MODELING DISPERSAL OF THE ASIAN LONGHORNED BEETLE

Jay S. Bancroft and Michael T. Smith

USDA Agricultural Research Service, Beneficial Insects Introduction Research Lab 501 S. Chapel St. Newark, DE 19713

Introduction

Numerous exotic invasive species pose a grave threat to the biodiversity and economic interests of the USA (Bright 1998). Typically, invasive species are introduced, establish breeding populations, and then spread rapidly (Parker et al. 1999). Inevitably, the introduction and establishment of some invasive species will occur. When an established species represents a major threat, it may still be eradicated. The Asian longhorned beetle (ALB), *Anoplophora glabripennis* Motsch., is a recent invader with extremely high risk to native deciduous forests (Pasek 1999). ALB serves as a test case for eradication because it produces relatively few progeny and is not prone to disperse

from suitable host-trees. Feeding by ALB larvae can girdle the cambium and kill a large host-tree in about 4 years. Although immature beetles cause most of the damage, factors affecting adult dispersal, rather than development or reproduction, are the most important processes influencing the invasion of exotic species (Higgins et al. 1996; Fig 1).

Once breeding populations of ALB were found in the U.S., state and federal agents undertook a major effort to eradicate the beetle. ALB readily attacks 29 species including healthy, full-grown maple, poplar, elm and willow trees. If allowed to spread, losses for maples alone could potentially include: destruction of the maple syrup industry, Fall foliage tourism, and urban street trees (30% Maples). Forest inventory analysis (FIA) shows the importance value of ALB host-trees is extensive within the Eastern US (Iverson et al. 1998). Importance value is relative to 80 species in the Eastern forest. The index ranked red maple 1st, American elm 3rd, and sugar maple 4th most important species (Fig. 2).

Intensive survey for infested trees, followed by felling, removal and chipping, is currently the only available method of



Fig.1. Interaction with host-trees and conspecifics are the focus of current research. Specifically, we are investigating factors associated with dispersal in the US.



Fig. 2. Sugar maple, a preferred host-tree of ALB, is common in much of the Eastern forests of the US.

population suppression. Effective surveys require establishment of boundaries around infestations (referred to as quarantined and/or eradication survey boundaries), inside of which surveys are conducted. However, delineation of boundaries is based upon the dispersal potential of ALB. Current guidelines for APHIS eradication surveys are 1/2 mile from the closest known infested tree (Dr. Alan Sawyer, per. comm.), which are based upon rate of detection of infested trees.

If ALB populations become large and spread beyond the urban areas, eradication of ALB is unlikely. In such an event, Cavey (1999) suggests that \$137 billion could be needed for management of ALB. Immediate action is important to protect the vast hardwood forests of the upper Midwest and Northeast. Understanding dispersal by ALB is critical to the eradication effort. Accordingly, this study provides critical new information on the dispersal of ALB. This information forms a basis for the delineation of the quarantine boundaries and concentrating survey and detection efforts, and thereby lowers the detection threshold for nascent infestations. We describe our ongoing efforts to predict ALB distribution and enhance quarantine efforts.

Individual Based Simulation

Environmental cues that are used by ALB have been programmed into an individual-based simulation. We are using the simulation of dispersal to create hypotheses about the importance of candidate dispersal mechanisms and predict ALB dispersal. In turn, the hypotheses are tested with discriminating experiments and lead to more accurate prediction and better control strategy. The

simulation was designed for flexibility, which is facilitated by implementation in the object-oriented language C++. A simplified flowchart shows how the simulation runs (Fig. 3). Because the focus is on predicting dispersal for one generation, estimation of reproduction was not needed. However, high mortality reduces dispersal distance. Mortality rate over time was calibrated with data from an age-specific-fecundity experiment (Smith et. al. 2001).

P(death) = N(t, b, c)Where N = Normal pdf t = time - start at age 0 b =92 (mean of normal distribution) c = 25 (variance of normal distribution)

Figure 4 shows that the fit of three common probability density functions offer adequate approximations of the mortality data. Field data on mortality is being acquired, which will improve the characterization of the mortality agents.

The dispersal model was tested with data from dispersal experiments. Because the release of





Fig. 3. At each one hour time-step, all cells and beetles within a cell updated their age and used a random number to determine if their position changed.

ALB is prohibited in North America, a mark-recapture experiment was conducted in Gansu province, China, in order to estimate ALB dispersal rate. A total of 188 marked ALB were recaptured in weekly samples (Smith et al. 2001). Trapping data was fitted with a time-integrated, two-dimensional diffusion model (Turchin and Thoeny 1993), but more realistic dispersal may include individual variation, reaction to local abundance of either, host trees or beetles of the same sex. Because data was gathered at discrete spatial and temporal intervals, an individual based model was a more intuitive approach.

A "random walk" model technique was used to simulate beetles moving on a grid of cells. The lattice of 30 m cells accommodates remotely sensed data, which will be discussed later in this paper. Conditions used by the model mimicked those from the dispersal experiment. The habitat or lattice size was set at 66 x 66. Each cell has a single "quality" that was set to a uniform value (128). The simulation runs were set to 56 d with samples taken every 7 d. The dispersal probability for a given cell was calculated as follows.

p(leave) = i (b + r (D/Q))where i = individual variation - uniform distr. b = base emigration rate r = scaling of ratio dependence D = density of same sex in cell Q = quality of cell

An interesting challenge to our understanding is evident in US survey reports and our field data. Infestations in the US have been largely located by the identification of infested trees, rather than by the collection of adult beetles. Similarly, in our field studies in China, while average annual emergence of adult beetles has been about 10 ALB / tree, numbers of resident adult beetles inhabiting trees has averaged only about 0.55 ALB / tree / week. Therefore, large numbers of ALB are either dying or dispersing without being captured. Furthermore, our studies have shown that ALB are capable of flights over a kilometer. Many explanations explain why live or dead adults are not observed. We restrict speculation to testable hypotheses in our experimental area in China. One possible explanation for this phenomenon is that many ALB are dispersing into the surrounding areas due to the lack of suitable hosts within our study area. In the U.S., host trees are plentiful, and vigilant surveys are needed to ensure that infested trees do not go undetected.

Results and Discussion

The test data-set consisted of numbers of ALB captured at each of nine distances. These values were normalized by dividing by their total (188). Similarly, simulation data was grouped into distance bins and normalized to one. The proportion of population dispersing a given distance was then compared between the simulation and observed data. The response measure of simulation's fit consisted of the weighted sum of squared error at each of nine distances. Powell's algorithm is a well tested technique for fitting multvariate functions such as our individual based simulation (Press 199). Dispersal parameters in the simulation were manipulated to find values that provided the best match of the simulation with observed data.

Numerous versions of the dispersal function were tested. A detailed explanation of the possible mechanisms of dispersal and the rationale behind the mathematical representation is beyond the scope of this paper (see Tilman and Karieva 1997 for an excellent overview). In each case parameters were fitted so as to minimize the mean square error of the ALB at the nine distances. We chose two versions of the simulation that show the process of evaluation and selection of best models. The first version is a simple random walk model (Turchin 1998). Using only one parameter this model was able to explain 88% of the variance in the data (Fig. 5a). The second version includes three parameters that represent processes that likely influence dispersal (Fig. 5b). While the second version is slightly more complicated, it better explains the data $(R^2=0.95)$. The density parameter in the better model indicates that the abundance of host material per beetle will be important for dispersal and a fruitful avenue of continued research. Similarly, the other parameter, individual variation, suggests that studies of the propensity of individuals to disperse should help explain important population level effects.





Our estimates for dispersal distance were much larger than previous estimates (Wen et al.1998, Yan 1985) because of variation in size and arrangement of tree species. Huang (1991, 1992) found ALB dispersal distance was generally within 200 m. However, his studies were conducted in a homogeneous young poplar plantation (3 by 5 m tree spacing). ALB dispersal distance may be greater in the U.S. where preferred host trees are more widely spaced. Our future studies will strengthen the understanding of host tree interaction and dispersal in response to landscape elements.

Simulation development has occurred concurrently with six experimental projects: mass-mark recapture, which provides large-scale seasonal movement; individual tracking, which provides daily movement and activity; flight propensity, which provides environmental impetus for movement behavior; host utilization in China, which provides adult emergence and death rates; host suitability, which screens possible USA host trees; and age-specific fecundity, which compares oviposition and death rates on host-tree logs in the laboratory. Each experiment fills a gap in our understanding. For example, dispersal differences among individual ALB was not evident in the data used to calibrate the current model, but the individual tracking study provides an independent measure of the importance of individual variation in dispersal. Generally, our studies provide a backbone of basic biology for predictions of ALB populations and development of control techniques.

The results of simulations have determined gaps in our ecological knowledge that need further research. There are two major processes that we plan to experimentally quantify and incorporate into the dispersal model. When ALB of the same sex meet, repulsion due to fighting causes a local uniform distribution (contest competition within trees). We are addressing interaction in individual mark-recapture studies in 2001. At a larger spatial scale, attraction to preferred host-trees results in congregation. Separate experiments on flight propensity, flight behavior, and host utilization are being used to understand interaction with host-trees.

Data acquired on reproduction and mortality enables multi-year prediction of spread. We are pursuing host-tree preference and suitability as well as detailed data on trees in our field site (including species, size, position, and health). We are pursuing techniques to use biological control agents with pilot experiments on attack and culturing of natural enemies. The simulation will incorporate this information and make quantitative predictions of ALB abundance and distribution for successive years.

The use of satellites and remotely sensed data has become a promising tool for ecological habitat classification. These rapidly improving tool will help predict areas with high risk of infestation. This involves combining images from different spectral sensors and classifying the landscape to identify host-trees. The development of high-resolution digital imagery involves geographic specialists at universities, the US Geological Service and private companies. These images, along with host-preference experiments, increase the applicability of ecological understanding to the predictions of ALB spread in the US. This proactive approach will form the basis for development of adaptive management strategies for this and other invasive species.

Our studies use rigorous experimental designs to understand basic biology about the population dynamics of ALB in nature. This fieldwork provides a critical bridge between numerous laboratory efforts and the ongoing eradication efforts in U.S. landscapes. Collectively, these approaches enable reliable predictions of ALB infestations in the U.S.

In summary, the leptokurtic or 'fat tailed' redistribution allows for an accelerating spread that is seen in many exotic invasive species (Shigesada 1997). Removal of infested trees in urban areas may provide containment. However, if ALB abundance in undetected populations are allowed to build, containment and eradication will be much more difficult. Our use of multiple experimental approaches and simulations has provided rapid progress in dispersal prediction, which is critical for eradication.

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