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Invasion by Exotic Forest Pests: A Threat to Forest Ecosystems

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Invasion by Exotic Forest Pests: A Threat to Forest Ecosystems

ABSTRACT For millions of years the distribution of the world's biota has been restricted by oceans and other natural barriers. During the last 100 years, human activities, especially international travel and trade, have circumvented these barriers and species are invading new continents at an increasing rate. Biological invasions of insect, plants, and fungal pest species often cause substantial disturbance to forest ecosystems and as well as severe socioeconomic impacts. The invasion process is composed of three phases: arrival, establishment, and spread. Arrival occurs when a species is initially transported to the new area (e.g. transportation to a new continent). Establishment is essentially the opposite of extinction; it is the process by which a population becomes abundant enough to prevent extinction. Spread is the process by which a species expands its range into adjoining uninfested areas. Management of pest invasions focuses on preventing arrival, establishment, or spread. We present case histories that illustrate the invasion process via details of the arrival, spread, impact, and management of selected exotic forest pests. Biological invasions are probably the most significant environmental threat to the maintenance of natural forest ecosystems in North America and elsewhere. The magnitude of this problem necessitates increased efforts to reduce the incidence and impacts of pest invasions.

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The term *biological invasion* connotes the expansion of a species' geographic range into new areas. The paleontological record indicates that species ranges are not static but instead are in constant flux. Technological advances have greatly increased the incidence of invasions over the last century via movement of humans and their goods and by disturbance of ecosystems. Most of these invasions have gone largely unnoticed but some have developed into serious pest problems of enormous ecological and economic impact. Pimentel (1986) estimated that 19 of 70 major insect pests of U.S. forests were imported and that the corresponding proportion for forest pathogens may be even greater. In this paper we present an overview of the ecological processes at work during invasions of forest pests and the implications of these invasions to forest management. Histories of the invasion by specific pests are described.

The two determinants of a species' range are the spatial distribution of the habitat (i.e., the geographical range of areas where an available ecological niche exists) and the accessibility of habitats suitable for existing populations. Barriers, such as oceans and mountain ranges, have greatly influenced species divergence and speciation (Mayr 1963). Probably the most important barriers that have facilitated the differentiation of terrestrial species have been the oceans, which have separated the continents since the Cretaceous period. These barriers are relatively impenetrable and permanent obstacles to invasions except during extreme deviations in climate (e.g., the land bridge across the Bering strait). Darwin's (1859) landmark studies on the Galapagos Islands were perhaps the first to demonstrate how geographical isolation results in divergence of disjunct populations and that when species gain access to previously isolated habitats they are often able to exploit unoccupied ecological niches. The field of biogeography has formed more generalized and unified theories about the importance of geographical isolation on speciation and evolutionary change (MacArthur and Wilson 1967). Just as geographical isolation has profoundly affected species ranges, so have changes in the geographical distribution of suitable habitats. The paleontological record indicates that over the past several million years, species ranges have been in constant flux due to temporal variations in climatic conditions. Probably the best records of these dynamic patterns exist for woody tree species which retreated southward from northern latitudes during the ice ages and then spread to the north during periods of interglacial warming (Raven and Axelrod 1977, Huntley and Birks 1983, Davis 1976). During periods of flux in species ranges, geographical barriers have often diminished; movement into new habitats has often resulted in a rapid spread into new areas where ecological resources had previously been largely unexploited. This phenomenon is illustrated by the invasion of humans from Asia into North America over the Bering strait. Thus, many biological invasions are natural phenomena that have been occurring for millions of years, independently of any human activity.

As a result of technological and sociological changes, humans and their material goods are moved around the globe with an ever increasing efficiency and frequency. This movement has precipitated a dramatic increase in biological invasions by transporting organisms past the natural geographic barriers that limited their dispersal. As early as 900 A.D., the range of several European animal and plant species had expanded as a result of human movement (Crosby 1986). The rate of establishment of exotic arthropod species in

North America did not substantially increase until about 1800 but has been accelerating ever since (Fig. 1). Presumably this temporal change reflects the increases in intercontinental mobility that also began around 1800. At present, over 360 exotic insect species and over 20 exotic diseases are known to attack woody plants in the US (Hack and Byler 1993, Mattson et al. 1994)

The increase in introductions of exotic organisms generally has resulted in a substantially greater number of pests. For a variety of reasons, introduced species are more likely to be pests than are native species (Simberloff 1986, di Castri 1989). Pimentel (1986) estimated that of the 70 major insect pests of U.S. forests, 19 were introduced species. This proportion (27%) is slightly less than the proportion of agricultural pests that are exotic (40%) but the impacts of exotic pests on forestry are characteristically severe (Elton 1958, Pimentel 1986). The increasing load of pest species is likely to result in large and long-term impacts on forest ecosystems. Introductions of major forest pests to North America, such as the gypsy moth and the fungi that cause Dutch elm disease and chestnut blight, are examples of introductions that have caused catastrophic tree mortality and in some cases caused the virtual elimination of previously dominant tree species. Thus, the accumulation of biological invasions could be considered an ecological problem comparable in many respects to some of the more well-known contemporary environmental problems such as atmospheric warming and acidic deposition.

Since the time of Elton's seminal book on the topic of biological invasion (Elton 1958), there has been growing attention by ecologists to various aspects of this subject. Out of this work has come a recognition of at least three processes underlying all invasions: arrival, establishment, and spread (Dobson and May 1986). Because of the accelerating frequency and economic importance of invasions, all three phases have recently have been the object of increased study (di Castri et al. 1990, Drake et al. 1989, Hengeveld 1989, Groves & Burdon 1986, Mooney & Drake 1986).

ARRIVAL

Humans have accelerated the natural intercontinental ebb and flow of species in two ways. First, we augmented the natural movement of organisms both by accidental transportation of species (e.g., in the ballast of ships) and by intentional introductions (e.g., introduced agricultural plant species). Simberloff (1986) noted that patterns of species introductions parallel intercontinental commerce patterns (e.g., most introductions to North America have come from Europe). The second way in which we have accelerated the natural rate of biological invasions is by disturbance of habitats. These disturbances do not alter the arrival process but instead may enhance the establishment of certain species.

The gravity of the problems created by biological invasions was not fully realized until the early 1900s. Before then, most governments had a rather *laissez faire* attitude about exotic organisms. For example, faya tree, *Myrica faya*, was repeatedly introduced to the Hawaiian Islands around the turn of the century for the purpose of reforestation (Whiteaker and Gardner 1992). After it was extensively established, it became clear that this species crowds out native species. In 1912, the U.S. Congress enacted the Domestic

Plant Quarantine Act, which gave authority to the U.S. Department of Agriculture (USDA) to regulate the movement of plant and animal material into and within the U.S. (Weber 1930). These regulations have been modified substantially since then. The current federal quarantine measures are designed to decrease invasions by limiting the arrival process and thus represent a first line of defense against invasions.

Over the last 100 years, the shipment of raw and processed wood has greatly increased (Fig. 2). Economically developed countries are typically the largest importers of wood products, and it is likely that the rate of intercontinental flow of wood will greatly increase over the next century (Laarman and Sedjo 1992). Intercontinental movement of wood products has recently been recognized as posing a major risk to importation of many exotic forest pests (USDA Forest Service 1991, 1992, 1993).

ESTABLISHMENT

Every seed that falls to the ground does not develop into a reproducing plant. Similarly, many invaders may arrive in a new habitat, but few become established. Here we define establishment as the process that results in a population that persists for many generations. Founder populations are typically small and consequently are at great risk of extinction. Generally, the smaller the founder population, the less likely is establishment (MacArthur and Wilson 1967). Though many scientists have referred to a "minimum viable population," there is rarely a distinct threshold. Instead it is more realistic to consider the *probability* of establishment as being a continuous function of the initial population size. This function reflects many characteristics of the species, such as its intrinsic rate of reproduction, mate location abilities, and genetic diversity (Mollison 1986).

The dynamics of all animal and plant populations are highly stochastic and typically strongly affected by environmental factors, such as weather. When viewed over small areas, even well-established populations may become locally extinct as a result of stochastic variation. When populations are established over large areas, zones of local extinction are quickly recolonized from adjoining areas. The invading population also may follow the same pattern and become locally extinct, but because its initial distribution is completely isolated, the result is total extinction (Figure 3). It is for this reason that most arrivals of exotics do not result in establishment.

Understanding this process has important implications for management. The activity we call "eradication" is aimed at reversing the process of establishment; eradication is forced extinction. It follows from the above description that eradication is only likely to succeed in situations where the target population is both low in density and highly restricted in its spatial distribution.

SPREAD

Once a population is established, its density will typically increase and it will expand into adjoining areas of suitable habitat. For most biological invasions this spread is the only process that we are able to observe directly, since the arrival and establishment

phases usually occur without notice by humans. For example, the pine shoot beetle, *Tomicus piniperda*, was already established in six states by the time it was discovered (Hack and McCullough 1993).

The spread of a species is driven by two processes: population growth and dispersal. Most models of population spread have therefore focused on these processes. The simplest and probably the most widely applied population spread model was developed by Skellam (1951). This model combined Fick's law of diffusion with an exponential model of population growth.

Fick's law states that the concentration, C , of particles is normally distributed across any dimension, x , and thus the concentration at any point in time after release at point $x = 0$ is described by:

$$C_{x,t} = \frac{M e^{-x^2/4Dt}}{2\sqrt{pDt}} \quad (1)$$

where t is the time since the initial release of M particles at point $x = 0$ and D is the "diffusivity" or "diffusion coefficient" (Okubo 1980). The diffusion coefficient is constant for any class of particles and set of environmental conditions; C is distributed normally at time, t , with a variance of Dt . Fick's law assumes that particles move randomly.

The exponential population growth model describes the concept of unlimited population growth:

$$N_t = N_0 e^{rt} \quad (2)$$

where N_t is the number of individuals at time t and r is the "intrinsic rate of natural increase" (birth rate - death rate under optimal condition; i.e., no crowding) (Varley, et. al. 1973).

Skellam (1951) combined Fick's law of diffusion with the exponential growth model to obtain a generalized model of the spread of an invading organism:

$$N_{x,t} = \frac{N_{00} e^{rt-x^2/4Dt}}{4pDt} \quad (3)$$

where $N_{x,t}$ is the density of organisms distance, x , from the point of release and time, t , from the time of release of $N_{0,0}$ organisms at time 0. The assumption of random movement in this model implies that the population will spread radially, at an equal rate in all directions. Skellam (1951) showed that for any detection threshold, T , such that the infested area at any time t is restricted to points where $N_{x,t} > T$, the expansion velocity of the infested front, V , is constant and can be described:

$$V = 2\sqrt{rD} \quad (4)$$

The above model assumes that r and D are constant through time and space during the period of range expansion of the invading organism, an assumption that does not intuitively seem likely (e.g., spatial variation in the habitat may profoundly affect birth/death functions as well as dispersal rates). Nevertheless there has generally been good congruence between predictions of this model and observed rates of spread of most exotic organisms (Levin 1989, Andow et al. 1990). For example, Long (1979) found that the larch casebearer, *Coleophora laricella*, has been spreading in the northern Rocky mountains at a constant radial rate, as predicted by Skellam's (1951) model.

An invading organism does not always become a pest. There are certain organisms, such as the brown tail moth, *Euproctis chrysorrhoea*, that despite considerable concern over their accidental introduction, never became a serious pest in North America (USDA Forest Service 1985). This phenomenon is also illustrated by the European strain of the scleroderma pathogen, *Gremmeniella abietina*, that was discovered in the Northeastern U.S. in the early 1970's (Setliff et al. 1975). This fungus caused local damage accompanied by great alarm that it would spread throughout the coniferous region of North America. However the fungus never spread well beyond the area of discovery, apparently because of climatic limitations (O'Brien 1984).

There is no question that many invading organisms become serious pests. The lack of evolutionary balance in herbivore-plant relationships may be a major cause of the outbreak dynamics that is common in many invading species (Pimentel 1986, Gibbs & Wainhouse 1986). The extent to which a foreign habitat matches the pre-evolved biology of the invader is a major determinant of the likelihood that the invader will become a pest. For example, the causal agent of Dutch elm disease, *Ophiostoma ulmi*, behaved more aggressively after introduction to North America than it apparently behaved after initial introduction to Europe (Gibbs 1978). This difference in population behavior can be at least partially attributed to differences in the susceptibility of host trees and abundance of vectors.

The ecological and economic impacts of invading forest pests on forest resources are quite similar to those of native pests. Forest pests can have substantial effects on tree growth, mortality, and reproduction. Several exotic forest pests have had spectacular and long-term effects on forest ecosystems. Perhaps the best example of this in North America is the chestnut blight fungus which has resulted in the elimination of American chestnut, *Castanea dentata*, as a dominant species throughout the eastern U.S. and forever change important forest ecosystem processes (Kuhlman 1978).

Invading forest pests can affect uses of forest resources for timber, recreation, wildlife, etc. A good example of the complexity of these impacts is the interaction between grizzly bears (*Ursus arctos horribilis*), whitebark pine (*Pinus albicaulis*), human habituation, and white pine blister rust (*Cronartium ribicola*), an invader. The grizzly bear, like many other mammals, uses whitebark pine seeds because of their high fat content and abundance during pre-hibernation feeding activities. In years of prolific seed crops, bears tend to remain and feed in high elevation areas until hibernation. However, when seed crops are small, they expand their feeding activities with a tendency to range closer to human facilities, which usually results in increased bear mortality and conflicts with humans (Kendall and Arno 1990). White pine blister rust is currently epidemic over most of the range of whitebark pine and is considered the major cause of its reduced seed production, damage, and mortality (Hoff and Hagle 1990). As a result, this disease will undoubtedly greatly reduce densities of several wildlife species, especially the grizzly bear.

Another important aspect of the impacts of invading forest pests to society is their impacts on endangered species or endangered ecosystems. This impact is illustrated by the balsam woolly adelgid, *Adelges piceae*. Feeding by this insect and possible interactions with atmospheric deposition have caused extensive mortality in relict stands of Fraser fir, *Abies fraseri*, in the southern Appalachian mountains (Witter and Ragenovich

1986, Hain and Arthur 1985). If this damage continues, some of these stands may be greatly reduced or completely eliminated, possibly resulting in extinction of native species that are tightly associated with Fraser fir.

WHICH SPECIES ARE LIKELY TO INVADE?

There is a clear need to identify specific organisms that have the potential for invading new areas and becoming pests. Such evaluations must consider if the organism has a high probability of successfully invading and if there is a high probability of it becoming a pest.

In considering an organism's probability of being an invader, it is useful to examine the organism's attributes relative to both the arrival and establishment phases of invasion (Table 1). Traits that will promote arrival are fairly obvious. Affinity to humans and their objects is an important trait that can be used for screening potential invaders. When considering the causes of the exponential increase in invasions (Fig. 1) it is obvious that the increase can mostly be traced to increases in human mobility. Therefore, species that are prone to be transported as a result of this increased mobility should be identified as high-hazard species. The recent discovery of numerous gypsy moth egg masses on Russian grain ships in western ports of North America illustrates this point. Prior to oviposition, females were attracted to artificial lights during loading and unloading of ships in eastern Russian ports (Schaefer and Wallner 1992). This behavior obviously creates a high risk that these gypsy moth populations will arrive in new areas. Association of a pest with shipments of raw or processed wood creates substantial risk of invasion. The recent attempt to identify pest species that are prone to accidental importation to North America with raw larch logs from the Russian far east (USDA Forest Service 1991) is an excellent example of how the risk of arrival and establishment can be estimated from existing information.

Establishment is another important process in determining the success of an invasion. An obvious factor that is important here is the ability of the habitat to support development of the exotic organism. This includes both the suitability of the climate and the availability of hosts. Organisms most likely to become established are those capable of utilizing diverse food sources and reproducing under various environmental conditions (Long 1981). High reproductive capacity also is an important trait for an invading species, since high initial reproduction is advantageous for avoiding extinction (Ehrlich 1986).

Gibbs and Wainhouse (1986) proposed that establishment in the Northern hemisphere by forest pests from the same hemisphere is more likely to be successful than establishment of species from the southern hemisphere. They noted that most of the common genera of forest trees had their origins in the Tertiary when a land bridge linked the continents in the northern hemisphere. This origin resulted in a distribution of the same genera across most portions of the northern hemisphere. The presence of closely related tree species in North America and Eurasia would increase the probability of establishment of pests within the hemisphere. Pimentel (1986) and Mattson et al. (1994) presented data showing that most exotic forest pests in North America originated in the northern hemisphere and thus supported Gibbs and Wainhouse's (1986) hypothesis,

though the increased level of trade with countries in the northern hemisphere is a confounding factor.

It is also important to evaluate the potential of the invading organism to be a pest. If a species is a pest in its native range, then it will probably be a pest after it has invaded another continent. Many species that are not considered destructive in their native range may ultimately develop into destructive pests after introduction to a new area. This is a particularly common trait for pathogens (e.g., the pinewood nematode, *Bursaphelenchus xylophilus* is rather inconsequential in its native North American habitat but in Japan it is the most destructive pest of pines [Dwinell and Nickle 1989]) and it is also true for many insect pests.

Often we think of exotic pests as either insects or pathogens, and most of the information presented in this article describes these types of organisms. Many introduced plant species have also become pests, creating major disruptions in natural forest ecosystems. Hundreds of exotic species of woody plants have been introduced into the United States, largely for ornamental purposes. A few of these species have developed into pest species, displacing native flora and fauna, and disrupting certain human activities. Tropical and subtropical areas seem to be particularly vulnerable to these invasions (Ewel 1986, Moulton and Pimm 1986). In Florida, exotic woody plants that now pose a problem include Brazilian pepper tree, *Schinus terebinthifolius*, Australian pines, *Casuarina spp.*, and *Mimosa pigra*, a relatively new introduction. Currently, more than 170 species of exotic plants have escaped and become established in Florida alone (Schmitz et al. 1991). In Hawaii, nearly 900 plant pest species have become established.

WHAT HABITATS ARE LIKELY TO BE INVADED?

Another factor important to the management of invasions is the identification of areas where conditions facilitate invasions of new pests. It is obvious that the arrival process is important in identifying these areas: regions where there is a great deal of human mobility and trade are probably at greater risk for invasions than are more isolated areas. Fortunately, forests have historically been not well traveled, thereby placing them at lower risk of invasion. However, as human population densities and forest land use increase, forests are increasingly at risk of invasion. Urban forests represent an increasing proportion of the forested land in North America, and these areas are often the first sites for invasions. This is illustrated by the arrival of the gypsy moth, which is one of the few examples of where the precise location of an introduction is known. In this case the introduction occurred in an urban forest, specifically in the backyard of an amateur naturalist's home, but subsequently spread into millions of acres of uninhabited forests (see case history #3 below).

Disturbance also facilitates the invasion of exotic pests. Picket and White (1986) define disturbance as the process by which a natural ecosystem is modified by human or other exogenous events (e.g., chance weather events) to a condition that is not otherwise common for that ecosystem. Disturbance may promote invasions; competition is typically lower in disturbed ecosystems and thus they leave open niches that permit increased reproductive rates for invading organisms (Di Castri 1989). This would result in a higher

probability of establishment. Some argue that disturbance is an important reason for the increase in successful invasions over the last 100 years (Fig. 1; Di Castri 1989). This argument also could be used to explain the success of some of our most spectacular invading forest pests. For example, one of the reasons for the immense success of the gypsy moth in North America is because of the large expanse of forests dominated by oaks in northeastern North America. This large expanse of oaks is not a natural situation and is largely a result of reforestation of areas cleared over 100 years ago by humans (Smith 1976). The elimination of American chestnut by the chestnut blight fungus also contributed to the increased dominance of oak and thus also served as an agent of disturbance.

Niemela and Mattson (1992) noted that invasions of North America by pests of European origin far outnumber invasions of Europe by North American pests. They hypothesized that this disparity was caused by a high probability of establishment by invading organisms introduced to North America caused by the greater abundance and diversity of tree species here. This theory is based upon previous biogeographical studies that have documented a correlation between herbivore diversity and the geographical range and diversity of hosts (e.g., Karban and Ricklefs 1983, Lawton and Shroder 1977).

MANAGEMENT OF FOREST PEST INVASIONS

Given the tremendous potential impact of invading pest species, it is important to focus management activities on them. The choice of an appropriate management strategy against an invader depends entirely on the current phase of the invasion. Specific strategies are appropriate to the arrival, establishment, spread, and persistence phases.

MANAGEMENT OF PEST ARRIVAL

One of the most efficient methods of preventing the impact of an invading pest is to exclude it from the region. A requisite to any exclusion program is the identification of a species or a group of species as potentially hazardous (e.g., USDA Forest Service 1991, 1992, 1993). This process, referred to as pest risk assessment, can be difficult because species that are pests on one continent may not be pests in a new region and conversely species that are innocuous in their native habitat may become pests after introduction to a new area (Kahn, R.P. 1989).

The two major approaches to exclusion are inspection and quarantine. With increasing recognition of the threat of biological invaders, Congress enacted the plant quarantine act in 1912 and it has been periodically updated (Rosenburg 1989, Weber 1930). These quarantine laws prohibit the importation of specific commodities from certain regions in the world and they restrict interstate movement of specific commodities within certain portions of the U.S. These laws often permit importation of commodities after mitigative procedures, such as fumigation or inspection in the country of origin (Rohwer 1979, Roth 1989, USDA Animal and Plant Health Inspection Service 1991). The enactment or threat of these laws can be so economically disruptive to the exporting country that it is forced into eradication or other mitigative programs (Dahlsten 1986). Inspection of commodities on entry from another continent is a useful method of excluding unwanted species. With the steady increase in international trade, the need for inspection has expanded. Furthermore, technological changes in shipping, such as the widespread use of containerized cargo, has made inspection more difficult. In the U.S., quarantine and inspection are largely the responsibility of the USDA Animal and Plant Inspection Service (APHIS), although states enforce their own quarantine regulations and conduct their own inspection programs (Rosenburg 1989).

MANAGEMENT OF PEST ESTABLISHMENT

As described earlier, the process by which a pest species becomes established is highly variable and often results in extinction. During the establishment phase, when population levels are low and the geographic range of the pest is restricted, it may be possible to apply population suppression tactics that force the population to extinction. This process, termed eradication, can be an effective way of preventing pest impacts. The monetary gain of avoiding an eternity of damages may justify the expenditure of great sums on eradication (Knipling 1978).

Extensive monitoring is essential in any program where the objective is to prevent pest establishment. Eradication programs are less expensive and more likely to succeed when populations are detected early. The discovery and synthesis of insect pheromones and other attractants have provided powerful tools for detecting insect invasions. For example, APHIS and state agencies deploy a network of over 300,000 traps across the

U.S. every year to detect new gypsy moth infestations. Captures of adult males are usually followed the next year by a denser array of traps that are used to delimit the extent of the infestation. This information can be used to effectively restrict eradication activities to specific areas where reproducing populations exist (Schwalbe 1981).

Because eradication necessitates destruction of nearly every individual in the target pest population, potent population suppression techniques are needed. Historically, chemical pesticides have been widely used in eradication programs, but biological pesticides, such as *Bacillus thuringiensis*, are becoming more common. In many cases, little is known about the biology of the target species and its susceptibility to various pesticides. In these cases, research on biology and pesticide toxicity are necessary before eradication can be effective (Dahlsten 1986). Isolated infestations of exotic pests are often found in urban or semi-urban habitats or other ecologically or politically sensitive areas where extensive applications of pesticides may be undesirable. For species that have been intensively researched, such as the gypsy moth, alternatives to pesticide applications may be available. These alternatives include sterile insect releases, mating disruption (with pheromone treatments), and trap-out, although the effectiveness of these treatments is often limited to specific population conditions. For many pests, especially forest pathogens, the only effective treatment for eradication is destruction of infested material (trees).

Eradication is a subject of considerable controversy. While it has been argued that eradication is an effective way of dealing with invading pests (Knipling 1978; Eden 1978), others have argued that it is often inappropriate and can result in considerable ecological damage (Dahlsten 1986, DeBach 1964, Morse and Simmons 1978, Perkins 1989). Efficacy evaluation of eradication projects is typically impossible since check plots would negate the objective of total population elimination. Although data documenting the efficacy of eradication programs are typically lacking, it is clear that many eradication programs are ineffective. In several historical situations, eradication may not have been necessary because populations may have gone extinct on their own, and in other historical examples, eradication attempts have been futile because populations were already extensively distributed. An example of the latter situation is the effort from 1909 to 1941 to eradicate white pine blister rust from North America (Benedict 1981). When a pest population is widely dispersed across large areas, total population elimination is impossible. In those situations it is more appropriate to design management programs that reduce impacts without total population eradication.

MANAGEMENT OF PEST SPREAD

It is sometimes difficult to classify the expansion of a pest's range as being part of the arrival and establishment process or as merely the continuous spread of the same infestation. Regardless of difficulties in terminology, the methods used for eliminating or reducing the spread of pests are essentially the same as the methods used to prevent arrival and establishment. Exclusion via inspection and quarantine have been effectively used to minimize the spread of forest pests (Weber 1930, Rohwer 1979). Currently there are domestic quarantine regulations that limit the interstate movement of introduced forest pests, such as the gypsy moth, the larger pine shoot beetle, the oak wilt pathogen, and the *Scleroderris* canker pathogen. These quarantines can be effective in limiting the spread of forest pests by hauling logs, Christmas trees, and other raw forest products.

Pest detection and eradication along the expanding front of the infested area can slow the rate of expansion. While such "barrier-zone" projects have often failed to halt the spread of an infestation, they may be effective in slowing the spread (Liebhold et al. 1992). It may be impossible to affect the rate of spread by organisms that are extremely mobile, such as fungi that have wind-borne spores.

MANAGEMENT OF PEST POPULATIONS AFTER ESTABLISHMENT

Once an invading pest species has become established over an area that exceeds the size where eradication is possible, the options for its management become essentially the same as for any other pest species except that classical biological control is likely to be a useful approach. When pests arrive in a new habitat, they typically are not accompanied by their natural enemies such as parasites, predators and pathogens. Therefore, the exploration of the native range of the pest species for natural enemies can be quite fruitful. In a well-planned biological control program, these exotic natural enemies are collected and held for several generations in a quarantine facility where they are observed and a pure strain is isolated (e.g. insect hyperparasites are eliminated). Successful biological control with introduced agents has historically been obtained in about half of attempts (Laing and Hamai 1976, De Bach 1964, DeBach et al. 1971, Crawley 1989). There are numerous examples of invading insect species that may have become major pests in North American forests but were successfully controlled via the importation of natural enemies. These species include the winter moth, *Operophtera brumata* (Embree 1971), the European spruce sawfly, *Diprion hercynia* (McGugan and Coppel 1962), and the larch casebearer (Ryan 1990). Introduced biological control agents maintain populations of these species at densities that do not cause significant damage. The importation of natural enemies from the native habitat of an invading pest may restore a level of population regulation comparable to that present in the native habitat. In some cases, escape from hyperparasites or other sources of mortality to natural enemies, may contribute to a greater level of control (Roland 1990).

Certain insects (e.g., the balsam woolly adelgid [Mitchell and Wright 1967]) and pathogens may have few or no natural enemies in their natural habitat or their population levels may be so low in their native habitat that it is difficult or impossible to locate natural enemies. Therefore these pests may not be successfully controlled using classical biological control. However, in recent years research has been directed at reducing the impact of plant-pathogenic fungi by introducing, or genetically engineering, hypovirulent strains that transmit debilitating viruses to pathogenic strains, thereby reducing their ability to cause damage (MacDonald and Fulbright 1991).

MANAGEMENT OF FORESTS TO REDUCE THE IMPACT OF INVADING PESTS

Invading pests are particularly important problems in forestry (vs. agriculture) because the length of forest rotations limits management flexibility. We generally know which exotic forest pests have already arrived in North America, and some guidelines are available for reducing impacts of these agents via manipulation of stand structure, species composition, or genetic composition (e.g., Gottschalk 1993, Hoff et al. 1976, Ostrofsky and McCormick 1986).

Despite efforts to prevent it, many new and damaging forest pests will arrive and become established in North America in the future. What can forest managers do now to protect forests from these unpredictable impacts? Probably every North American tree species could be affected by one of many possible pest invasions. Therefore, it is impossible to recommend conversion to any one species that will be immune to all pests. Probably the best strategy for avoiding catastrophic impacts would be to manage for a diversity of tree species. While pests may eliminate one or more of these species before the end of a rotation, growth losses and mortality are likely to be partially compensated by unaffected species. For example, Masson pine, *Pinus massoniana*, was widely planted in monocultures from 1950 to 1990 over 23 million ha in China. The pine needle scale, *Hemiberlesia pitysophila*, now threatens to destroy most of these plantations (Wilson 1993). This extensive loss could have been reduced had a diversity of tree species been used in reforestation.

When considering the potential impact of unknown pest invaders one also could recommend that exotic tree species be avoided. One of the reasons why the representation of exotic pests is higher in agriculture than in forestry is because agricultural crops are typically composed of exotic plants. Exotic plant species provide excellent habitats for invading species; even specialist herbivores may thrive when they exist on their preferred hosts in an area devoid of their natural enemies (Pimentel 1986). This point is well illustrated by *Dothistroma* needle blight; in the native range of *Pinus radiata* in North America, this disease is of little consequence, but it is extremely damaging in *P. radiata* plantations in New Zealand (Gibson 1972).

CASE STUDIES OF PEST INVASIONS

Many of the most damaging insect and disease agents in North American forests have been introduced from other continents (Table 2). An extensive list of exotic insects is available elsewhere (Mattson et al. 1994). Below we provide descriptions that provide details of a few specific introduced forest pests. These case studies illustrate the processes and ecological relationships involved in the various phases of pest invasion.

CASE HISTORY NO. 1: CHESTNUT BLIGHT IN NORTH AMERICA

BACKGROUND

The devastation of the American chestnut by the fungus *Cryphonectria parasitica* represents one of the greatest recorded changes in a natural plant population caused by an introduced organism. American chestnut once comprised 25% of the eastern hardwood forest, an area that included 200 million acres of land. No other single tree species can be credited with playing such an important role in the ecology and economy of the Appalachian area (Kuhlman 1978).

Chestnut blight actually is a disease of the bark. The microscopic hyphal threads that comprise the fungus thallus aggregate in fan-shaped structures that grow through bark layers causing dysfunction of the phloem and underlying xylem. Ultimately the canker that results girdles the stem (Hebard et al. 1984). The term "blight" was applied to describe

the gross foliar symptoms that developed as individual branches and eventually the main stem died from multiple infections.

Despite early attempts to control the disease, the fungus spread on average almost 25 miles a year, invading the entire natural range of American chestnut in about 40 years (Kuhlman 1978). The invasion occurred so rapidly that efforts turned from any hope of stopping the blight to the utilization of dead and dying trees. Today, American chestnut survives as an understory tree by producing a succession of sprouts that in time also become blighted. The best survival of the species has occurred on sites with relatively open canopies (Griffin et al. 1991).

ARRIVAL, ESTABLISHMENT, SPREAD

The fungus that causes chestnut blight undoubtedly was introduced into the U.S. before 1904 when it was discovered in New York City. Observers of Chinese (*C. mollissima*) and Japanese (*C. crenata*) chestnut growing in North America noted that these species had more natural resistance than the American species. This led to the suggestion of a Far Eastern origin of the pathogen and its eventual discovery there in 1913 (Roane et al. 1986). Remarkably, plant introduction records show that Chinese chestnut had been imported for more than 50 years before the blight fungus became successfully established in eastern North America (Anagnostakis 1989).

Conditions in North America favored the establishment, survival and rapid spread of the pathogen. The American chestnut was highly susceptible and evenly distributed throughout much of its range, and no natural barriers limited spread of the fungus. Both windblown sexual spores and rain-splashed asexual spores contributed to its spread. Furthermore, the organism was capable of infecting a variety of bark wounds on chestnut and other hosts, and it reproduced on dead substrates.

The blight fungus also was introduced into Europe, with the first infections reported near Genoa, Italy, on European chestnut (*C. sativa*) in 1938 (Mittempergher 1978). The course of the disease in Europe somewhat paralleled that in North America, except the invasion appeared to be slowed by a slightly less susceptible host and more significant mountain barriers that restricted spread throughout the natural and cultivated range of *C. sativa*.

C. parasitica was well-adapted for establishment and dissemination once it arrived in North America and Europe. Its potential to spread in both settings probably was influenced more by the availability of susceptible host material than by any other factor. This fungus infected and colonized susceptible hosts under the many moisture and temperature regimes that exist in the various ecological niches chestnut exploits.

MANAGEMENT

As chestnut blight progressed unabated in North America, researchers shifted their attention to their only hope for control, breeding blight resistant trees. The early breeding programs were designed to preserve the best traits of the American chestnut while incorporating resistant germplasm from Chinese and Japanese chestnut (Clapper 1952). This approach relied almost entirely on one strategy, making large numbers of crosses. There were few second-generation trees grown from first-generation hybrids, and most of the F₁ hybrids were backcrossed to a resistant parent, typically one that lacked the desired

traits of the American chestnut (Burnham et al. 1986). These undertakings met with limited success and were never designed to control chestnut blight in North America. Currently, there is renewed interest in breeding resistant trees using the well-established backcross method. With this method, American cultivars that are susceptible to blight are crossed with resistant species, and the first-generation hybrids then are backcrossed to the cultivar being improved rather than to the source of resistance. Resistant plants are selected from the backcross progeny (Burnham 1988).

A second approach to the control of chestnut blight came in the 1950s when natural abatement of the disease was discovered in Italy (Mittempergher 1978). This change was attributed to the development and/or dissemination of cytoplasmically transmitted double-stranded RNA viruses that reside within *C. parasitica* (MacDonald and Fulbright 1991). Strains of the fungus debilitated by these viruses have been termed "hypovirulent", and they appear responsible for the significant biological control of blight that has occurred in many chestnut growing regions of Italy (Grente and Barthelay-Sauret 1978). A similar phenomenon has been observed among populations of American chestnut that grow outside the natural range of the species in Michigan (Fulbright et al. 1983). Comparable spread of debilitating viruses has not been observed among the sprout populations of American chestnut that exist within the natural range, however limitations to the use of transmissible hypovirulence as a biological control for chestnut blight are discussed by MacDonald and Fulbright (1991). Nuss (1993) describes the implications of using genetically engineered hypovirulent strains for biological control.

Cryphonectria parasitica should reside at the top of the list of devastating organisms introduced to North America by humans. This introduction was not surprising given the large immigrant human population, their long-standing interest in bringing plant material from their native lands, and the lack of appreciation during the 17-19th centuries of the risks associated with intercontinental movement of plants and their associated organisms. Whether this invasion could have been prevented had the problem been recognized and adequate quarantines established will remain a matter for discussion. Ironically, the long-term fate of the American chestnut may reside with the natural or artificial development of a second epidemic, one that results in the debilitation of *C. parasitica* by hypovirulent disease agents as is occurring in Italy and Michigan.

CASE HISTORY NO. 2: WHITE PINE BLISTER RUST IN NORTH AMERICA

BACKGROUND

White pine blister rust (WPBR) is caused by the rust fungus, *Cronartium* and needs no introduction for foresters and plant pathologists in North America. This rust is considered the most important disease of the Hapoxylon (5-needle or white pines) pines, especially eastern white pine (*Pinus strobus*), western white pine (*P. monticola*) and sugar pine (*P. lambertiana*).

Cronartium ribicola is an obligate parasite that has a complex life cycle involving five different spore stages and two different hosts (white pines and *Ribes* spp.). Spores from the leaves of *Ribes* infect pines during periods of wet weather in late summer and early

fall. The leaves of *Ribes* plants become infected each spring by wind-blown spores from white pines. The complete life cycle requires 4 years or longer.

After infection of pines, the blister rust fungus grows throughout the inner bark, eventually girdling infected branches or the main stem, resulting in the characteristic dieback of branches (flagging) and/or tops. Diseased trees often are predisposed to attack by secondary insect pests and fungal pathogens, both of which will hasten tree mortality (Kinloch and Dulitz 1990, Kulhavy et al. 1984).

ARRIVAL, ESTABLISHMENT AND SPREAD

Cronartium ribicola has a well-known history as an introduced pest in both Europe and North America. This rust is believed to have had its evolutionary development in the native ranges of *P. armandi*, *P. griffithii* and *P. koraiensis* in eastern Asia because these pines express a relatively high degree of resistance (Hoff et al. 1980, Soegaard 1969). The rust was probably introduced to Europe some time before the mid-1800s on infected plant material during a period of expanding trade with eastern Asia, but there is no conclusive proof. Moir (1924) and Spaulding (1922, 1929) reviewed the history of WPBR and its initial spread through Europe. They reported that Dietrich found the first known specimens of WPBR on pines and *Ribes* in the Baltic region of Russia in 1854. Prior to that time, eastern white pine was extensively planted throughout Europe using planting stock produced in Europe during the early 1800s. By the mid-1800s WPBR was widespread in northern and western Europe. Both native and ornamental *Ribes* spp. (especially *R. nigrum*) grew throughout Europe and served as efficient alternate hosts.

White pine blister rust is believed to have been introduced to North America from Europe on diseased nursery stock sometime in the early 1900s. However, earlier reports indicate the rust had been found on *Ribes* as early as 1898 and was probably introduced sometime during the 1890s. One of the first records of the rust on eastern white pine was from Philadelphia, PA in 1905, and by 1909 the rust had been discovered in seven northeastern states (Mielke 1943). There is no question that diseased nursery stock was introduced to many areas of eastern North America in the early 1900s and therefore is most likely responsible for the rapid spread of WPBR throughout the native range of eastern white pine.

The introduction of WPBR to western North America is attributed to a shipment of 1000 seedlings of eastern white pine to Vancouver, British Columbia from France in 1910 (Spaulding 1922). Some of these seedlings were diseased and the native *Ribes* population around the Vancouver area probably became infected (Spaulding 1922). It was later discovered on western white pine in various field locations during 1921 (Mielke 1921). Since then, WPBR has spread throughout the entire range of western white pine, from British Columbia to New Mexico, and it has also been found as far south as New Mexico on southwestern white pine, *P. strobiformis* (Hawksorth 1990). In certain areas of the Rocky Mountains, *P. flexilis* (limber pine) and *P. albicaulis* (whitebark pine) have been severely affected and even eliminated from some sites (Hoff et al. 1980, Hoff and Hagle 1990, Meilke 1943). Although Hapoxylon pines occur in Mexico and extend into Central America, WPBR is not known to occur there.

White pine blister rust is found on *Ribes* throughout Eurasia, where the most common pine hosts are *P. cembra* and *P. peuce* (Mielke 1943, Merrill 1988). The rust has recently

been reported on several herbaceous species of Scrophulariaceae in Asia (La and Yi 1976) so the range of potential alternate hosts still remains a question, suggesting more diversity in the pathogen population than occurs in North America. Similar species of Scrophulariaceae are also widely distributed throughout North America, and WPBR has been reported capable of infecting *Castilleja minuta* in Canada (Hiratsuka and Maruyama 1976). Hoff and McDonald (1993) summarized the current status of variation in virulence of the white pine blister rust fungus. Evidence of variability within the fungus substantiates the need for strong quarantines to restrict the importation of any susceptible plant material or different collections of the fungus into North America. Hoff and McDonald (1993) also suggest that movement of the rust fungus, even within the continent, should be restricted.

IMPACT AND MANAGEMENT

White pine blister rust has been ranked as one of the major causes of timber loss and has been credited for creating major ecological impacts on the coniferous forests of North America (Ketcham et al. 1968, Kinloch and Dulitz 1990, Mielke 1943, Merrill 1988). Enormous economic losses attributed to WPBR derive from tree mortality and reduced wood product value associated with resinous cankers and top killing of trees. In addition, secondary attack by bark beetles that vector wood-staining fungi hasten tree mortality and add to wood quality defects. The costs of control programs, such as *Ribes* eradication, chemical application, resistance breeding, and other research, are estimated in hundreds of millions of dollars (Anonymous 1991, Benedict 1981).

The ecological impact of WPBR on the white pine region of North America has been profound. White pines once occupied some of the most productive forest land in North America, but today many of these areas in the west are not being managed for white pine because of the threat of WPBR (Hagle et al. 1989, Ketcham et al. 1968, Merrill 1988).

Up to 95 percent of the original stands of western white and sugar pines have been either killed or damaged by WPBR. In the early 1980s, the prospects for ecosystem management of sugar pine in California were great. By 1990 optimism was diminished because WPBR infection was killing both pole-sized and mature trees or was predisposing trees to attack by other organisms (Kinloch and Dulitz 1990).

Since the introduction of WPBR to North America, plant pathologists and foresters have waged a constant battle against it. Early attempts to halt the spread were aimed at eradicating *Ribes* in and around white pine stands. This approach has been reasonably successful in areas of eastern white pine (Ostrofsky et al. 1988) but not in the western pine regions, where eradication work was discontinued in 1966 because *Ribes* populations could not be decreased to a level that would have had a significant impact on infection rate (Ketchum et al. 1968).

In 1966, the U.S. Forest Service temporarily abandoned white pine for timber management by implementing the following three major changes: (1) planting of western white pine on an operational basis was discontinued; (2) thinning and weeding operations were used to favor other species; and (3) salvage of blister-rust-infected white pines was accelerated (Hagle et al. 1989, Ketcham et al. 1968). These management techniques have had a profound impact on the western white pine region of North America.

In the early 1960s, a rust hazard rating system based on the environmental factors affecting infection of pines was developed in the Lake States (Van Arsdell 1961). Similar

rating schemes were later developed for other regions (Charlton 1963, Lavallée 1986). These systems established "hazard zones" that allow forest managers to evaluate the WPBR risk for sites prior to planting white pine. Microclimatic conditions vary with site topography, local environmental factors, and certain stand conditions and must be taken into consideration in WPBR management (Hagle et al. 1989, Hirt 1942, Van Arsdel 1965). WPBR can be managed in low- to medium-hazard zones by not planting small stand openings, by pruning lower branches and by keeping the canopy closed. These activities reduce the probability of dew formation and therefore opportunities for infection. Also, stand treatments, such as pruning, thinning and canker excision, are considered successful management options in certain stands (Hagle and Grasham 1988, Hagle et al. 1989, Hunt 1982). Thus it appears that the probability of WPBR infection can be reduced through manipulation of the forest environment and cultural.

Resistance to WPBR was first observed in the field in the 1930s but research to determine if genetic resistance existed in North American white pines was not initiated until 1949 (Bingham et al. 1953). A selection program was introduced for both eastern and western white pines and eventually included studies of the Eurasian pines. This initial selection program was quite successful for western white pine, and today seed orchards are producing F₂ generation seed with a high degree of resistance to WPBR. Currently, up to 65% of the genetically improved F₂ seed will produce trees that should remain disease free. Unfortunately, the amount of seed available does not begin to meet overall planting needs. Therefore, resistant seedlings are being selectively deployed to certain field sites in an attempt to maximize benefit (Goddard et al. 1985). Also, a "plus tree" selection program that promotes the practice of leaving superior (disease resistant) trees as parents for the next generation is being evaluated but its success in the field has yet to be determined (Hoff and McDonald 1977).

When developing a host-resistance program it is important to consider pathogenic variability and potential for genetic change in the pathogen. Variability in virulence is known for *C. quercum* f.sp. *fusiforme* (Snow et al. 1975) and has been shown in WPBR for major gene resistance in sugar pine, *P. lambertiana* (McDonald et al. 1984). Also, other forms of variations are known for WPBR as summarized by Hoff and McDonald (1993).

The rapid spread of WPBR throughout the white pine regions of North America resulted from an introduction of a virulent pathogen to highly susceptible pine and *Ribes* host populations growing in close proximity and in favorable environments for rust infection. The only possible means of introduction of *C. ribicola* to North America was by movement of diseased pine or *Ribes*. It is ironic that European plant pathologists, with a knowledge of WPBR, had warned of impending disaster associated with importation of diseased nursery stock (Merrill 1988), but there were no quarantine laws in the United States or elsewhere in North America, and therefore there was no legal way to prevent shipments. Had this movement of living plant material not occurred, WPBR might not be present in North America today.

The gypsy moth, *Lymantria dispar* is a foliage-feeding insect that probably evolved in eastern Asia. Its natural range now extends from Japan and central China across Siberia to Europe and Northern Africa. This insect is univoltine throughout its range, but there is considerable geographical variation in traits such as larval coloration, number of instars, and ability of females to fly (Goldschmidt 1933, Baranchikov 1989). The gypsy moth is highly polyphagous, but population growth is greatest on *Quercus*, *Populus* and other preferred tree species. Throughout most of its range the gypsy moth historically exists at endemic population levels but there are other areas within its natural range where outbreaks are quite common. These sites are typically dominated by *Quercus* and many are xeric (Montgomery and Wallner 1988).

ARRIVAL, ESTABLISHMENT, AND SPREAD

Around 1869 the gypsy moth was accidentally released in Medford, Massachusetts, a Boston suburb, by a French immigrant, E. Leopold Trouvelot (Forbush and Fernald 1896, Liebhold et al. 1989). At the time, Trouvelot supported himself as an artist but had an amateur interest in natural history; his specialty was the evaluation of native silkworms for potential in commercial sericulture. It is not clear what Trouvelot's intentions were when he transported gypsy moths from his native France to Massachusetts, nor do we know the exact details of their release in his yard. There are records that Trouvelot contacted several prominent entomologists to notify them of his accident but none of these people initiated any control action.

After Trouvelot's accident, there was an establishment period of over 10 years during which gypsy moth populations remained at undetected levels. The first outbreak appeared around 1885 in Trouvelot's neighborhood. Because of strong reaction by Medford residents and concern among government officials, a major effort was initiated around 1890 to eradicate gypsy moth populations. This effort was jointly funded by the state and federal governments. Activities consisted of scouting the area for new populations, manual removal of egg masses, chemically treating life stages with primitive pesticides and destruction of infested host material (i.e., burning forests). By 1900, there was some evidence of success; it had become nearly impossible to detect any gypsy moth life stages in the area. Consequently, many declared the eradication a success, and the state legislature withdrew funding of the eradication work. High population densities returned again in 1905, and eradication efforts resumed. Dunlap (1980) speculated that had eradication efforts continued during the lull in populations, eradication would probably have been successful and the current gypsy moth problem would have been avoided. However, given our current knowledge about gypsy moth demography, it is doubtful that eradication of such an extensive population would have been possible.

Since the turn of the century, the range of the gypsy moth in North America has expanded (Fig. 4). Liebhold et al. (1992) analyzed historical records and determined that there were three periods of relatively constant rates of spread. From 1900-1916 the radial rate of gypsy moth spread was ~8 km year. From 1916-1965 the rate of spread was only about 2 km per year. From 1966-1990 spread occurred at a rate of about 21 km/year. During the latter period, spread in the northern states and Canada was much slower, reflecting previous observations of high overwintering mortality in extremely cold climates. Liebhold et al. (1992) also used estimated life history parameters in Skellam's

(1951) model to predict a rate of ~2 km/yr based upon spread due to only natural dispersal of first instars. They concluded that the currently observed (~21 km/yr) rate of spread is much higher than the predicted (~2 km/yr) rates because humans are inadvertently moving life stages beyond the infested area at a greater rate than would occur naturally. Liebhold et al. (1992) also concluded that the much slower rates of spread from 1916-1965 may have been caused by management activities. During that time the U.S. Department of Agriculture (USDA) and state agencies conducted an intense program of detection and suppression in and around the Hudson River valley aimed at preventing the spread of gypsy moth to the west. The extensive use of DDT and other materials became a subject of criticism by environmentalists (e.g., Carson 1962), and the program was eliminated in the early 1960s. During the peak of this "barrier-zone" program there were great expectations that ultimately gypsy moth would be eradicated from North America (Felt 1942). These projections were overly optimistic because, as we now know, a gypsy moth population established over such a large area (all of New England) is impossible to eradicate. Nevertheless, the control program did apparently retard westward spread.

While the concept of a barrier zone has been abandoned, there is new interest in programs aimed at slowing the spread along the infested front. From 1988 to 1992 the U.S. Forest Service sponsored the Appalachian Integrated Pest Management Program whose objectives included slowing the spread of the gypsy moth infestation through the central Appalachian mountains. In 1992 the Forest Service initiated another demonstration program in portions of North Carolina, Virginia, West Virginia and Michigan aimed at slowing the spread of the gypsy moth via intensive monitoring of low-level populations using pheromone traps and suppressing isolated populations just beyond the infested front. Clearly, this is a novel approach to managing an invading species and eventually it should be possible to determine if these types of programs are technically feasible and economically justified.

While the generally infested area enlarges continuously, isolated gypsy moth populations often develop in areas far removed from its current distribution. A spectacular example of an isolated population was in Michigan (Dreistadt 1983). The gypsy moth was first detected in Michigan in 1952, and several attempts were made to eradicate populations between 1954 and 1967. The eradication efforts were assumed to be successful, but extensive populations were again discovered in 1973 and subsequent eradication efforts failed. Since that time, the gypsy moth has developed into a major forest pest in Michigan, defoliating large areas. This example illustrates the importance of an intensive monitoring program that uses sensitive traps; had populations been detected earlier, eradication attempts would have likely succeeded.

As the area of the generally infested area continues to increase (Fig. 4) the probability of accidental transportation of life stages into currently uninfested areas increases. From 1980 to 1990, gypsy moth males were trapped in all of the 48 coterminous states. Historical trapping data indicate that most introductions fail to establish and disappear after only a single year of detection (E. LaGasa, unpublished data). However, isolated populations have temporarily become established in varying habitats including scrub oak communities in Utah, Douglas fir mixed with oak species in Oregon, and swamp oak in Georgia. These populations were apparently successfully eradicated. Nevertheless, the behavior of these isolated populations indicates that gypsy moth will eventually become

established in a large number of habitats throughout North America. It is unknown in which of these areas, populations will ever reach defoliating levels. Historically gypsy moth outbreaks developed in areas where at least 20% of basal area was represented by preferred species (Herrick and Gansner 1986). This suggests that gypsy moth may become a major pest in much of the southeastern, midsouthern, and northcentral U.S. and will possibly be a pest in certain western states.

IMPACTS AND MANAGEMENT:

The impacts of gypsy moth in North America are manifold. Defoliated trees grow slower, but this growth loss is sometimes compensated by increased growth of non-hosts (Wargo 1981a, Campbell and Sloan 1977a). Oaks that are completely defoliated will typically produce a new flush of leaves. Defoliation and refoliation cause a net decrease in the tree's balance of nutrients; trees that are already under another form of stress and healthy trees receiving consecutive years of defoliation often die. Mortality is typically caused by a reduction in defensive reactions to secondary agents such as the two-lined chestnut borer, *Agilus bilineatus*, and the root rotting fungus, *Armillaria mellea* (Wargo 1981b).

Defoliation can cause a major shift in stand species composition directly as a result of mortality of overstory trees or indirectly via seed failures and mortality of oak seedlings (Gottschalk 1990). The net effect in these situations may be to increase dominance of non-hosts. Though there is evidence for major stand conversion in areas receiving catastrophic tree mortality (Allen and Bowersox 1989), the species composition in most stands have probably not changed dramatically. Indeed, Gansner et al. (1994) showed that over large regions receiving several years of defoliation, the total volume of merchantable oak actually increased. Thus, the ecological impact of gypsy moth on stand species mixtures is probably not as dramatic as problems such as chestnut blight and Dutch elm disease.

The major impact of the gypsy moth in North America is probably sociological. Defoliation can have dramatic effects on aesthetic quality, recreational values, and residential values. Much of the concern about gypsy moth has arisen due to defoliation in densely populated portions of the northeastern U.S. Home owners are often willing to pay substantial amounts to protect their shade trees from gypsy moth defoliation (Payne et al. 1973).

During the early 1900s considerable effort went into biological control of the gypsy moth. Much of this work came about as a result of the success of C.V. Riley (then chief entomologist, USDA) in biological control of several exotic agricultural pests. From 1905 to the present, over 40 gypsy moth parasitoids have been introduced to North America from Europe and Asia (Hoy 1976). There has been recent criticism of early efforts in that little, if any, effort was made to restrict introductions to specific natural enemies (Washburn 1984) and many introductions were carried out without adequate quarantine procedures, which resulted in the introduction of several hyperparasitoids that ultimately limited the effectiveness of parasitoids. Nevertheless, at least 10 parasitoids have been established (Hoy 1976).

The question of the effectiveness of these natural enemies in regulation of populations remains a matter of some debate (Berryman 1991, Liebhold and Elkinton 1991, Elkinton

et al. 1989). North American gypsy moth populations continue to behave in an eruptive manner; populations exist at very low levels but occasionally rise to very high densities that result in considerable socioeconomic damage. However there is evidence that natural enemies do contribute to the regulation of populations. The imported tachinid parasitoid *Compsilura concinnata* can cause spatially density-dependent mortality and therefore may cause small areas of elevated gypsy moth population densities to be reduced to endemic levels (Gould et al. 1990, Liebhold and Elkinton 1989). Small mammals that are endemic to North America, such as *Peromyscus* spp. and *Sorex* spp. are thought to be the most important mortality agents that maintain gypsy moth populations at low levels (Elkinton and Liebhold 1990, Elkinton et al. 1989, Campbell and Sloan 1977b). A nuclear polyhedrosis virus (NPV) is usually the principal agent causing the decline of outbreak gypsy moth populations. NPV apparently was introduced to North America in the founding gypsy moth population, since epizootics have been recorded from even the first outbreaks in Medford (Forbush and Fernald 1896).

In 1909 an entomopathogenic fungus, *Entomophaga maimaiga* was introduced from Japan to New England to control the gypsy moth but it was assumed that the fungus never became established (Speare and Colley 1912). A very wet spring occurred in New England in 1989, and *E. maimaiga* was discovered to be causing considerable mortality in New England gypsy moth populations for the first time. The most likely explanation for the occurrence of this fungus was the original release in 1909 (Hajek et al. 1990, Andreadis and Weseloh 1990). Very wet conditions appear to promote *E. maimaiga* epizootics, but this agent has continued to cause high levels of gypsy moth mortality in subsequent years even in the absence of unusually damp conditions. Since 1989, the fungus also has apparently spread very rapidly from New England and now is present in nearly every portion of the area infested by the gypsy moth (Hajek et al. 1994).

Despite intensive efforts at biological control of the gypsy moth, this insect remains a serious pest in North America. Several other forest pests, such as the winter moth and the European spruce sawfly, have been successfully controlled using classical biological control (Dahlsten 1986). It is doubtful that the "failure" of biological control can be attributed entirely to mistaken tactics in natural enemy importations. One explanation of the failure in gypsy moth biological control is the very nature of the insect. It is a highly plastic organism, capable of exploiting a wide variety of host plants in a wide variety of climates. It may be even more important to consider that the gypsy moth is an eruptive insect through much of its natural range and is thus not entirely regulated by natural enemies even under endemic situations.

CASE HISTORY NO. 4: *MELALEUCA* IN NORTH AMERICA

Dozens of exotic species of woody plants have been introduced into the U.S., largely for ornamental purposes. The tree species, *Melaleuca quinquenervia*, has been recognized as a problem in southern Florida. This species, which is a native of subtropical Australia, New Guinea and Caledonia (Hofstetter 1991), is known by a variety of common names: *Melaleuca*, cajuput tree, punk tree and paper tree, but we will use "*Melaleuca*" here. The genus, *Melaleuca*, includes approximately 250 species and is a member of the Myrtaceae or myrtle family.

ARRIVAL, ESTABLISHMENT, AND SPREAD

Melaleuca was intentionally introduced to the U.S. on several occasions. One of the earliest documented introductions was in 1906 when seeds were received by a University of Miami Forestry professor, Dr. J. C. Gifford. These were subsequently planted at his home on Key Biscayne and at a nursery in Broward County, Florida (Meskimen 1962). Early introductions of this tree were viewed as beneficial. It was thought that, because of its high transpiration rates, stands of the tree had the ability to lower the water table and to dry wetlands, making them suitable for development. Also, the tree was viewed as a potential source of wood and fiber. One individual aerially seeded a section of the everglades in 1936 in an attempt to make it suitable for development (Meskimen 1962, Hofstetter 1991). In the 1940s, the Army Corps of Engineers' Lake Okeechobee Levee Project planted large numbers of *Melaleuca* seedling for their rapid growth and potential bank stabilization properties. In the 1950s, the tree was also used extensively by the landscape nursery industry for ornamental planting in Florida, and it also was widely planted for windbreaks and stabilization of shore lines.

Melaleuca is a plastic species in that it will grow in a variety of soil types and climatic conditions (Myers 1983). There are apparent differences in site susceptibility to invasion by *Melaleuca* that have not been fully explained. Hofstetter (1991) speculated that shortened hydroperiods and dry season fires stress native vegetation, making sites more susceptible to invasion.

In its native range, *Melaleuca* trees normally flowers once a year, but in Florida trees may bloom as many as five times a season (Hofstetter 1991). Seed release from the persistent seed capsules is stimulated by drying. Fire also aids in this process, often resulting in a massive seed release. In the absence of fire, seed release is almost continuous.

Seed and seed capsules are buoyant and dislodged seeds can be carried along canals or streams, aiding in the tree's invasion of new areas. Seeds can survive up to six months submerged (Meskimen 1962) and up to 10 months in some soils (Myers 1983, Woodall 1983). Natural seed dispersal from a tree is limited and under most conditions does not exceed 170 m from a source tree (Meskimen 1962, Browder and Schroeder 1981). Invasion of new areas is generally a steady slow advance, but because two-year-old seedlings can flower and produce seeds, the advance is fast relative to other tree species. LaRoche and Ferriter (1992) studied the rate of expansion of *Melaleuca* in newly invaded areas. They found that after 25 years, 95% of an area would be occupied by *Melaleuca*, when initially, it only occupied 2-5% of the land area.

Woodall (1978) projected that the potential range of *Melaleuca* will include the majority of the Florida peninsula south of Lake Okeechobee. Its northern limit is restricted by its sensitivity to cold temperatures; several hours of -5°C are capable of killing trees near ground level. The exact area now infested with *Melaleuca* is not precisely known, even though there have been a number of efforts to determine the acreage and its geographic distribution. Probably the most complete information is provided by a 1980 aerial survey that was conducted by the U.S. Forest Service and the Florida Department of Agriculture and Consumer Services (Cost and Carver 1981). They found that approximately 200,000 ha out of the total 3.2 million ha surveyed in 10

counties were infested. Pure stands of *Melaleuca* occurred on about 16,600 ha. A later estimate of the infested area indicated that *Melaleuca* occupied about one million hectares (DiStefano and Fisher 1983). Thayer and Bodle (1990) estimated that in 1989 *Melaleuca* occupied about 10 percent of its potential range. Laroche and Ferriter (1992) noted that *Melaleuca* has historically spread from multiple sites of introduction in Southern Florida

IMPACTS AND MANAGEMENT

Melaleuca commonly forms dense, pure stands. Densities in young stands can be as high as 250,000 stems/ha (Hofstetter 1991). As stands mature, stem counts decline, but commonly, native vegetation is displaced and overall species diversity is less (Woodall 1978, 1981, Austin 1978). These pure stands also have limited wildlife value. Stands of *Melaleuca* have replaced sawgrass marshes and other vegetation types, dramatically changing many natural ecosystems in southern Florida and potentially displacing rare and endangered species. Balciunas and Center (1991) report that if left unchecked, *Melaleuca* will occupy all of the Everglades National Park.

The Florida Department of Natural Resources Economic Impact Statement on *Melaleuca* offers the most comprehensive list of potential impacts of *Melaleuca* invasion (Diamond and Davis 1991). Foremost is the possibility that extensive coverage of the Everglades with *Melaleuca* could substantially decrease the fresh water supply to South Florida. Hofstetter (1991) found on a per unit leaf area basis sawgrass and *Melaleuca* transpire similar quantities of water. Leaf area in stands of *Melaleuca*, however, are much greater than sawgrass, and Woodall (1983) notes that the loose papery bark of *Melaleuca* has a higher potential to intercept rainfall than most other vegetation in the everglades ecosystem. Though the relative impacts of increased invasion by *Melaleuca* on the surface water supply are estimated to be three to six times greater than native vegetation, the precise impact has not been determined (Diamond and Davis 1991, Balciunas and Center 1991).

Another negative impact of *Melaleuca* invasion is increased fire hazard. The tissues of the tree have a high volatile oil content which makes it highly flammable. Crown fires can occur in dense stands (Hofstetter 1991). Diamond and Davis (1991) and Wade et al. (1980) indicate that conversion of native vegetation to stands of *Melaleuca* will significantly increase fire protection and control costs.

The introduction and spread of *Melaleuca* may have some positive impacts. Because the tree flowers profusely nearly throughout the year, it offers a winter pollen source for bees. Diamonds and Davis (1991) report a possible loss of millions of dollars to the bee industry if *Melaleuca* were eliminated entirely, but there is no clear evidence that other plant species could not provide alternative sources of winter pollen and the honey produced from *Melaleuca* is of poor quality. Balciunas and Center (1991) state the economic and environmental damage associated with *Melaleuca* infestation far overrides any minor benefits such as to the bee industry.

The greatest estimate of negative impacts of *Melaleuca* are associated with losses in tourism and outdoor recreation. Annual losses were estimated to be between 150 million and 1 billion dollars annually (Diamond and Davis 1991, Balciunas and Center 1991). Although it is likely that the *Melaleuca* invasion further threatens endangered species (Diamond and Davis 1991), these impacts have not been estimated.

Melaleuca is included on the Federal Noxious Weed List and the Florida Prohibited Aquatic Plant List. Inclusion in the latter list prohibits transportation and possession of live *Melaleuca* within the state. Before *Melaleuca* was included under state law, several county and local government entities had adopted regulations or laws which restricted the cultivation, sale or transportation of this species; in some cases, municipalities even required mandatory removal of trees.

Control of *Melaleuca* currently consists of manual or mechanical removal of individual trees or treatment with herbicides or a combination of tactics. Physical removal of seedlings is expensive, and in remote and environmentally fragile areas, crews have to be ferried to trees by helicopter adding additional expense. Mechanical removal of large trees is only possible in accessible areas. Extensive studies have been conducted on the efficacy, selectivity and persistence in the soil and water of various herbicides (Burkhead 1991, Maffei 1991, Molnar et al. 1991, Timmer and Teague 1991). Herbicides are now used in several management programs.

Melaleuca appears to be a good candidate for classical biological control. Exploration for biocontrol agents should yield insect species which are host specific. In southern Florida, there are few closely related native plant species and no crop species that introduced biological control agents that prefer *Melaleuca* are likely to attack. Pure stands of *Melaleuca* should be well suited for establishment and maintenance of biocontrol agents. The continual flowering of *Melaleuca* in Florida may also be beneficial for maintaining high population levels of flower-feeding natural enemies (Balciunas and Center 1991).

In 1987, foreign exploration for natural enemies of *Melaleuca* was initiated in Australia. Early work indicated that Australia contained large numbers of these agents (Center 1991). Thus far, exploration has yielded over 400 species of insects associated with the tree, and approximately 100 of these occur commonly. The goal of this biological control effort is to introduce and establish natural enemies that will limit seed production and seedling growth and survival (Balciunas et al. 1992, Center 1991). This project has progressed to the point where two species are being screened in a quarantine facility in Florida for host specificity. Other species' life cycles and host specificity are being studied in Australia. Prospects for eventual introduction and establishment of biological control agents appear to be very promising and may eventually mitigate some of the impacts of *Melaleuca*.

CASE HISTORY NO. 5: PINE SHOOT BEETLE - A NEW IMMIGRANT

The pine shoot beetle, *Tomicus piniperda*, was first detected in North America in a Christmas tree plantation in Ohio in July, 1992. As of November, 1994, the known distribution in North America included 118 counties in six U.S. states (PA, NY, OH, IN, MI, and IL), and 8 counties (all in southern Ontario) in Canada. The known infested area will undoubtedly increase as intensive delimitation surveys continue. The likely source of introduction(s) was from infested crating or ship dunnage which were off-loaded in port areas in the Great Lakes. Current federal regulations prohibit off-loading of this material until APHIS is notified and approval is granted. After inspection, if no pests are found, the material may be off-loaded. Inspection of this material is difficult under the best

conditions as bark is often concealed inside of the crating, making pest detection nearly impossible. A new proposed regulation would prohibit off-loading any wood or wood product with bark attached regardless of the presence or absence of exotic pests.

The pine shoot beetle's native range includes most of Eurasia from western Europe to Japan and from the Arctic Circle to North Africa (Langstrom 1980a,1983). Within its native range, it is a significant forest pest when conditions are suitable for large population increases. Damage is caused by shoot pruning which results from feeding by adult beetles (Langstrom 1980a, 1980b, 1983). At high population levels, terminal damage can be severe enough to result in up to a 60 to 70 percent loss of increment growth. In young trees, terminal feeding results in stunting and malformed growth (Eidmann 1992, Ericson et al. 1985, Langstrom and Hellquist 1991). Brood development occurs in injured pines or in recently cut pine logs or logging residue. Population density and host damage increase when logging practices or natural occurrences (i.e. storm damage) provide abundant brood material (Langstrom and Hellquist 1991). In northern Europe, the pine shoot beetle is principally associated with Scots pine, *Pinus sylvestris*. However, it attacks other pine species and occasionally will utilize larch (*Larix*), spruce (*Picea*) and fir (*Abies*) for brood development. Adults usually do not successfully attack live healthy pines.

The area in the United States that is currently known to be infested by the pine shoot beetle is regulated under a Federal quarantine. Movement of pine nursery stock, Christmas trees, logs, stumps and pine bark products are all covered by this quarantine. In the known infested area, most host material is in nurseries, Christmas tree plantations and in stands of planted and native pines. Impacts to date have been largely to the nursery and Christmas tree industries which must meet inspection certification standards to move host material to areas outside of the regulated infested area.

The potential impacts on the U.S. pine timber industry, at this time, are unknown. The host range of the pine shoot beetle in North America is currently under investigation. In addition to Scots pine, beetles have been confirmed to shoot feed on eastern white, jack , Austrian, and red pines as well as a number of other pine species. Preliminary findings indicate that several native pines are acceptable hosts for brood production (pers. comm. W. Berisford, T. Eager, R. Haack, and R. Lawrence). In a previous study, lodgepole pine, *P. contorta*, was shown to support the entire life cycle of this pest (Langstrom and Hellquist 1985).

In Scandinavia, pine shoot beetle populations are managed by adopting practices that minimize brood material. This is accomplished by timing cuttings and by the removal of logs and cutting residue from the forest before or during the adult spring flight and ovipositional period (Langstrom 1984, 1986, Schlyter and Löfquist 1990). Although this management strategy is very successful in Europe, it is doubtful whether this strategy could be successfully incorporated into North American forestry practices. If the pine shoot beetle is able to utilize native pines as hosts, current forest practices in the U.S. would probably promote population density increases. In addition, the conditions that provide suitable material for brood development (i.e., wind, snow or ice damage to trees) also would promote local population increases. The pine shoot beetle is thought of as a secondary pest (i.e., it does not normally attack and kill healthy trees), however, its impact on increment growth, due to shoot feeding, clearly is a direct and a primary impact. Its interactions with native insects infesting pine and native disease organisms are also

unknown. How the pine shoot beetle interacts with other pine-feeding insects or alters their interactions with host pines will, in part, determine long-term impacts. The interaction with other organisms within the pine shoot beetles' native range are not completely understood (Gibbs and Inman 1991, Lieutier et al. 1989, Piou and Lieutier 1989).

The pine shoot beetle's potential impacts in North America are difficult to predict, but it is an additional pest which forest managers will have to consider in planning for the future. Its shoot feeding behavior exploits a niche for which there were few native Scolytid competitors, although this niche is exploited by a number of Lepidoptera. Prospects for eradication at this point are remote. Further research is needed to identify regulatory measures and control treatments that will minimize this pest's distribution and damage.

CASE HISTORY NO. 6: ASIAN GYPSY MOTH - A NEW IMMIGRANT

In 1981 a few gypsy moth egg masses were observed on Soviet freighters docked in Vancouver, B.C. In the spring of 1991, a very large number of egg masses were detected on several Russian vessels in Vancouver, BC, and Portland. That summer, several Asian gypsy moth males were trapped in the Vancouver area and around Tacoma, Washington, and one Asian male was trapped near Portland, Oregon. A large detection and aerial spray program was conducted in 1992 in order to eradicate Asian gypsy moth from British Columbia, Washington and Oregon. The program apparently was successful; no Asian gypsy moths were trapped in 1992 or 1993.

The Asian strain of the gypsy moth is similar in many ways to the European strain present in the Northeast (Schaefer and Wallner 1992). The most significant difference is the Asian female's ability to fly. This mobility could allow the Asian strain to spread quickly and this would make eradication more difficult.

One of the most important obstacles to eradication of Asian gypsy moth from North America is the difficulty in differentiating Asian individuals from Europeans. Although there are slight morphological differences, the most definitive method used for identification has been the sequencing of mitochondrial DNA. Since mitochondria are maternally derived, matings between Asian males and European females will result in individuals that can not be identified using this method (Wallner 1993). The problems in identification have been acute in the Pacific Northwest region, because isolated populations of the European strain exist there that could easily be confused with the Asian variety. Furthermore, the Asian and European strains will freely mate and produce viable offspring and hybrids may be phenotypically intermediate. New diagnostic tests based on an analysis of two separate nuclear loci have recently been developed and should provide more definitive identifications (J. Slavicek and T. Grigliatti, pers. comm.).

These recent introductions illustrate the significant danger of permanent establishment of Asian gypsy moth in North America. As trade between the Far East and North America increases, the danger of repeating the incidents of 1991 are substantial at many ports. In July, 1993, a military cargo vessel arriving from Germany at the port of Wilmington, NC, was found to be contaminated with flying gypsy moth males and females. Preliminary investigations of the incident indicate that these individuals were accidentally transported on containerized cargo from a hybrid (European x Asian) population that had previously been undetected in Germany (Hofacker et al. 1993). An extensive eradication program was conducted in the Wilmington area in 1994. New introductions of Asian gypsy moth have apparently recently been discovered in Long Island, NY and in South Carolina. This example illustrates the need for international efforts in monitoring pest populations in both exporting and importing countries.

CASE HISTORY NO. 7: POPLAR LEAF RUST - A NEW IMMIGRANT

Many species of *Populus* and their hybrids are increasingly being grown in plantations for wood fiber production (Widen and Schipper 1981). These trees are grown on a short rotation and are usually established from stem cuttings and then regenerated by coppice methods. The parent trees most often are selected for growth rate and fiber quality. This

selection has limited the number of genotypes and thus increased genetic uniformity in plantations. This uniformity along with dense, even-aged plantings may allow disease-causing agents to rapidly spread once they are introduced.

Some of the most important diseases of poplar are the leaf rusts caused by *Melampsora* spp. These rusts are of major concern not only because they cause defoliation and growth retardation, but also because they occur over a wide geographic area and their host range includes many species, clones, and interspecific hybrids of *Populus*. The rusts are known to have different physiological races that vary in virulence on resistant poplar clones (Pinon et al. 1987).

Several species of *Melampsora* have histories as introduced pests in certain areas of the world. The genus contains both autoecious (single host) and heteroecious (host alternating) forms; however, the host alternating macrocyclic rusts are believed to be of greatest importance to forest trees.

Recently, *Melampsora larici-populina* (larch-poplar leaf rust) was reported for the first time in the United States from hybrid poplar plantations along the Columbia River in Washington and Oregon, and in California (Newcombe and Chastagner 1993, Newcombe, pers. comm.). This pathogen alternates between species of *Larix* and *Populus*. However, this rust also has been reported on *Pinus radiata*, and the full host range has not been systematically investigated (Newcombe and Chastagner 1993). Conclusive documentation as to how or when this rust was introduced is lacking.

Spores of this rust are wind disseminated, sometimes over great distances, and may infect native host species (Widen and Schipper 1980). Aeciospores or wedinospores initiate infection on poplars, and the uredinial (repeating) stage is responsible for intensifying infections, often resulting in extensive premature defoliation. The potential for damage to intensively managed fiber plantations is worrisome primarily because premature defoliation is reported to greatly reduce annual fiber production and even cause dieback of young trees, as reported for *M. medusae* (Widen and Schipper 1981). To date, the distribution and potential impact of *M. larici-populina* in North America are not understood.

Epidemiological opportunities for *M. larici-populina* in North America appear to be great, considering the variety and widespread distribution of hosts trees and the opportunity this rust may have once it becomes established in poplar plantations of clonal origin. Virtually nothing is known about host resistance or pathogenic variability of the rust in North America.

Current research is designed to assess the distribution of *M. larici-populina* in North America and to determine if different physiological races occur here (G. Newcombe, pers. comm.). In the future, use of rust resistant poplar clones or their hybrids may be the only way to effectively manage this disease.

CASE HISTORY NO. 8: PINE WOOD NEMATODE - A HIGH RISK AGENT

The pine wood nematode (PWN), *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae) is believed to be native to the conifer regions of North America, but it is not considered a forest pest there (Dwinell and Nickle 1989). PWN was apparently

introduced to Japan near the beginning of the 20th Century and there it is considered a serious pest of pines (Kishi 1988) and for that reason it is now considered a high-risk disease-inciting agent for other pine-growing regions of the world.

Nematodes of the genus *Bursaphelenchus* inhabit wood and bark tissues of branches, stems and roots of many species of conifers. In pines, PWN can incite "pine wilt disease." In North America, PWN is considered a component of a disease complex that includes coniferous hosts (Robbins 1982), PWN races or pathotypes (Bolla et al. 1986, 1988, Webster and Baillie 1988), insect vectors and associates (Linit et al. 1983), bacteria, fungi, and pathotoxins as summarized by Bergdahl (1988). A number of abiotic and biotic stress factors, including drought, high temperatures and infection by other pathogens, are known to predispose trees to infection/infestation by PWN (Mamiya 1983, Wingfield and Blanchette 1983, Wingfield et al. 1982). These nematodes infect trees during either the feeding or breeding/oviposition activities of pine sawyer beetles (*Monochamus* spp.) (Edwards and Linit 1992, Linit 1990, Wingfield 1983). These insect vectors do their maturation and maintenance feeding primarily on healthy pine trees, but during breeding activities they will use stressed, dying pines or freshly cut trees or logs for oviposition.

PWN was first described from longleaf pine (*Pinus palustris*) in 1929 by Steiner and Buhner (1934). This early report did not indicate the nematode to be pathogenic, and even today there is no evidence of it causing pine wilt disease in conifers growing in natural North American habitats. The PWN resides in dead and dying trees in forests and landscape settings and is commonly found in raw wood products (especially cut logs) or associated with conifers dying from a variety of causes (Bergdahl et al. 1985, Linit and Tamura 1987, Wingfield 1983, Wingfield et al. 1982). PWN has been reported to persist for extended periods of time (5 yrs) in asymptomatic living trees following inoculation but this relationship is poorly understood (Bergdahl and Halik 1993).

PWN occurs throughout most of the U.S., including all states east of the Mississippi River (Robbins 1982). There are a number of reports from across southern Canada and a recent report from Mexico (Dwinell 1993) but none from the Caribbean islands. PWN is most frequently recovered from pines, especially from Scots pine, *P. sylvestris*, which appears to be one of the most susceptible species. The PWN has also been found in other coniferous genera including *Abies*, *Cedrus*, *Larix*, *Picea*, and *Pseudotsuga*, but reports for these genera have been rare (Malek and Appleby 1984, Robbins 1982).

PWN is known to kill exotic pines growing in the central United States. Most of this reported mortality has occurred in Scots pine growing on poor sites (sandy soils, dry sites, or in urban settings) and in areas where climatic conditions are much warmer than in the species' native habitat of Eurasia (Linit and Tamura 1987, Wingfield et al. 1982). PWN also has been associated with mortality of some North American pines growing in overstocked plantations and in seed orchards (Blakeslee et al. 1987, Dwinell and Barrows-Broadus 1983).

In Japan PWN has caused major epidemics of pine wilt since the early 1900. By 1984 it was estimated that approximately 25% (650,000 ha) of pine forests were infested (Mamiya 1987). PWN is thought to have been introduced to Japan in logs imported in the early 1900s. Since then the movement of infested wood has spread PWN and its vectors to the islands of Okinawa and Taiwan and to mainland China (Mamiya 1984, Yang and Wang 1989). Pine mortality has been most extensive in the warm coastal areas of Japan;

however, the most aggressive forms of PWN have been observed in the northern extremes of the nematode's range where introduction from other areas of that country is believed recent (Kiyohara and Bolla 1990, Mamiya 1987). In these cooler inland and northern regions, low temperatures often cause a delay in host symptom development and a slower rate of nematode population increase (Mamiya 1983).

In China the PWN is currently causing serious pine wilt disease problems in their native pines in the localized areas of introduction. The new areas of infestation have been associated with the movement of infested wood into the region (B. Yang, pers. comm.).

CURRENT REGULATIONS

PWN has a history of transcontinental movement in raw wood products, such as logs, lumber, crating materials and wood chips (Mamiya 1984, Rautapaa, 1986, Tomminen and Lahtinen 1990). Eurasia represents the most extensive conifer resource in the world and it is feared that if PWN ever became established there it would cause serious disease problems over a vast region. Large economic losses and drastic changes in the ecology of coniferous forests could result. The most likely way that PWN could be introduced to Europe would be importation of infested raw wood products from North America.

In September 1984, the Finnish Plant Protection Organization intercepted PWN in shipments of wood chips from North America. This discovery prompted an embargo against the importation of certain coniferous wood products from regions of the world known to have PWN (Rautapaa 1986). Since then, Finland has found PWN in lumber shipped from eastern Canada (Tomminen and Lahtinen 1990) and more recently found it in wood crating and pallet lumber from Canada (J. Tomminen, pers. comm.).

Soon after the Finnish Plant Inspection Service intercepted the PWN in green lumber they amended their plant health regulations to require kiln-drying of all coniferous wood imported from areas known to have PWN (Anonymous 1990, Tomminen and Lahtinen 1990). However, Dwinell (1990) and Tomminen and Nuorteva (1992) reported that kiln-heating was just as effective in eliminating the PWN from infested lumber.

In 1986, the European Plant Protection Organization (EPPO) recommended that all member countries adopt import restrictions on raw wood products from regions of the world reported to have PWN. Recently, the European Economic Community (EEC) established a position that all coniferous wood, with the exception of cedar (*Thuja* spp.), entering the European market must be heat-treated or kiln-dried so that all parts of the wood reach a temperature of at least 56° C for 30 minutes. This new regulation was promulgated in 1993 (C. Twarok, USDA, FAS, FPD; pers. comm.).

IMPACT ON NORTH AMERICAN FORESTRY

Since 1984, European import restrictions have had a significant negative impact on export trade of coniferous wood from North America to Europe (Bergdahl 1988, Dwinell and Nickle 1989, Nickle 1985). In 1991, the value of green wood lumber shipments from the west coast of the U.S. that would have been directly affected by EEC restrictions was estimated at about \$150 million (C. Twarok, USDA, FAS, FPD; personal communication) however much of this wood was kiln dried to avoid restrictions. The estimate for potential annual loss in export trade of unseasoned softwood lumber for British Columbia alone exceeds \$700 million (Anonymous 1991). In addition, the multimillion dollar wood

chip markets that had been established in northern Europe prior to 1984 have been lost due to import restrictions (Bergdahl 1988, Bracht 1987, Davis et al. 1987). The new EEC ruling that includes all member countries will significantly add to the North American wood export problem. In the future, these restrictions may impact our long-term forest management and timber harvesting decisions, therefore potentially reducing forest productivity and suppressing the economics of forest-related industries and the rural areas they support.

The current demand for coniferous wood in Europe far exceeds the kiln capacity of North American lumber mills, so current restrictions will reduce export trade of wood products to the EEC. Since "heat treating" is not considered a value-added process as is kiln drying, the producer will have to absorb the additional cost to remain competitive. The EEC is considering requiring phytosanitary certificates even for kiln-dried material, and this action also may have a negative impact on trade for the North American wood industry.

POTENTIAL IMPACT TO OTHER REGIONS OF THE WORLD

In North America, PWN has been found in many genera of conifers but as an introduced pest elsewhere in the world, it is primarily found in pines. *Pinus sylvestris*, although one of the more susceptible hosts for PWN, may not suffer great losses because its native range is in the cooler northern regions of Eurasia (Critchfield and Little 1966, Rutherford and Webster 1987). PWN probably could persist in northern Eurasia without inciting pine wilt disease. However, in the warm, dry climate of southern Europe (Mediterranean area), PWN would come in contact with a variety of other conifers, including *P. nigra*, which is also highly susceptible. This pest could be very devastating in southern Europe.

PWN is not known to occur in Eurasia except in portions of Japan and China (Yang and Wang 1989). If PWN expands its range in Eurasia beyond Japan and China, it will be exposed to a large number coniferous species whose susceptibility is currently unknown. Until a better understanding of the risks associated with importation of wood products infested with the PWN is available, the European position on import restrictions against PWN is justified.

CASE HISTORY NO. 9: OAK WILT - A HIGH RISK AGENT

Few forest pathogens are as capable of killing their hosts as is the oak wilt fungus, *Ceratocystis fagacearum* (Bretz) Hunt. This fungus causes a wilt disease of oaks, chestnuts, chinkapins and tan oaks. The most susceptible species are members of the red oak group (subgenus *Erythrobalanus*). Most North American white oaks possess appreciable resistance, but no oak species is known to be immune.

Oak wilt is known only in the U.S. where the organism is assumed to be native. The disease was first described in Wisconsin in 1942 (Anonymous 1942). Several years later the causal agent was described by Henry (1944). Recognition and proof that the fungus occurred in other states came rapidly, so that by 1951 it had been reported in 18 states from Minnesota to Pennsylvania in the north and Arkansas to North Carolina in the south (Fowler 1952). Its current distribution includes a few additional southern states with the

most destructive recent outbreaks being in Texas. There is some historical evidence that the disease was killing oaks at the beginning of the century in Wisconsin and Minnesota (Gibbs and French 1980). Most investigations have discounted the possibility that *C. fagacearum* is of foreign origin, because it is difficult to envision a fungus becoming established over such a wide area of North America when local dissemination occurs so poorly. Various theories as to the origin of *C. fagacearum* were reviewed by True et al. (1960).

If *C. fagacearum* is a North American pathogen, then its threat lies in its possible introduction to other continents or in some modification of its ability to spread in North America. In recent years, oak wilt has been of particular interest in Europe because it has been hypothesized that the fungus could be destructive to European oaks. To better understand the risk that this organism poses to oaks everywhere, it is important to understand the biology of the disease.

The oak wilt pathogen survives primarily by invading and colonizing the current year's xylem of infected trees. The fungus is poorly adapted to a saprophytic existence apart from recently killed trees (Shigo 1958). It therefore relies on continued dissemination and re-establishment. Dissemination depends either on insect vectors to spread fungal spores overland or on root grafts that allow fungal hyphae to grow between diseased and healthy oaks (True et al. 1960, Kuntz and Riker 1950).

The insects most commonly associated with transmission of the oak wilt pathogen are in the Nitidulidae. These sap-feeding beetles are attracted to fragrant vegetative structures, commonly known as fungus mats, produced by *C. fagacearum* (Boyce 1954). These structures develop between the bark and wood on some infected trees, which cause the bark to split, and allow insects access to the spore producing surface (Dorsey and Leach 1956). As insects frequent the fungal mats, they become contaminated with spores that can be transmitted to healthy trees. A second group of insects, the oak bark beetles (*Pseudopityophthorus* spp.) also have been implicated in vectoring the fungus directly to healthy oaks when they emerge from breeding galleries in diseased trees (Rexrode 1976). Fortunately, in North America the conditions for successful vectoring of spores by insects are seldom met. If they were, the disease would be of far greater consequence.

Spread by root grafts is known to create large infection centers particularly in the Lake States and Texas (Anderson and Anderson 1963). In live oak (*Quercus fusiformis* and *Q. virginiana*) in Texas, disease centers expand because of the clonal development of extensive root systems from which many stems grow (Appel et al. 1989). In the Appalachians, the occurrence of large oak wilt centers is less common, perhaps because of greater species diversity and soil conditions that are less conducive to root grafting.

Once introduced into a susceptible host by insects or root grafts, the fungus spreads rapidly within the current year's xylem vessels by hyphal growth and spores (Young 1949). The host responds by forming tyloses, gums and other compounds that rapidly occlude vessels (Struckmeyer et al. 1958; Jacobi and MacDonald 1980). Susceptible hosts rapidly develop foliar symptoms that include wilting, browning, water soaking and leaf abscission (True et al. 1960).

Factors that influence the distribution of oak wilt are complex and not completely understood (MacDonald and Hindal 1981). Host abundance and disease incidence appear related only in areas where high stem density results in frequent root grafting (i.e., Lake

States, Texas) (Gibbs and French 1980; Appel et al. 1989). Long-distance spread of the fungus occurs by insect vectors, but these have apparently been inefficient because the disease has remained rather static in many eastern states. The pathogen has not become established in areas where highly susceptible oaks grow and efficient vectors are common, specifically areas of the South, Northeast and western U.S. that contain major populations of oak.

Most studies that have examined the relationships among environmental or site factors and disease incidence have been inconclusive (Cones 1968; MacDonald and Hindal 1981). However there is convincing evidence that forest practices do affect local spread of *C. fagacearum*. Spring wounds on trees have been documented as ideal inoculation sites for nitidulid beetles (Juzwik and French 1983). In some areas, such as in central Wisconsin, extensive populations of root grafted red oaks became established after logging and fire destroyed much of the original diverse woodland (Gibbs and French 1980). In areas of Texas, rangeland has become colonized by populations of live oak that have developed from root sprouts. Both of these situations have resulted in extensive root grafting, which is ideal for local spread (Appel et al. 1989)

POTENTIAL IMPACT

Oak wilt is considered to be an internationally important disease because the susceptibility of oak species on other continents is unknown (Gibbs et al. 1984). This is particularly true in Europe where oaks are highly valued for their economic, ecological and cultural uses. In recent years, European concern about oak wilt has increased primarily because imports of oak logs, lumber, and veneer have increased substantially, thus raising the risk of intercontinental movement of the pathogen. There also has been an increase in the planting of susceptible northern red oak (*Quercus rubra*) in many areas of Europe, particularly in France (Pinon et al. 1993). Further, the European experience with reintroduction of Dutch elm disease, a disease with many similarities to oak wilt, has raised fear that oak wilt will cause a similar epidemic.

From our knowledge of the biology of *C. fagacearum*, it is possible to make assumptions about factors that would most influence disease development if the fungus were introduced to Europe. The two issues seemingly of greatest importance are the susceptibility of European oaks to *C. fagacearum* and the mechanisms by which the disease would spread if introduced.

Oak is the most common timber species within the European countries that comprise the EEC, with France being the leading producer (Pinon et al. 1993). Only a small number of species that belong to the white oak group (subgenus-*Lepidobalanus*) occur in Europe (Gibbs et al. 1984). Northern red oak was introduced to Europe near the end of the 17th century but at that time was considered an amenity tree. Because of its rapid growth a significant number of plantations of this species have been and continue to be established there.

Until recently, the only information on the resistance of European oaks was from a 1950s study that indicated 1-2 year-old seedlings of several European species developed symptoms 3-5 weeks after inoculation (Bretz 1955). Because of the lack of resistance information, especially for older trees, cooperative arrangements were made in the early 1980s to establish plantings of European oak in the U.S. Two sites were chosen, one for

northern European provenances (West Virginia) and a second for southern provenances (South Carolina). Preliminary susceptibility data indicate that many of the European provenances developed symptoms more typical of susceptible North American red oaks than white oaks to which they are more closely related. The European trees are scheduled to be challenged with *C. fagacearum* again at ages 12 - 15 in the mid-1990's (Pinon et al. 1993).

A second area of concern is the mechanism of disease transmission. Root graft transmission is accepted as critically important for local spread of the fungus. Root graft studies conducted in southern England have documented root graft formation in ancient coppice stands as well as between 30-year-old plantation trees (Gibbs et al. 1984). Therefore, root grafting would likely play an important role in disease transmission in Europe. A greater unknown regarding transmission is the potential importance of insects as vectors. Insect transmission is a weak link in the disease cycle in the U.S. However, there has been speculation that several insects in Europe are better equipped to be vectors than are their North American counterparts. The chief candidate is the bark beetle *Scolytus intricatus*. This species is relatively large and aggressive and capable of invading the trunk and main branches. Hence, it may be a better vector of *C. fagacearum* than are nitidulids or *Psuedopityophthorus*. The potential of a variety of European beetles to serve as vectors is reviewed by Yates (1984).

CURRENT REGULATORY PROCEDURES

In the late 1970s, the EEC passed Directive 77/93 which dealt with methods of log and lumber treatment to minimize the risk of introducing *C. fagacearum* into Europe. Unfortunately, the procedures outlined in this directive were so restrictive that both the U.S. and European wood industries believed it would significantly reduce or eliminate U.S. oak exports (Jakes 1992). As a result of these concerns, research was initiated to develop more practical certification procedures.

Studies funded by The National Lumber Exporters Association and coordinated by the U.S. Forest Service were conducted to evaluate the efficacy of methyl bromide fumigation to kill the oak wilt fungus in logs and lumber and to measure fungus survival in air-dried lumber. Air drying of lumber required unacceptably long time periods to kill the fungus (Tainter et al. 1984), but methyl bromide fumigation effectively eradicated *C. fagacearum* from logs without product degradation (MacDonald et al. 1985). As a result of this experimentation, EEC directive 77/93 was amended in 1983 to permit importation of fumigated oak logs (Table 3), though some EEC member nations (England, Greece, Ireland, Italy and Portugal) prohibit the importation of any oak logs with bark. Details of the other aspects of the coordinated European and U.S. research efforts on oak wilt are given by Gibbs et al. (1984).

The spread of oak wilt in the U.S. has been slow and sporadic, and a relatively small number of infected trees exist. Even though most scientists have accepted the premise that the risk of export and establishment of the pathogen elsewhere is quite small (even without fumigation), no one should accept the argument that the experience with oak wilt in the U.S. reflects its potential on other continents.

CONCLUSIONS AND RECOMMENDATIONS

Introduced forest pests represent a major environmental problem that is likely to escalate in the future. The rate of invasions by exotic pests has been accelerating over the last 200 years (Fig. 1), and given current trends in human demography, this acceleration will likely continue. The ecological and economic impacts of invasions to forests is comparable to several other important environmental problems, and considerable international attention should be given to reducing or mitigating potential impacts (U.S. Office of Technology Assessment 1993).

Although some measures are currently being taken to prevent the transportation of exotic pests, relatively little additional effort in this area could substantially reduce the frequency of forest pest invasions. There is a need for all countries to assess the potential risk for introduction of a variety of potential exotic pests, many of which have not been identified (Ciesla 1993). Evaluation of risk may entail conducting additional research on forest pests in their country of origin in order to better understand the biology of these agents. There also is a need to increase inspection and quarantine efforts. As shipping technology changes, inspection, quarantine, and mitigative procedures must be adapted to prevent increases in pest introductions.

Special attention should be focused on introduced plant species. Many of the historical introductions of exotic plants were the result of ill-conceived actions, and similar introductions continue to occur. Under current U.S. federal regulations, there are no barriers to importation of new plant species, unless they are listed on the Federal Noxious Weed List. Under the current Federal Noxious Weed Act, interstate movement of exotic plant species is permitted, unless a quarantine and eradication or control program is present. Schmitz et al. (1991) stress that this policy fails to prevent the interstate shipment of several federally prohibited plant species that are being sold commercially. A new federal noxious weed policy has been proposed which, if approved, will include many additional species.

Whether importation and naturalization of any plant species will be beneficial or harmful is debatable. However, such actions should be approached with as much caution as we approach the introduction of biological control agents. Development of a set of principles and guidelines for importation of exotic plant species should be a high national priority. Implementation of such a risk assessment system may be expensive, but long-term savings would be realized when the cost of control measures for introduced pests are considered (U.S. Office of Technology Assessment 1993).

The probability of pest establishment could be greatly decreased if a greater effort went into detecting new infestations (Wylie and Peters 1987). Risk analysis data could be used to identify high-risk species and intensively search for new populations. Such a program would increase the chances of eradicating introduced pests while their populations are small and localized.

Given the magnitude of exotic pest problems that are expected in the future, considerable attention should be given to this problem in forest management. Clearly, planting exotic tree species is a risky venture both because of the potential for the tree

species to become a pest but also because exotic plant species are bigger targets to exotic pests (Pimentel 1986). Exotic pests are an even greater problem in agriculture, where most plants are exotic, and foresters should take a lesson from these experiences. Given the uncertainty about precisely which exotic pests will become established in the future, foresters should avoid relying on one or only a few tree species to meet society's demands for wood and fiber in the future. A diversity of tree species would decrease the odds that an exotic pest would devastate forest resources.

A final recommendation for minimizing the impacts of exotic forest pests in the future is to promote self-sufficiency in wood products. Importation of both raw and processed wood products increases the odds of pest introduction and should be avoided in order to minimize impacts on forest resources. Thus, although not initially obvious to all, the most efficient way to protect and preserve our native forests may be to wisely manage them for wood products.

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Table 1. Biological attributes of invading forest pests.

Traits related to arrival	Traits related to establishment
Naturally mobile	High reproductive rate
Affinity for humans and their technology	Wide host preference
Resistant or dormant life stage(s)	Tolerant of climatic extremes
	Efficient mate location
	High genetic or phenotypic plasticity

Table 2. Some of the more important introduced forest pests and diseases in North America.

Agent	Latin Name	Origin	Hosts	Tissue Attacked
INSECTS				
Gypsy moth	<i>Lymantria dispar</i>	Europe, Asia	Hardwoods	Foliage
Winter moth	<i>Operopthera brumata</i>	Europe	Hardwoods	Foliage
European pine sawfly	<i>Neodiprion sertifer</i>	Europe	Pines	Foliage
Balsam woolly adelgid	<i>Adelges piceae</i>	Europe	True firs	Phloem
Hemlock woolly adelgid	<i>Adelges tsugae</i>	Asia	Hemlocks	Foliage
DISEASES				
Chestnut blight	<i>Cryphonectria parasitica</i>	Asia	Chestnuts	Cambium, phloem
White pine blister rust	<i>Cronartium ribicola</i>	Europe, Asia	white pines	Needles, stems
Beech bark disease	<i>Nectria coccinea var. faginata</i>	Europe	Beech	Bark, cambium
Dutch elm disease	<i>Ophiostoma ulmi</i>	Europe	Elms	Xylem, phloem
PLANTS				
Banana poka	<i>Passiflora mollissima</i>	S. America		
Australian pines	<i>Casuarina spp.</i>	Australia		
Brazilian pepper tree	<i>Schinus terebinthifolius</i>	S. America		
Faya tree	<i>Myrica faya</i>	mid-Atlantic islands		
Melaleuca	<i>Melaleuca quinquenervia</i>	Australia		

Table 3. Current EEC oak export requirements described by EEC directive 77/93 as amended in 1983.

Commodity	Required treatment
Oak lumber (all species)	Boards must be stripped of all bark and square edged, or treated by kiln drying, hot air, or hot water
Oak logs (white oak Oct 15-April 30)	Shipped freely after chemical color test to confirm species identification
Oak logs (red oak-year round/white oak May 1-Oct. 14)	Fumigation treatment (APHIS PPQ Manual/T-312) with methyl bromide required

Figure Captions

Fig. 1. Cumulative number of exotic species of insects and mites introduced to the United States (from Sailer 1978)

Fig. 2. Major flows of forest products in international trade (modified from Laarman and Sedjo 1992).

Fig. 3. Dynamic patterns in a hypothetical invading population that fails to establish (solid line) and a hypothetical established population that reinvades from adjoining populations.

Fig. 4. Historical spread of the gypsy moth in North America.