EXOTIC INSECTS IN NORTH AMERICAN FORESTS: ECOLOGICAL SYSTEMS FOREVER ALTERED

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ABSTRACT. More than 400 species of exotic phytophagous insects have become established on native and introduced woody plants in North America. About 5 percent of these invasives have well-recognized, severe ecological impacts on the trees and ecosystems that they occupy. For the others, very little is known about their influence on natural processes. However, evidence suggests that all may irrevocably change their respective, invaded ecosystems. In the worst cases, the exotics insects have become the "final straw" causing their adopted host plants to fall into perennial decline-death spirals.

EXOTIC FOREST INSECTS: PILING STONES UPON A SAGGING BACK

In North America, there are currently at least 400 species of exotic insects which have become naturalized on native and introduced woody plants in forests, parks, and urban landscapes (Mattson et al. 1994, Niemelä and Mattson 1996). Many of these invaders, such as the gypsy moth, *Lymantria dispar*, the balsam woolly adelgid, *Adelges piceae*, and the beech bark scale, *Cryptococcus fagisuga*, have precipitated serious ecological and economic consequences, the full magnitudes of which are not yet fully appreciated (Liebhold et al 1995, Wallner 1996, see also Wallner this volume). In fact, Liebhold et al (1995) and Wallner (1996) astutely observed that biological invasions, i.e., the wanton spread and establishment of alien organisms in native ecological systems, can have local ecological consequences as important as those resulting from rising levels of pollution and global climate change. Yet, the number of exotics continue to rise along with international trade, and travel (Liebhold et al. 1995, Wallner 1996).

In trying to simply comprehend the general physiological and ecological effects of exotic insects and pathogens upon their newly adopted host trees and forests in North America, it is instructive to invoke the metaphor of loading stones upon the back of an already laden beast of burden. The metaphor, though imperfect, is apt because it emphasizes that the trees which serve as new hosts for the alien herbivores are already carrying a significant burden of native herbivores, most of which have long been associated with the particular trees--for at least hundreds of thousands if not millions of years (Tahvanainen and Niemela 1987, Labandeira et al. 1994). The effects of loading yet another one, two, or even more new species of insects on top of a typical, already in-place load of about 50 species (Strong et al. 1984, Niemelä and Mattson 1996) are not simply linear, but are decidedly nonlinear. In other words, the impacts of the new, additional species are often vastly out of proportion to their number. Why? For one, the host tree has no evolutionary history with the new consumer and thus (a) may have minimal defenses (including damage repair, recovery) with which to respond to it, or even worse, (b) the tree may over react (in terms of a rapid inducible resistance) and in the process kill itself, such as in auto-immune disorders in humans. Moreover, the exotics are invariably lacking in natural enemies and hence can cause vastly more feeding damage than the natives. The net result is that exotics, when coupled to the natives, and the normal, abiotic stresses and strains, may induce total herbivory to overshoot the "load bearing" limit, the resilient capacity of the tree, causing it to become physiologically depressed and ecologically disadvantaged. In fact, this is the thesis of the paper. Moreover, I propose that the host tree and its ecosystem is forever altered as the result of the invasion of the exotics.

THE DEATH, DECLINE SPIRAL: EXOTICS AS INCITING FACTORS

When subjected to numerous simultaneous stresses or debilitating experiences, trees and even whole ecosystems may end up slipping from their normal growth and development trajectories onto the slippery slopes of a death-decline (D/D) spiral from which recovery is difficult because of many reinforcing feedback loops that inexorably push (ratchet) toward further plant/system dysfunction, weakness, and ultimately death (Fig. 1, Manion 1981). Manion (1981) classifies the many interacting factors surrounding the D/D spiral into predisposing, inciting, and contributing factors. Predisposing factors are usually the background abiotic components of a particular environment, and the unique properties of the trees therein (e.g. their genetics, age, etc.). On the other hand, the inciting and contributing factors are mainly the background of biotic stressing agents. However, severe, episodic "acts of god" such as frost, drought, or human-caused stresses are also included among the inciting factors. Using this framework, I would argue that exotic insects and diseases often behave as severe, inciting stress factors during their "initial" contacts with new host populations. In a particular landscape, this "early" period of intense and severe (inciting) impact of invasive insects on hosts may play out for many decades or even centuries before the interactions "evolve" to become less intense and less severe owing to critical changes in the gene pools of hosts and invasive insects, and heightened deleterious impacts of natural enemies upon the invasive insects as more and more native predators and parasites eventually adopt the exotic as host and food. Over the long-haul, as the exotics spread everywhere, and the systems adjust ecologically and evolutionarily, the invasive exotic may eventually change into the role of a contributing factor. When this happens, probably no less than a hundred years from its first contact with any particular local landscape, no one will remember and few people will understand how the system has been changed as the result of the invader(s). Just as we accept the presence of dandelions, *Taraxacum officianale*, without thinking about their exotic origins and ecological impacts, we now also indifferently accept the absence of American elms, *Ulmus americana*, or only a small fraction of the number that used to occur in urban, rural and forest landscapes before the spread of dutch elm disease by introduced and native species of bark beetles. Few ask what, if anything, was lost when so many elms disappeared? Is it possible that the American elms will ever recover their former prominence? Not likely—at least within any time frame meaningful to *Homo sapiens*.

TREES PUSHED TO THE EDGE

Fortunately, not all of the 400 or so exotics insects which are now naturalized and living on woody plants in North America have become the final "straw" leading to the general breakdown and collapse of the plants they attack. In fact, most exotic species, though common and widespread, seem to have only very localized severe effects, i.e. their severe impacts are limited to very few, and particular trees. One such exotic is the eastern spruce gall aphid, *Adelges abietis*, which forms small pineapple-like galls on the tips of elongating white spruce, *Picea glauca*, shoots. Although most trees are infested to some extent, only few trees are so heavily attacked that they are rendered incapable of competing with their neighbors (Mattson et al. 1996). However, the impacts of most species are not known but suspect. For example, there are 20 plus species of introduced, root-feeding weevils (e.g. *Otiorynchus, Polydrusus, Phyllolobius* spp) which are incredibly abundant in forests. Their huge numbers suggest that they must be taking a toll, although it has yet to be determined. In addition, their serious impacts on woody ornamentals in nurseries and in urban settings also imply that these inconspicuous, unstudied immigrants may be having important, though unappreciated, ecological impacts (Drooz 1985).

On the other hand, about 20 species of exotics typically have frequent and extensive, severe effects on their host plants. These are the subject of the following discussion. Insects in this category seem to be either (a) the definitive "final straw," or (b) the conditional "final straw." The mere presence of the former type seems to start the unraveling of the system, whereas the second type precipitates an unraveling usually only under conditions of concomitant abiotic stresses. The "overloading" of trees with exotic insects and pathogens can easily render them ecologically "incompetent" in their natural ecosystems and hence lead to their ultimate displacement by other species. And, it can also render them economically unsuitable for use in commercial forestry applications owing to their diminished growth rates, and high probability of failure before harvestable products are produced.

EXOTICS AS THE DEFINITIVE "FINAL STRAW"
SOME EXAMPLES

Beech: One of the premiere examples of an exotic insect precipitating serious and widespread debilitation of its newly adopted host plant is the case of the European beech bark scale on North American beech, *Fagus grandifolia* (Houston 1994, also Houston this volume). The scale's feeding stylet penetrates and alters the bark such that formerly innocuous, native *Nectria* spp fungi can also enter the bark and trunks and trigger rapid decline and death of the trees.

Elm: A similar example of an exotic insect and pathogens in tandem pushing a tree species to an ecological precipice is the well-known case of the European elm bark beetle, *Scolytus multistriatus*, vectoring the deadly Eurasian fungus, *Ceratocystis ulmi*, along with three other exotic bark and several American bark beetles. Although most of the American elms in urban and rural landscapes of eastern North America have long since been killed and removed, and out of public attention, elms are still dying in great numbers in the forests at the western edge of the advancing infestation wave. For example, between 1980 and 1993 in the Upper Peninsula of Michigan, the number of elms declined by 65%, from 66.1 to 22.9 million, and growing stock volumes dropped 75%, from 189.5 to 47.3 million ft^3 (Spencer 1982, Leatherberry 1994, Schmidt 1993).

Firs: Another exotic insect renown for its high damage potential is the balsam woolly adelgid, (BWA) which feeds by means of its hair-like stylet, on the boles, twigs and buds of Fraser fir, *Abies fraseri*, and bracted fir, *A. balsamea* var. *pheneroleopis,* in the southern Appalachians. Although some may argue that acidic deposition and drought were also involved, the BWA appears to be the most parsimonious explanation for the rapid death and decline of 80-95% of mature firs in several locations, but especially at Mt. Mitchell, North Carolina (Witter and Ragenovich 1986).

Hemlock: Three species of exotic sucking insects could ultimately prove to be important inciting factors in the death and decline of eastern hemlock, *Tsuga canadensis*. The hemlock woolly adelgid, *Adelges tsugae*, which is currently confined to a handful of mostly eastern seaboard states, and two exotic scales (*Fiorinia fioriniae*, and *Fiorinia externa*) need to be vigilantly monitored for their expanding impacts along with natives such as the ever-devastating hemlock looper, *Lamdina fiscellaria*, and the hemlock borer, *Melanophila fulvoguttata* to guard against escalating hemlock losses.

White Pine: Two exotic defoliators, the introduced pine sawfly, *Diprion similis*, and the pine falsewebworm, *Acanthodyla erythrocephala*, coupled to the lethal, Eurasian-origin, white pine blister rust, *Cronartium ribicola*, and the native white pine weevil, *Pissodes strobi*, have caused many to question white pine's, *Pinus strobus*, utility as a commercial tree species, not to mention its capacity for long-term survivability and regeneration in the wild. Besides these concerns, white pine is also noted for its high susceptibility to damage by tropospheric ozone which is rising in the United States.

Red Pine: Two exotic defoliators, the European pine sawfly, *Neodiprion sertifer*, and the pine falsewebworm, coupled to two rather recently introduced sucking insects, the red pine adelgid, *Pineus boerneri*, and the red pine scale, *Matsucoccus resinosae*, and European scleroderris canker, *Gremmeniella abietina*, may eventually threaten the usually high commercial potential of *Pinus resinosa*. Red pine is not known for its high genetic variability and hence may have limited genetic resources to call upon for surviving the onslaughts of devastating exotics.

EXOTICS AS A CONDITIONAL "FINAL STRAW" SOME EXAMPLES

Paper birch: Four species of sawfly leafminers from Europe, especially *Fensusa pusilla*, are well known for their chronic and heavy defoliation of paper birches in North America. These insects, when coupled to several native defoliators, aphids, and especially to drought, and then to the very lethal bronze birch borer, *Agrilus anxius*, can wreak havoc on urban and forest-growing birches. The one-two punch of drought and bronze birch borer are bad enough, but to further debilitate the trees through heavy defoliation virtually guarantees that birch growth rates, and life expectancy will be significantly diminished. For example, following a series of dry summers, there was a 400% rise in birch mortality in Minnesota in the years 1990-92, translating to over 105 million dead trees (Twardus and Mielke 1995). At the same time, about 75% of the birches in Wisconsin had at least low levels of crown die back.

Sugar Maple: The exotic pear thrips, *Taeinothrips inconsequens*, a cell-sap feeder, when coupled to several native defoliators like the forest tent caterpillar, *Malacosoma disstria*, the bruce spanworm, *Opheropthera bruceata*, the maple leafcutter, *Paraclemsia acerifoliella*, and root pathogens may together be important inciting factors in the decline and death of sugar maple, *Acer* *saccharum* (Parker et al. 1991). However, abiotic factors like drought, acidic deposition, and stress-induced flowering are also likely to be crucial contributing factors.

Oaks: The European gypsy moth has caused cyclical and heightened defoliation of eastern North American oaks for over 100 years. They, along with several native defoliators like the forest tent caterpillar, and random weather stresses (e.g. severe spring frosts and drought) and follow-up attacks by the two-lined chestnut borer, *Agrilus bilineatus*, on weakened trees, are undoubtedly changing the structure of mixed oaks forests (Wallner 1996). For example, in the state of Michigan, this very combination of factors has precipitated the death (varying from 10-100%) of northern pin oak, *Quercus ellipsoidalis*, on about 387,000 acres (Twardus and Mielke 1995).

Spruces: The European aphid, *Elatobium abietinum*, has sporadically caused severe outbreaks on western spruces, *Picea* spp, precipitating the extensive decline and death of trees both in urban and forested environments along the west coast (Furniss and Carolin 1977). During 1995-96, in the Rocky Mountain region of the United States more than 10,000 acres of blue spruce, *P. pungens*, forests were severely defoliated and may very likely succumb to attacks by bark beetles. Nothing is known about the particular circumstances leading to the severe outbreaks, but it is likely that unusually favorable weather for aphid survival and reproduction is part of the story.

IS THERE A SOLUTION?

Given that there are no less than 400 exotic insects, and 20 or so exotic pathogens now naturalized in the forests, parks, and urban landscapes of North America (Liebhold et al 1995, Niemela and Mattson 1996), is there anyway to minimize the potentially negative impacts of these biological pollutants?

First thought. We must minimize the spread of exotics. Therefore, we need to aggressively plug the leaky "dikes"at crucial environmental boundaries, staunching the influx of new invasive organisms. This is an absolute given. The same should apply to the movement of already existing exotics in North America.

Second thought. We must find inexpensive and ecologically tenable ways to limit population growth of the exotics species. This will be possible through several avenues: (1) enhance the build-up of natural enemies of the exotic pest by facilitating the transfer of natives to it, and by importing natural enemies from the exotic's ancestral environment, (2) facilitate the development of natural plant defenses (including tolerance) that are efficacious against the exotics by employing classical and novel genetic engineering methodologies, (3) discover, create, and restore ecological, environmental conditions that are inimical to the exotics through special forest management, silvicultural approaches, (4) invent and employ special methods to lower the effective breeding stock of the pest, such as the "sterile male," trapping out, and pheromone bewilderment methods, and most importantly, (5) brainstorm entirely novel approaches.

All of the potential solutions will have substantial costs, and none is likely to yield overwhelming results in the short run (10 years). In fact, it is unrealistic to expect significant break-throughs until 2 decades of effort have been invested. Fortunately, there have been some remarkable success stories that justify the substantive investments. For example, the outbreaks of at least three very damaging exotic defoliators (*Coleophora laricella, Gilpinia hercyniae, Pristiphora erichsonii*) and one shoot borer (*Rhyacionia buoliana*) have been essentially eliminated following the establishment of parasites and pathogens from the ancestral home of the exotics. In other words, though still present in North America, their numbers have been brought down to tolerable levels and hopefully so have their ecological and economic impacts.

Of course, such timetables for attaining success are dependent to a degree on the amount of effort and money expended. In any case, developing methods for stopping and managing exotics is a trench war that will never be won with weak resolve and capricious support. However, it's not the only problem begging for attention. Because the world is now changing at a record pace owing to the huge (6 billion) population and its unprecedented impacts on fundamental life support systems, incredible numbers of critical issues need to be addressed simulataneously. It provokes one to ask whether there is enough money to go around.

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Figure 1. The decline-death spiral showing the many interacting factors, from Manion (1981), printed with permission of Prentice-Hall, Inc.