Eastern Asia	Europe: Gibbs et al., 1972 Asia: Brasier & Afsharpour, 1979 Australasia: Cooper, 1991
Alder disease *Phytopthora alni* Brasier & S.A. Kirk	Live plants 1970s to 1990s	Interspecific hybridation event	Europe: Brasier et al., 1995 North America: Adams et al., 2008
Sudden oak death *Phytophthora ramorum* Werres, De Cock, & Man in t'Veld	Live plants 1990s	Eastern Asia	Europe: Werres et al., 2002 North America: Garbelotto et al., 2001 North America: Hepting & Roth, 1946
Pitch canker *Fusarium circinatum* Nirenberg & O'Donnell	Seeds, live plants	Mexico	Asia (Japan): Muramoto & Dwinell, 1990 Africa: Viljoen et al., 1994, South America: Wingfield et al., 2002, Europe: Lander et al., 2008, Asia: Durgapal, 1971
Horse chestnut bleeding canker *Pseudomonas syringae* pv *aesculi* (ex Durgapal & Singh) Young, Bradbury et al.	Possibly live plants 1990s	Himalayas	Europe: Webber et al., 2008
Kernoviae dieback *Phytophthora kernoviae* Brasier, Beales & S.A. Kirk	Live plants 1990s	Asia, or possibly New Zealand	Australasia: McAlonan, 1970 Europe: Brasier et al., 2005

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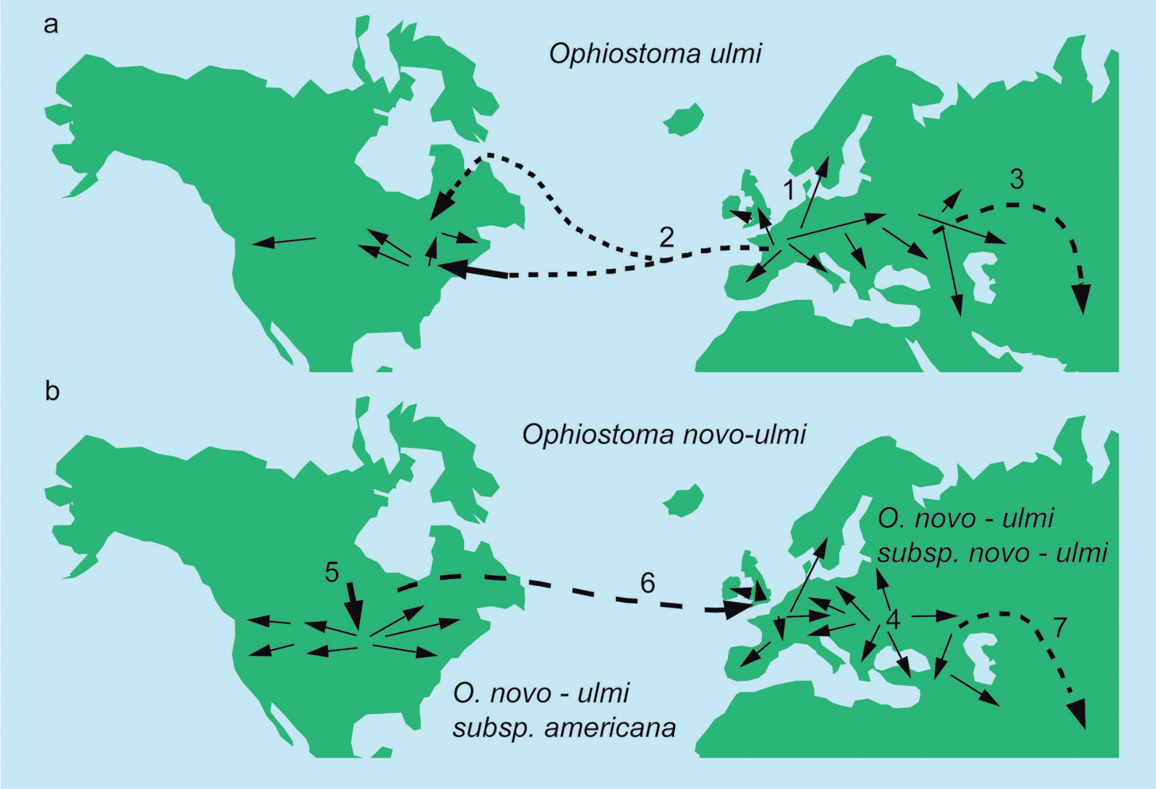

FIGURE 1: Spread of *Ophiostoma ulmi* and *O. novo-ulmi* during the first and second pandemics of Dutch elm disease (taken from Brasier et al., 2004a). Solid arrows indicate natural migration from probable sites of introduction; dashed arrows indicate subsequent spread via importation/timber movement.

(a) Spread of *O. ulmi* following the first appearance in western Europe in around 1910 (1); the introduction to North America in the1920s (2); introduction from Krasnodar to Tashkent in the late 1930s (3).

(b) Spread of the two subspecies of *O. novo-ulmi*. Original centres of appearance of subspecies *novo-ulmi* and *americana* in Romania-Moldova (4) and southern Great Lakes region (5), respectively; introduction of subsp americana from Toronto area into Britain around 1960 (6); introduction of subsp *novo-ulmi* into the Tashkent area in the 1970s (7).

Invasive pathogens

Introduced pathogens capable of causing damage to the environment are often described as 'alien invasive species'. The Convention on Biological Diversity (CBD, adopted in 1992) highlights the threat that such aliens pose to plants and to biodiversity, as well as to ecosystem function (CBD, 2002). Typically, invasive micro-organisms are highly mobile and show evidence of changing and evolving once they are in a new environment. In many instances, they are also classified as quarantine pests – organisms that are already present and damaging in one region and therefore subject to plant health controls to prevent their international spread and introduction into endangered areas.

The devastation that can be caused by alien invasive plant pathogens to natural ecosystems is well illustrated by the two pandemics of Dutch elm disease that have occurred over the past 100 years. The combined actions of two pathogens, *Ophiostoma ulmi* (responsible for the first pandemic from the early 1900s) and *Ophiostoma novo-ulmi* (first detected in the late 1960s and the cause of the second pandemic) have destroyed millions, probably billions, of elms across Europe, Asia and North America; even the Southern Hemisphere has not been left untouched as the disease was reported in New Zealand in 1989 (Cooper, 1991). Again, the history of this disease tells a story of serial introductions across the globe (Figure 1), usually via logs infested with one of the species of bark beetle vectors that spread Dutch elm disease. Moreover, the appearance of the new highly aggressive Dutch elm disease pathogen (*O. novo-ulmi*) initially went undetected because of the masking presence of *O. ulmi* in both Europe and North America. Even today, almost a 100 years after the disease was first identified, the impact is clearly visible on the landscape in many parts of the world.

In an analysis of the most frequently cited drivers of emerging fungal diseases injurious to plants, Anderson et al. (2004) identified three factors as important: (i) pathogen pollution (ie introduction); (ii) changes in cultivation techniques; and (iii) changes in weather. This paper focuses on the first of these factors. It is widely acknowledged that the opportunities for introduction have grown hugely in recent decades as the increase and diversity in free trade has never been greater, particularly the trade in living plants and timber products. Growing affluence and disposable income mean that consumers can demand food and plants from all over the world, whilst markets continually look for new products and more cost-effective production methods. At an individual level, the international movement of people has also greatly increased. Despite this, hard evidence is still lacking that correlates the effect of growing global trade with increasing numbers of successful pathogen introductions (Jones & Baker, 2007). Perhaps this is because some of these introductions are, in fact, re-introductions and go unrecorded, but also because what we see now may have resulted from earlier trade activity and we have yet to see the outcome of the current and expanding scale of global trade. If, as Waage et al. (2005) predict, many invasives that escape into the natural environment are initially very slow spreading, then years may elapse before their detection, while associated losses to biodiversity or ecosystem services only start to occur by the time pathogen populations have reached high densities and are beyond control measures. This also raises the question of how long the lag phase is for different pathogens following initial introduction, a critical issue when it comes to understanding how long they are likely to remain below the radar of surveillance. If the true time period between the introduction event and the first report is unknown, tracing the source of the outbreak may never be possible.

Allied to the process of introduction, a range of other factors can play a part in promoting invasive behaviour. Once removed from native ecosystems, pathogens escape from stabilising selection (Brasier, 1986) and are instead exposed to new environments and hosts. If hosts have not co-evolved with the pathogen (sometimes referred to as naive host populations) then they are less likely to have resistance mechanisms to combat the new threat. Association with a vector – and this can include man – can also be highly effective at moving pathogens over long distances and promoting invasive behaviour. Some insect-vectored pathogens have proved to be highly adaptable and able to transfer to other insect vectors that are available in a new environment, sometimes with devastating results. For example, when rock elm (*Ulmus thomasii* Sarg.) logs from Canada infected with *O. novo-umi* were imported into Britain, they also contained the North American bark beetle *Hylurgopinus rufipes* Eichhoff (Brasier & Gibbs, 1973). However, although this vector species was effective in transferring the aggressive elm pathogen to nearby elms it failed to establish itself. In contrast, *O. novo-ulmi* established quickly as it linked into the life cycle of native scolytid vectors and ultimately eliminated *O. ulmi* from elm habitats (Brasier, 1983).

A move to a new environment almost inevitably means being subject to extreme levels of disturbance; the likely outcome is episodic selection which drives genetic change and adaptation in fungal species (Brasier, 1986). Indeed, without change, extinction is the likely outcome for most newly introduced pathogens, and founder populations may fail to survive because of limited genetic diversity or if they comprise just a single mating type or even a single clone. Once again Dutch elm disease has provided a blueprint for how introduction can be the starting point of far reaching genetic changes in a pathogen (Brasier, 1991). Evidence indicates that *O. novo-ulmi* arose from an introduction into North America, but as a quite separate episode from the 1920s' introduction of *O. ulmi* from Europe (see Figure 1). Since then, episodes of hybridisation and genetic introgression between *O. ulmi and O. novo-ulmi* have created the North American subspecies (*O. novo-ulmi* subsp. *americana* Brasier & S.A.Kirk), and it is this new form of *O. novo-ulmi* which has effectively eradicated most mature elms from many western European countries. In eastern Europe and central Asia, another genetically distinct Eurasian subspecies of *O. novo-ulmi* (subsp. *novo-ulmi americana* Brasier & S.A.Kirk) has caused similar levels of damage. This Eurasian sub-species was probably the second Dutch elm disease pathogen to be introduced into North America, and in this genetic melting pot it eventually gave rise to *O. novo-ulmi* subsp. *americana*. As *O. novo-ulmi* has migrated across the Northern Hemisphere in the past 30-40 years, it has replaced *O. ulmi*, leading to its virtual extinction. Not surprisingly given this history of rapid evolution, the two *O. novo-ulmi* subspecies have started their own process of hybridisation and genetic exchange in the regions of Europe where they now overlap, underlining once again the genetic flexibility and dangerous potential of some invasive pathogens (Brasier & Kirk, 2009).

Insights from such studies provide a valuable framework for identifying the factors that interact together to make some introduced fungal pathogens capable of causing long term damage to trees. Increasingly, climate change is likely to add to the disturbance which drives genetic change, but predicting its effect on any introduced organism is likely to be a complex task because of the uncertainties in climate models and the complex interactions and feedbacks that are innate to all ecosystems.

Managing the risk of introductions

Responding to concern about the spread of plant diseases, the World Trade Organisation (Sanitary and Phytosanitary Standards agreement) first put international regulations in place in the 1950s to reduce the risk of accidental introductions of harmful organisms (World Trade Organisation, 1995). The agreement requires member states to have phytosanitary measures in place that are based on an assessment of risk to plant health. The context of national Plant Health Regulations also influences the approach to managing the threat from exotic pathogens. For some countries or trading blocs the focus is on 'known risks' – pathogens that already have a proven track record as damaging agents and are therefore listed and regulated to minimise the likelihood of introduction and spread. Inclusion of organisms onto the list must be based on 'sound science'. However, this also means that organisms that are not listed remain unregulated. In contrast, a precautionary approach is adopted by other countries, which effectively means that any introduced organism is regarded as potentially harmful until proved otherwise.

Pest Risk Analysis

Assessing risk, undertaken as Pest Risk Analysis (PRA), evaluates the probability and potential impact of a plant health risk and operates within the framework of relevant International Standards for Phytosanitary Measures (ISPM) developed under the International Plant Protection Convention (IPPC). The methodology for PRA is not prescriptive and both quantitative and qualitative approaches are valid (Food & Agriculture Organisation, 2004; Vose, 2008), although lack of data often limits quantitative methods. Over the past decade the process of pest risk analysis has become increasingly sophisticated, and techniques such as Geographic Information Systems (GIS), environmental and climatic modelling, economic analysis and pathways analysis are used to make it more powerful.

International Standards for Phytosanitary Measures (ISPM) number 11 (Food & Agriculture Organisation, 2004) gives three main initiation points for a PRA: (i) when an organism is recognised as a new or potential threat; (ii) if a particular pathway identified as high risk; or (iii) if there are changes or revisions to phytosanitary policy. For pathogens, PRAs are invoked most commonly as a result of evidence-gathering and horizon-scanning. These two approaches identify plant health risks when major disease episodes become apparent somewhere in the world, mainly as a result of introduction and invasive spread. Typically, a PRA will include information on the identity of the pest organism, hosts (known/potential), likely pathways, associated risk, as well as exclusion and management options for eradication. Recent examples of tree pathogen threats that have spawned PRAs from several countries include sudden oak death (*Phytophthora ramorum* Werres, De Cock & Man in 't Veld), pitch canker (*Fusarium circinatum* Nirenberg & O'Donnell), and Port Orford cedar root rot (*Phytophthora lateralis* Tucker & Milbrath) (e.g. Sansford, 2009). Increasingly, however, the high risk associated with particular pathways is being acknowledged and evaluated using PRA, when a pathway is defined as any means that allows entry or spread of a pest (Food & Agriculture Organisation, 2007). Spread of Dutch elm disease from continent to continent highlighted the dangers of logs and timber as a pathway, particularly for insects or insect vectored pathogens. Wood packaging material that frequently accompanies non-wood imports has also proved to be another high-risk pathway and consequently international regulations (ISPM number 15) now require its treatment before export to eliminate any associated pests (Food & Agriculture Organisation, 2002).

Weaknesses in PRA

Pest Risk Analyses have a structured and logical approach to evaluating risk and undoubtedly are useful in pinpointing what additional research is needed when an emerging pathogen threat is identified, but they also have weaknesses. These include the tendency for PRAs to be focused on named pests associated with defined hosts, and to be defensive and reactive once a threat has emerged but not able to anticipate new threats such as those posed by as yet unknown pathogens.

In taking a 'pest-by-pest' approach, PRAs and Plant Heath Regulations also often assume that the pest, identified at the species level, is a relatively homogeneous and genetically stable organism. This can be a critical oversimplification when it comes to micro-organisms with short generation times that can promote rapid genetic change. Unfortunately, acknowledging this complexity raises a huge regulatory problem, as it means that risk analysis and regulation at only the species level may often be insufficient. Thus, even if an introduced pathogen has breached biosecurity measures and the species is now considered to have established in a new region, there may still be strong arguments to keep measures in place that prevent further introductions. This is because arrival of new genotypes may not only create a significantly increased risk to an environment but an increased risk of genetic exchange and adaptation. There are also a growing number of instances where a single species of pathogen may comprise more than one taxon which, singly or in combination, pose differing threats (Brasier, 2008). Recently, for example, it has emerged that *Phytophthora ramorum* (cause of sudden oak death) consists of three genetically distinct lineages – two now present in North America, the other in Europe. These lineages apparently diverged in their native habitat thousands of years ago, and were sufficiently isolated from each other to allow independent evolution prior to introduction to North America and Europe (Goss et al., 2009). Because of the genetic differences between the lineages and the likely isolation which has allowed this divergence, there are strong biosecurity reasons to recognise and regulate these different entities to prevent their intermixing. It also suggests that pathways for the introduction of this pathogen into Europe and North America have included more than one geographical origin. A somewhat similar situation exists for the alder phytophthora, *Phytophthora alni*

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Brasier & S.A.Kirk, although this species has arisen through a process of interspecific hybridisation and consists of several heteroploid taxa, now named at the level of subspecies (Brasier et al., 1999; 2004). The most common hybrid type or subspecies is *P. alni* subsp. *alni* which is the most pathogenic subspecies and present throughout much of Europe, apparently spread on alder plants infected in nurseries (Jung & Blaschke, 2004). The other hybrid types are collectively known as *P. alni* subsp. *uniformis* Brasier & S.A.Kirk and subsp. *multiformis* Brasier & S.A.Kirk, and have a much more limited distribution, although recent reports indicate that *P. alni* subsp *uniformis* has now been recorded on a number of occasions in the USA – several times in Alaska and possibly also from a nursery in Michigan (Schwingle et al., 2007; Adams et al., 2008). As before, this raises the issue of regulating distinctly different taxa classified as the same species, but also understanding the circumstances that have lead to their occurrence on at least two continents.

Lack of PRA

Despite being identified as potential threats many pathogens are not subject to risk analysis. This can simply be due to a lack of resources to undertake PRA, but often it is due to the lack of information about a pathogen despite evidence that it is capable of causing very significant damage. One such current example is the disease 'daño foliar del pino' of *Pinus radiata* D.Don caused by *Phytophthora pinifolia* Alv. Durán, Gryzenh. & M.J.Wingf. (Durán et al., 2008).

Challenge of regulating known threats

Current plant health measures still rely heavily on visual inspection to pick up symptoms or other tell-tale signs as the first step in the interception of known quarantine pests infecting plants or wood products. Modern molecular diagnostic methods undoubtedly help in this process as highly sensitive tools for the rapid and accurate detection of potential pathogens, but again identification is geared to detecting known and listed pathogens. Despite this, effective inspection is probably becoming untenable because of the sheer quantity and range of imported products from around the globe. Living plants (often referred to as 'plants for planting') and potentially any associated pests and pathogens, are traded around the world from increasingly exotic locations. The demand for plants and thus the extent of the trade has grown hugely since the World Trade Organisation regulations were originally framed in the 1950s to prevent pathogen movement via this route. Single consignments can now consist of several thousand plants, and it is not unusual to trade plants the size of specimen trees (5-10 m tall) with intact roots and associated soil presenting, in essence, a small ecosystem in its own right. Inspecting this type of commodity in any meaningful way to detect the presence of known pathogens, quite apart from any unknown threats, presents a huge and probably impossible challenge.

Certain pathogens such as species of *Phytophthora* are particularly well-suited to moving along the live plant pathway. This genus includes species that are notable for the damage they cause to trees and associated ecosystems (see Table 1) and many new taxa have been discovered in the last ten years (Brasier, 2009). Soilborne species which often attack roots, may be present but in cryptic form, sometimes as resting propagules such as oospores or chlamydospores, so that even the soil associated with non-host plants can be contaminated and act as a carrier. Use of fungicides of the type commonly deployed in nurseries where plants are propagated and grown-on may add to the problem by suppressing symptoms but not necessarily eliminating the pathogen. More recently it has become apparent that the aerially infecting phytophthoras, *P. ramorum* and *P. kernoviae* Brasier, Beales & S.A.Kirk, can also infect foliage without inciting symptom development at least for a period of time and can even sporulate on infected but asymptomatic tissue (Denman et al., 2009). These features of cryptic or asymptomatic infection and non-host carriers further increase the difficulty of using inspection to detect and intercept known plant pathogens.

Change in approach – regulate pathways

With the realisation in the 1970s and 1980s that various wood products (particularly untreated logs or timber) presented high risk pathways, measures were developed to counter the threats associated with known pests. These included identifying tree species as particularly at risk of harbouring specified pests and pathogens, but also heat and chemical treatments capable of eliminating a wide range of pests. More recently it has been acknowledged that unregulated Wood Packaging Material (WPM) presents a similarly high risk pathway, hence the development of ISPM 15 (Food & Agriculture Organisation, 2002). Although this international standard addresses the risks associated with known pests and specifies certain treatments, it assumes that many unknown pests can be eliminated by the same treatments, providing the application of measures has fully met those specified in the international standard. This approach has marked a turning point, as ISPM 15 imposes measures aimed not only against known pests but also against unknown pests. It therefore regulates the pathway and not just named and listed pests or hosts.

The growing awareness that the trade in living plants has provided just as many if not more introductions of pests as WPM and is clearly a pathway of very high risk (cf. Brasier, 2008 and Table 1) highlights the need to regulate the pathway and not just individual pests. The difficulties associated with inspection and detection aimed at particular pests and pathogens mentioned earlier, just serves to emphasise the need for a changed approach which applies regulation to the pathway instead of known, listed organisms.

In recognition of this, a fundamental review of the 'plants for planting' pathway and how it could be regulated to reduce the risk it presents is now being addressed by a number of organisations, including the United States Department of Agriculture Animal and Plant Health Inspection Service (APHIS), the International Plant Protection Convention (IPPC) and the International Union of Forestry Research Organisations (IUFRO) (Unit 7.03.12 – Alien Invasive Species) (APHIS, 2005). However, regulating the pathway for live plants will require much more fundamental changes to be put in place compared with regulating timber or WPM pathways. Radical changes in practices are likely to be required from both importing and exporting countries. This could include pre-certification programmes by importing countries, whilst exporting places of production could develop controls such as only propagating from certified stock, effective diagnostic procedures, inspections at growing sites and clean packing practices. Appropriate quarantine procedures to prevent entry and establishment of plant pests could include inspection at the border, supplemented by quarantine periods of sufficient length to allow disease symptoms to develop on the plants so that unwanted pathogens can be detected. It still remains a huge challenge to detect cryptic pathogens that are present but not expressed on infected or carrier plants.

Greater knowledge of organisms that are innocuous and often go largely unnoticed in countries of production, but have potential to become significant pathogens when exposed to new host populations could also be explored through the use of sentinel plants. The impact of native pathogens on the non-native sentinel plantings put into areas of production in exporting countries could flag up species likely to cause damage if they were transposed to importing countries (Fagan et al., 2008). Another version of sentinel plant strategy is to harness the resources of botanic gardens and arboreta around the world with their stock of non-native plants, as a global plant network to share information about pests on non-native host plants (Britton et al., 2009). Such a scheme could provide valuable data about unknown pathogen threats, although it may be most effective at flagging up certain types of organisms such as foliar pathogens. Slow acting, long-lived pathogens with an extended cryptic phase such as root rot fungi, probably need another approach.

Although the global trades in plants and wood are undoubtedly the highest risk pathways for pests and pathogens, other routes are probably often underestimated. It is still permitted for individuals with an interest in plants to legally import a small number of plants within the EuroMed region, while plant hunters still travel the world looking for undiscovered or novel plants. There is an irony that these activities could ultimately introduce new pathogens that then threaten the specialist collections and historic gardens built from the expeditions of much earlier plant hunters such as Wilson and Forrest. Even the soil on hikers' boots can sometimes carry propagules of invasive and damaging pathogens - particularly phytophthoras (Cushman & Meentemeyer, 2008; Webber & Rose, 2008), although this pathway is usually considered too difficult or sensitive to regulate. However, the question is can we afford not to regulate this pathway when it can have far reaching consequences? Pathogen spread via this route has endangered the recently discovered Wollemi pine (*Wollemia nobilis* W.G.Jones, K.D.Hill & J.M.Allen) (Benson, 2000; NSW - Department of Environment and Conservation, 2007). Long isolated and undisturbed in a remote habitat in eastern Australia, this unique species is now under threat from *P. cinnamomi* Rands which appears to have been brought into this habitat by hikers.

Conclusions

In general, there continues to be a lack of awareness of how invasive pathogens emerge and spread into new environments among the sectors and trades that routinely work with plants, such as horticulturists, foresters and conservationists. It is also easy to become complacent if a recently arrived pathogen appears to cause little damage, and to assume that this status will continue indefinitely. Often it can be decades after an introduction before the scale of the threat posed by an invasive pathogen becomes apparent, or before it is possible to predict the long term impact on habitats or ecosystems. Limited resources for risk analysis of each known pest, quite apart from the many that have yet to appear, also highlight the need to focus on pathways and the types of pathogens associated with different pathways so we can better anticipate possible risks and impacts on this basis.

Unfortunately, the plant trade not only provides pathways for the entry of new organisms but unwittingly may also provide the ideal conditions for pathogen change. The close proximity and mixing of plants and pathogens in nurseries, sometimes from very different bio-geographical regions, can allow previously separated but related pathogen species to hybridise, offering opportunities for rapid evolution and the emergence of entirely new and destructive pathogens (Brasier, 2001; Webber & Brasier, 2005). Education to increase awareness of these risks as well as new approaches to biosecurity measures are vital if we are to counter the loss of biodiversity and degradation of forests and other natural ecosystems as a result of introduced pathogens. We clearly need to prevent pests and pathogens from entering new habitats, but this is best achieved if they never leave their native range. Thus, for biosecurity measures to be most effective, a two-way process is needed – this means greater awareness and counter measures at the pathway origin to prevent the accidental export of pests as well as effective measures to intercept any hitch-hiker pests on their arrival.

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