Forest Health & Biodiversity News
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Biodiversity, Food-web Complexity, and Spruce Budworm Cycles

A recent long-term study, conducted in the Acadian forest ecosystem of New Brunswick, revealed a remarkably complex, yet highly flexible food web on balsam fir (*Abies balsamea*). This food web changes consistently and dramatically both in time and space in response to natural changes in the abundance of one of North America's most eruptive and devastating forest pests - the spruce budworm (SBW) (*Choristoneura fumiferana*).

The SBW, being indigenous to North America, has developed intricate relationships with its host trees, other co-inhabiting herbivorous insects, and a myriad of natural enemies – insect parasitoids (parasitic wasps and flies), entomopathogens (viruses, fungi, and bacteria) and predators (vertebrates and invertebrates) - that attack the SBW and/or the other insect herbivores. The vast majority of ecological studies on the SBW have monitored the insect in isolation of much of the community in which it lives, focusing mainly on its interaction with its immediate (primary) natural enemies in attempts to determine why it undergoes large fluctuations in abundance over its 35-40 year outbreak cycles typical in eastern Canada. Virtually ignored are all the other species in the SBW community, namely, other insect herbivores with which it shares many natural enemies, and the secondary and tertiary natural enemies (hyperparasitoids) that feed, respectively, on primary and secondary natural enemies. Consequently, little is known about the identity and role of these organisms in shaping both SBW outbreak cycles and overall food-web structure within different landscapes (forest stands with different mixes of tree species) and how food-web structure could be influenced by fluctuations in SBW abundance - a natural perturbation effect.


Illustration : Deborah Perry

Diversity of parasitoid and hyperparasitoid species increases with increasing spruce budworm density.

Researchers at the Canadian Forest Service's Atlantic Forestry Centre documented and analyzed 20 plot-years of field data, coupled with manipulative field experiments, on the composition and structure of the balsam fir food web at three plots varying in landscape (resource) structure over a SBW outbreak and decline. The study revealed an incredibly complex and diverse assemblage of species interacting at five conventional trophic (feeding) levels: 1 host plant; 6 herbivores; 66 primary parasitoids and 21 primary entomopathogens; 23 secondary parasitoids and 1 secondary entomopathogen; and 6 tertiary parasitoids (Fig. 1). This parasitoid-entomopathogen assemblage is probably the most complete and diverse described to date for any insect herbivore community, rivaling that of many tropical food webs in terms of the total number of parasitoid species.

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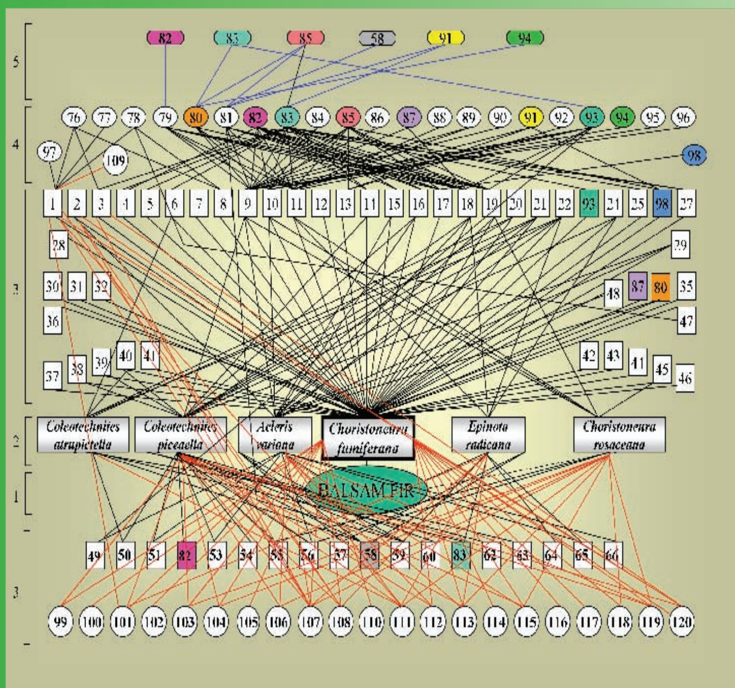

Fig. 1. Structure of the balsam fir food web. Trophic (feeding) levels are identified by brackets and numbers on the far left.

1st trophic level contains balsam fir;

2nd trophic level contains herbivores;

3rd trophic level contains primary parasitoids (squares) and primary entomopathogens (circles);

4th trophic level contains secondary parasitoids (ovals) and a secondary entomopathogen (circle); and

5th trophic level contains only tertiary parasitoids (octagons).

Numbers enclosed in polygons represent different species.

However, Fig. 1 is only a static representation of the many players and interactions found in the food web. In actual fact, the food web is a 'living' dynamic system that responds to variation in time and space. The incredibly flexible food-web architecture actually expands and contracts, like an accordion, with changes in SBW abundance. For example, as SBW increases in abundance, it attracts primary parasitoids (birdfeeder effect) and this increase in primary parasitoids attracts hyperparasitoids. In other words, an increase in SBW abundance is accompanied by an increase in insect diversity and in food-web complexity – the food web expands as progressively more generalist parasitoids (parasitoids that have multiple hosts) feed higher up in the food web. Conversely, when SBW populations decrease, diversity decreases and complexity decreases – in essence, the food web contracts and gets relatively shorter and simpler due to some omnivorous species switching to feed on hosts lower down in the food web, along with some higher-order generalist parasitoids leaving to find more profitable feeding areas. In addition, species composition changes somewhat from high to low SBW densities; certain primary parasitoid species common at high densities are not present at low densities, whereas a few other species are found only at low densities. Thus, both diet shifts and changes in species composition help to continuously shape and reshape food webs during a SBW outbreak. This inherent food-web flexibility is very important because, according to recent foraging-based food-web theory, it can play a major role in maintaining stable or persistent ecosystems.

Importantly, the study also revealed a greater diversity of generalist primary parasitoids and hyperparasitoids, as well as greater amounts of omnivory, at high SBW densities in heterogeneous than in homogeneous plots. This greater food-web flexibility in heterogeneous plots, augmented by the fact that heterogeneous plots also have more plant diversity to support more and diverse alternate and alternative host species (host species that parasitoids can attack in addition to SBW) than in homogeneous plots, can be extremely important in muting SBW damage in heterogeneous plots. In fact, food webs in the two most heterogeneous plots were characterized by a lower peak SBW density (and thus lower defoliation) than in the most homogeneous plot. Thus, the study provides a plausible mechanism for previously published observations (G. Su, D.A. MacLean and T.D. Needham; UNB) that the greater the degree of heterogeneity of a forest stand (amount of hardwood – balsam fir content) the lower the level of damage to balsam fir from SBW feeding.

Overall, the results have important implications for some key ecological issues:

(1) Biodiversity/conservation – the study provides clear evidence that food-web structure and complexity is not static in time and space but changes dramatically and consistently with natural changes in the density of the major food-web player – in this particular case, the SBW. Thus, SBW, despite its negative economic impact on the forest, is nevertheless an integral and vital player in the forest ecosystem. Further, it is evident that to understand how ecosystems function and how they can be affected by natural perturbations such as insect outbreaks, it is critically important to understand the network of trophic interactions (biostructure) in the ecosystem, not just the diversity of species contained therein;

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Are Urban Forests an Advanced Indicator of Climate Change?

Urban forests may offer advanced indication of the effects of climate change on forest ecosystems, given the specific physical conditions under which urban ecosystems and urban forests function. If this is the case, urbanized sites can be considered as tools for large-scale simulation of future climatic conditions or as amplifiers of climate change effects currently taking place. It is apparent that urban conditions (physical and otherwise) magnify the effects of climate events, increase physiological stress on trees, and lower species richness. For these reasons, urban ecosystems merit focused scientific investigation.

Specific Characteristics of Urban Ecosystems

Cities are hotter environments than geographically comparable natural sites. The measurable ambient temperature difference of urban forests (the urban "heat island" effect) has a direct effect on their composition and condition. Though rarely a consideration for northerly landscape planners at present, further south, nocturnal summer temperatures are a fundamental factor in tree species selection. For example, Norway maple (*Acer platanoides*), ubiquitous in cities in Hardiness Zones 7 and points north, cannot be grown with success in Hardiness Zone 8 or further south.

Due to human activity and vehicle emissions, many urban forests develop and function under elevated levels of atmospheric carbon dioxide, carbon monoxide and ground-level ozone. Urban forest sites often feature disturbed and nutritionally impoverished soils with limited flora for forming mycorrhizal associations and nutrient recycling. These conditions might also be expected to result from the extremes of an altered climate.

Modern architecture accelerates prevailing winds, meaning increased structural loading and increased transpiration for trees. Heat energy reflected and radiated from concrete exposes urban trees to intense fluctuations in microsite temperatures, particularly within the laminar boundary layer between the atmosphere and paved surfaces. In cities where snow accumulates in winter, the periodic removal of snow around street trees produces rapid freezing of root zones. When repeated several times in a winter, a series of extreme weather events is simulated.

Indication of climate effects on urban trees. Green ash (Fraxinus pennsylvanica) showing normal form (left) and form as affected by the ice storm of 1998 (right).

Similarly, the extensive non-permeable (paved) surfaces of urban environments magnify drought and rain events. Surfaces that do not absorb precipitation impede moisture uptake by roots but also facilitate the rapid local accumulation and violent outflow of storm waters.

Considered together, the above factors create a severe and dynamically altered climate for urban forests when compared to forests located "out in the country".

What, if Anything, are Urban Forests Telling Us?

Trees found on highly artificial urban sites (specimens trapped in containers or with root systems and crowns repeatedly exposed to mechanical damage) tell us little about climate effects and must be written off as artefacts. However, functioning urban trees (trees in remnant stands, ravines or parks) often exhibit characteristic differences in comparison to trees in natural forests and may be of interest to climate change researchers. "Generally observed" urban tree characteristics include: reduced life span; reduced crown size at maturity; altered crown and branch form; increased occurrence of crown scorch and leaf necrosis; seasonally advanced leaf color change; early leaf senescence; and increased pathogen and insect pest levels —all indications of physiological stress.

Are Urban Forests An Indicator of Successful Climate Change Adaptation?

If urban forests replicate (to any extent) a natural environment under intensified or accelerated climatic-induced stress, then tree species that are successful under urban conditions should present characteristics useful for forest ecosystems that must adapt to future climate change. The most striking feature of urban forests, from a horticultural perspective, is their severely limited species richness. Despite having an apparent wealth of material from which to choose, the majority of working horticulturalists employ a very short list of woody plant material — urban conditions mitigate against biodiversity. The short list of species that do thrive under urban conditions (in temperate urban forests at least) exhibit all the characteristics of, or are, invasive species.

Exotic species are selected by landscape planners to the point of monoculture creation. Examples include the maidenhair tree (*Ginkgo biloba*) or little-leaf linden (*Tilia cordata)*, as well as specifically adapted varietal forms of native species such as honey locust (*Gleditsia triacanthos* var. inermis) and green ash (*Fraxinus pennsylvanica* var. subintegerrima). Selection is based on the broad ecological amplitude (inherent tolerance of soil and site characteristics across a wide range of conditions) and superior resistance to drought, heat, pests and pollution. These are characteristics of invasive species — precisely opposite to what would be desirable in a highly adapted, site-specific species.

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Emerald Ash Borer: It's Here to Stay, Let's Learn How to Manage It

In an earlier issue of this newsletter (Volume 8, No. 1, Spring 2004), Hopkin *et al*. discussed the introduction, basic biology, signs and symptoms of attack, and research needs for control of the emerald ash borer (EAB), *Agrilus planipennis*. At that time, the known North American distribution of EAB was restricted to Essex County in Ontario, southeastern Michigan and northwestern Ohio. The spread of an invasive alien species can occur slowly by natural dispersal or more rapidly by human-assisted movement. For wood-boring beetles, like EAB, the latter may occur through the movement of unprocessed wood material, infested firewood, or nursery stock. Tree-dating techniques suggest that EAB was present in the Detroit area for about 10 years prior to its discovery in 2002. Consequently, the insect had a long period in which to spread unchecked and unregulated before it was discovered. In the intervening years, the beetle has been found widely distributed in Michigan, Ohio, Indiana, and in localized populations in Illinois, Maryland, Pennsylvania, and West Virginia. The recent discovery of EAB in Toronto is the most easterly population detected to date in Canada. Many of these populations were well-established when found and some may have pre-dated the imposition of quarantine regulations.

EAB, as its name suggests, attacks all species of true ash trees (*Fraxinus* spp). Since its arrival in North America, the beetle has killed millions of ash trees. In northeastern North America, there are five species of native ash trees: green ash (*F. pennsylvanica*, a.k.a. red ash), white ash (*F. americana*), black ash (*F. nigra*), blue ash (*F. quadrangulata*); and pumpkin ash (*F. profunda*). The first two are important hardwood species used in the manufacture of cabinetry and sporting goods. Black ash is favoured by First Nations people for the fabrication of baskets and other crafts. Pumpkin ash and blue ash are uncommon species in Canada that grow in extreme southwestern Ontario. Blue ash was designated a 'Threatened' species in Canada in April 1983 by the Committee on the Status of Endangered Wildlife in Canada. Its status was re-examined in November 2000 and the species was downgraded to 'Special Concern'. Blue ash appears to have some resistance to the beetle, but pumpkin ash, a species that was unknown in Ontario until 1992, is very susceptible. All native ashes are thus candidates for genetic conservation. Eleven other species of ash grow elsewhere in North America and, along with exotic ashes, are also at risk. Asian species appear less susceptible.

Adult emerald ash borer (top).
Dead ash trees in a woodlot in southwestern Ontario (bottom).

If the invasion rate of alien insects like EAB can be slowed, costs associated with managing the insect's impacts can be prorated over time. A slow-the-spread strategy also buys time for the development of other control options. Quarantines and regulations, under the authority of the Plant Protection Act, prohibiting or restricting the movement of potentially infested materials, are designed to slow the spread of invasives. Regulated materials for EAB include nursery stock, trees, logs, wood, rough lumber including pallets and other wood packaging materials, bark, wood chips or bark chips from ash (*Fraxinus* spp.), and firewood of all species. Currently in Ontario, the combined regions of Essex Co. and Municipality of Chatham-Kent (formerly Kent County), Lambton Co., Elgin Co. and Middlesex Co. are each quarantined under an Infested Places (Ministerial) Order prohibiting or restricting the export of ash materials and firewood beyond their borders. Within Lambton, Elgin and Middlesex Counties, properties within 5 km of infested trees are also quarantined via Notices of Quarantine issued to individual property owners. These quarantine measures restrict the movement of regulated materials from these properties. The net effect is a nested-quarantine (quarantine within a quarantine) structure.

For counties like these that are not believed to be completely infested, the nested structure reduces the risk of EAB being spread through human activities from known infested (and regulated) areas to other areas of the county that may not be infested, while still regulating high risk materials from leaving the county. This has the dual benefit of slowing both intra- and inter-county spread of EAB. For localized infestations, such as those recently discovered in Norfolk County and Toronto, only individual infested properties have been quarantined to this point through the issuance of Notices of Prohibition of Movement. This is an interim solution until other quarantines can be applied.

The greatest challenge to managing this insect has been our inability to locate new low-density populations. Although significant research efforts have been made in the identification of an attractant, an efficient lure for detection traps remains elusive. Thus, we must rely on the presence of signs and symptoms of the insect's activity to detect infested trees. Signs and symptoms include thinning and dieback of the tree crown, deformities of the

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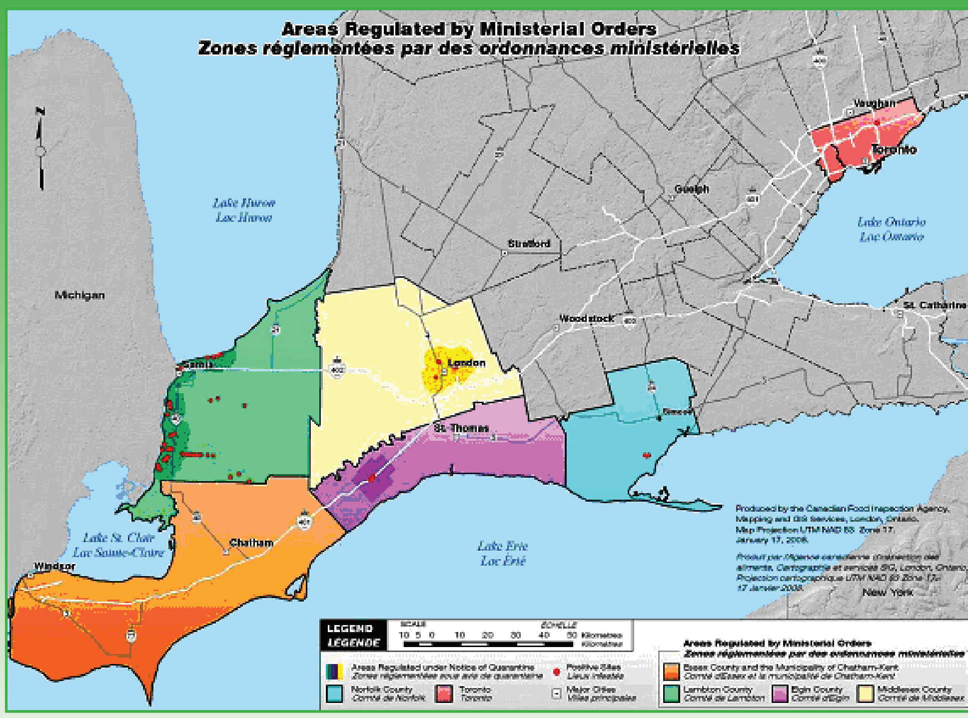

Distribution and regulated areas for emerald ash borer in Canada (prepared by Canadian Food Inspection Agency).

of the bark, development of shoots from the bark, D-shaped adult emergence holes, and holes created by woodpeckers searching for the larvae. The Canadian Forest Service (CFS) has produced two publications describing methods for detecting and surveying EAB populations. These are available at the following website: http://cfs.nrcan.gc.ca/index/invasive. However, by the time these signs and symptoms are evident, the beetles are well established and have spread further.

Biological control (the use of natural enemies to regulate pest populations) is one control strategy that might benefit from the slow-the-spread methodology. The classical biological control tactic involves exploration for natural enemies of the invasive alien species in their native habitats and re-associating the host insects with their natural enemies in their new habitats. The Animal and Plant Health Inspection Service (APHIS) and the Forest Service (FS) of the United States Department of Agriculture (USDA) have been actively involved in classical biological control of EAB since its discovery in Detroit. Steps in a classical biological control program include: 1) assessment of native natural enemies; 2) foreign exploration and collection; 3) propagation, mass-rearing, biological investigations and host-specificity testing; 4) field release; 5) impact assessment; and 6) long-term monitoring. Having satisfied the first three of these steps, the USDA released three parasitoids of EAB from China into Michigan in the summer of 2007. These included two parasitoids of larvae [*Spathius agrili* (Hymenoptera: Braconidae) and *Tetrastichus planipennisi* (Hymenoptera: Eulophidae)] and one parasitoid of eggs [*Oobius agrili* (Hymenoptera: Encyrtidae)]. The USDA plans to develop a mass-rearing facility for these parasitoids with the goal of making future releases. A second biological control tactic known as augmentation involves moving established or natural biocontrol agents from areas where they occur to areas where they don't occur (inoculation) or supplementing low numbers by propagation (inundation).

For step 1 of the classical tactic described above, USDA-FS scientists evaluated the impact of native parasitoids on EAB populations. Observations from Michigan populations indicated that native parasitism rates were <1%. However, through our regular rearing of EAB from log bolts in our quarantine facility in Sault Ste. Marie, we located an Ontario population of EAB that had high numbers of two larval parasitoids. The most abundant parasitoid was *Phasgonophora sulcata* (Hymenoptera: Chalcididae) and the less abundant parasitoid was *Balcha indica* (Hymenoptera: Eupelmidae). The former species is the most common parasitoid encountered in native *Agrilus* populations. The second species is itself an alien species that probably arrived in North America from Asia on some host other than EAB because it was first encountered in 1994 in Virginia. Subsequent trapping at this Ontario location using sticky bands suggested a parasitism rate of ~40% by *P. sulcata*.

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(2) Population and food-web ecology – the study provides new insights into the strong relationship between individual species dynamics and food-web ecology; it argues for an integrative approach to gain a better understanding of these traditionally separate branches of ecology. For example, it is evident that predicting what will happen to SBW populations at a given moment requires the integration of data on the status and composition of the food web with population data on the SBW; and

(3) Forest and pest management – the study provides a plausible mechanism for forest composition effects on insect pest populations. Importantly, the results indicate that large-scale homogenization of the base of the food web (for example, forest plantations) could inhibit the buffering effect of generalist parasitoids and, in combination with reducing vegetational biodiversity that supports important alternative/alternate hosts for parasitoids, it could lead to more severe and costly outbreaks of insect pests, such as SBW, in these areas.

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For further information, read:

Eveleigh, E.S., McCann, K.S., McCarthy, P., Pollock, S.J., Lucarotti, C.J., Morin, B., McDougall, G.A., Strongman, D.B., Huber, J.T., Umbanhowar, J. and L.D.B. Faria. 2007. Fluctuations in density of an outbreak species drive diversity cascades in food webs. Proceedings of the National Academy of Science. 104: 16976-16981.

Continued from pg 3. Are Urban Forests . . .

Much of the remaining biodiversity in urban forests and ecosystems comprises actual invasive alien plant species, such as European buckthorn (*Rhamnus cathartica*), Tatarian honey-suckle (*Lonicera tatarica*), Siberian elm (*Ulmus pumila*), and sycamore maple (*Acer pseudoplatanus*). All in all, there are two groups of successful tree species in urban forests: one artificially selected by horticulturalists for survival characteristics and the other a group of escaped volunteers that cannot be unselected. This suggests that under a stressful and dynamically fluctuating climatic regime, successful forest ecosystems will feature a limited number of tree species that feature strongly invasive characteristics.

Are Urban Forests Suitable Sites for Biodiversity Studies?

Studying current urban ecosystems will allow the application of concepts across a much larger area in the future, as natural ecosystems are converted to urban ecosystems. These areas will support most of the future human population and will experience its impact on biodiversity.

Thus, while it is critical to study natural ecosystems and work for their preservation, pragmatism suggests that urban forests are a *de facto* “growth market” for forest ecosystems in the future. Climate change will increasingly affect urban biodiversity (including people) and urban ecosystems will increasingly be agents of change at their interface with natural ecosystems. Thus, as sites for research, urban forests offer direct benefits to biodiversity science and to civil society. These benefits will increase as urban populations continue to grow.

Leaving aside the potential contribution of urban forests to the mitigation of climate change effects, studies of urban ecosystem biodiversity can provide:

- indicators of urban forest sustainability
- understanding of urban-wildland interactions
- urban genetic diversity and provenance information
- measurement and description protocols for urban systems
- taxonomy, ecology and biodiversity data

Whether or not urban forests are advanced indicators of climate change, they are without question the ecosystem where in future, the greatest part of the human population will interact with forests and forest biodiversity under a changing climate. As such, urban forests warrant increased attention and investigation.

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For further information on urban forests and urban forest research:

http://www.treecanada.ca/index_e.htm

http://www.fs.fed.us/ne/syracuse/

http://www.idrc.ca/en/ev-103884-201-1-DO_TOPIC.html

http://www.treelink.org/

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The emerald ash borer (EAB) has immediate economic and aesthetic impacts in Canada's rural and urban landscapes. It also has hidden impacts in terms of loss of the unique gene pools represented by populations of each of the native ash species. At the Atlantic Forestry Centre in Fredericton, initiatives are underway to ensure that if the EAB continues to spread across the country, all will not be lost.

Seed has been collected for the National Tree Seed Centre from black, green/red and white ash populations in the Maritime provinces, Quebec, Ontario and Manitoba. Most of the seed is destined for long-term storage for conservation and eventual restoration. The rest of the seed is used in studies to improve storage protocols, understand germination requirements, and evaluate genetic diversity using isozyme analysis. Seed collections from 1 blue ash, 1 pumpkin ash, 85 red/green ash, 120 black ash, and 215 white ash trees are in storage, representing more than 25 locations across the range of the species. Collection efforts will continue with the objective of capturing 90-95% of the common genetic diversity in each species.

– Judy Loo and Dale Simpson
Atlantic Forestry Centre, Fredericton, NB

Both species were encountered during the Michigan study. Investigations will continue to evaluate the impact these parasitoids are having on EAB populations and their potential value as augmentative biological control agents.

Ash trees are often important components of our urban forests because ashes are resistant to the harsh conditions we impose on our landscape trees. The Canadian Forest Service (CFS), in cooperation with the Canadian Food Inspection Agency, the Ontario Ministry of Natural Resources and the City of London, is developing a science-based management plan for EAB in urban/suburban areas. During the summer of 2007, a project was undertaken in London to demonstrate the usefulness of some of the tools currently available to manage this pest.

Among the tools used was the systemic injection of ashes in the vicinity of infested trees with a formulation of the biological insecticide neem, which was developed by the CFS in Sault Ste. Marie. The efficacy of this tool will be assessed in 2008.

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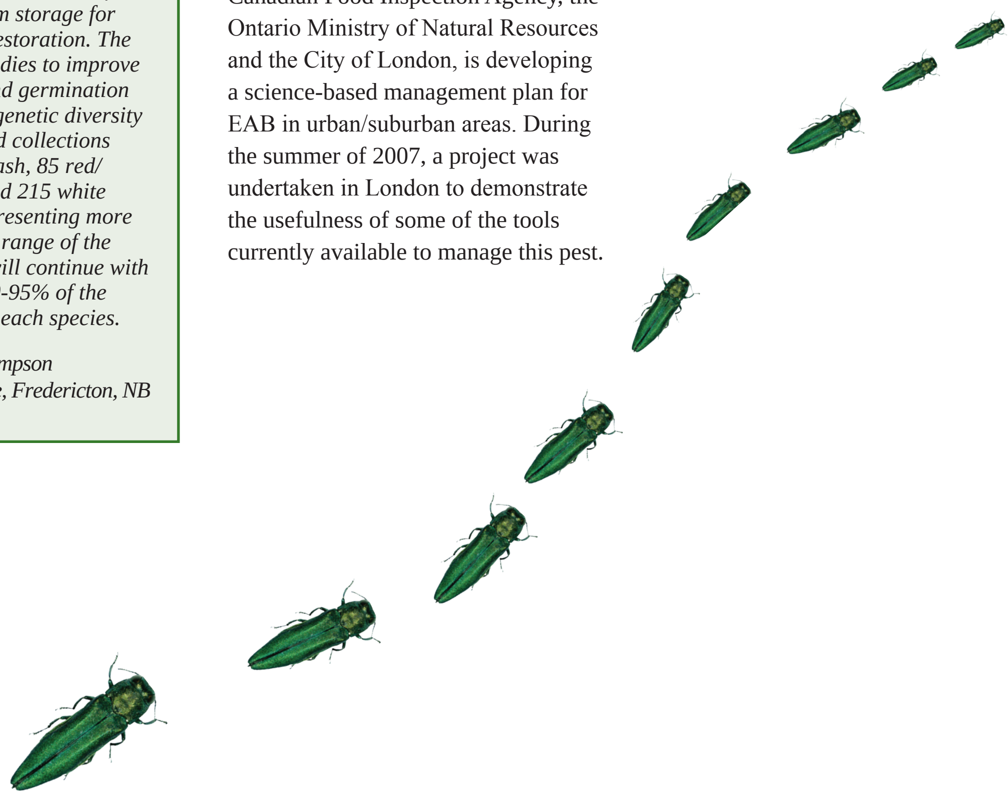

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