

POPULATION AND LARGE-SCALE DISPERSAL DYNAMICS IN THE BEECH SCALE INSECT *CRYPTOCOCCUS FAGISUGA*

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Abstract

Pathogens and parasites play important roles in ecological communities and their influence is meaningful when they represent a newly arrived invader. At geographic scales, invading tree pests have caused major disruptions of terrestrial ecosystems. The bark disease of American beech (*Fagus grandifolia* Ehrl.) is an example of a disease invasion that has had a major impact on forest composition throughout northeastern North America in the past 50 years. The combined infestation of the European beech scale insect *Cryptococcus fagisuga* Lind., and the subsequent invasion of fungi (*Nectria* spp.) have substantially altered the structure of American beech populations. Because the scale insect must precede the fungus, it is the key component of disease spread. Despite this, there is little ecological research in North America on the beech scale insect. I examined the population and local dispersal dynamics of the beech scale insect on American beech populations in continuous forest inventory plots within the Edmund Niles Huyck Preserve in eastern New York State. Range maps of the insect's dispersal were re-interpreted to model the diffusive spread of the beech scale insect. Results indicate that geographic dispersal does fit a diffusion model, however estimated velocity was less than expected.

Introduction

The limiting component in the spread of beech bark disease is the spread of the scale insect (Houston et al. 1979), because the attack by the scale predisposes the beech tree to an invasion by the *Nectria* spp. (Burns and Houston 1987). Without the scale, the fungi are unable to invade and the disease cannot progress. Knowledge of the patterns of scale reproduction and dispersal would help in understanding the disease's persistence in the aftermath zone of North America and would be beneficial to research on the original host, European

beech (*Fagus sylvatica*), for which mortality from the disease can be high on a local scale (Wainhouse et al. 1988).

The specific objective of this study was to quantify the spread of the beech scale insect over the past 100 years through the diffusive spread model. An understanding of the dynamics of the spread can help predict future spread of the disease, which has so far extended across less than half of the American Beech's geographic range (Houston 1994).

The diffusion coefficient D , can be calculated using mt , the mean squared deviation at time t , where $mt = 2Dt$. At time t , dispersing individuals are normally distributed about the release point with a mean of zero and a variance of $2Dt$. The mean square deviation of the distribution of the individuals is the variance of the normal curve and will increase linearly through time with a slope of $2D$ (Kareiva 1983, Dwyer 1992).

Velocity of the expansion front of an invading species (Skellam 1951), V , is constant and can be calculated as

$$V = 2\sqrt{rD}$$

where D is the diffusion coefficient and r is the intrinsic rate of increase. This is the speed that the population front moves outward from the origin. Expansion results from both population growth and diffusion (Shigesada and Kawasaki 1997).

Methods

To determine the diffusion coefficient, D , distance measurements were taken from the point of insect introduction in Halifax, Nova Scotia, to the extent of spread for each time interval delineated on published contour maps. Measurements were performed on my own digital projection of maps from Houston et al. (1979) and Houston (1994). Two sets of measurements were performed, one of maximal and one of minimal distances from the source introduction. Dispersal range boundaries limited by Atlantic coastal shores within the beech range were not included. In addition, satellite populations in Ohio and West Virginia were not included in diffusion coefficient measurements because their spread was apparently not due to diffusion, but possibly facilitated by human vectors (Houston 1994).

Table 1.—Mean fecundity for *Cryptococcus fagisuga* (eggs per adult) by host infestation level with corresponding minimum and maximum values. 100 colonies were sampled weekly (40 from low and 60 from high density infestation)

Density (colonies/cm ²)	Mean fecundity (eggs/adult)	SD	Maximum eggs/adult	Minimum eggs/adult
High = 15 trees	12.93	4.56	22.61	7.31
Low = 10 trees	10.30	2.22	14.30	7.02
Total (25 trees)	11.88	3.96		

(T 21.5 = 1.917, p = 0.069)

In order to determine the demography of the beech scale insect, I sampled a series of randomly selected colonies collected from the same 25 trees, in four different forest plots in the E.N. Huyck Preserve in Rensselaerville, NY. Each tree was first sampled in early spring (March) and once a week during the reproductive period of the insect's life cycle (June through October). Each weekly random sample consisted of four individual colonies from each tree, stratified into four major compass directions to take into account any microclimate variations due to colony orientation on the tree. Of the 25 adult beech trees that were sampled, fifteen trees were of relative high density (2.09 ± 1.14 colonies/cm²) (mean $\pm$ SD) and ten were of lower density (0.43 ± 0.184 colonies/cm²). For each colony, I recorded the number and size of adults, numbers of eggs and numbers of first instar (crawler) larvae.

In order to accurately estimate insect fecundity, I needed to account for all the eggs laid throughout the season. This required a reliable measure of adults present within a colony, along with an estimate of the cumulative egg total for a colony. A cumulative egg total was calculated by summing the weekly egg count with the cumulative egg count from the same tree 25 days earlier. This method takes into account both eggs present in the current sample and eggs that have hatched into crawler larvae. The estimate of the total eggs produced for each tree was calculated by averaging the cumulative egg total from the last 6 weeks of sampling. The mean egg total was then divided by number of mean adults per colony (calculated by averaging the number of adults per colony for each tree for the entire sample period before the presence of eggs) to determine a mean insect fecundity value for each tree.

Results

The linear relationship between the square root of the area and time indicates, for the most part, a constant velocity in the spread of the insect (Figure 1).

To calculate the velocity with which the beech scale insect spreads over space, the diffusion coefficient and intrinsic rate of increase were used. Substituting my estimate for r (2.47)(Table 1) and D (0.571 to 1.97 km²/year)(Figure 2) into the equation for velocity of the spread of the organism, the velocity of the insect was calculated to be between 2.38 to 4.41 km/year.

Conclusions

There was not a significant difference in fecundity among insects located on high infested and low infested trees. Results indicate that geographic dispersal does fit a diffusion model, however estimated velocity was less than

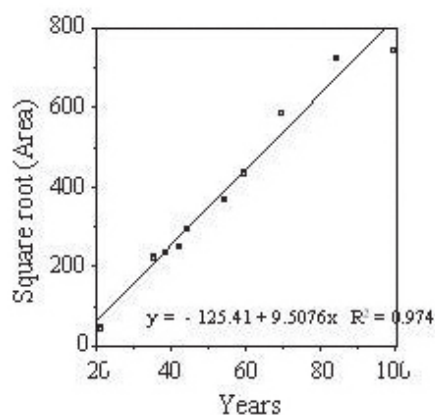


Figure 1.—Square root of the area occupied by the beech scale insect (*Cryptococcus fagisuga*) in years following 1890 introduction. The straight line is the least-squares fit.

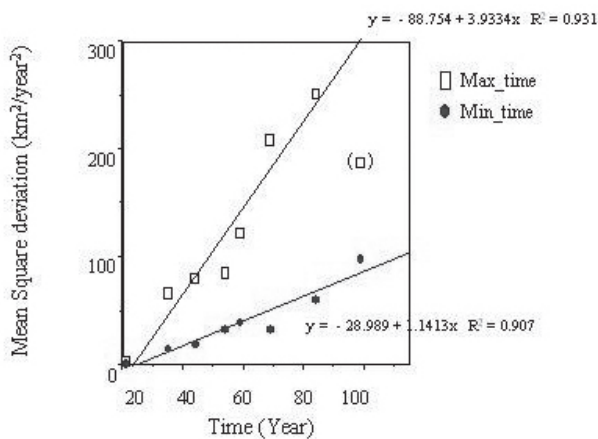


Figure 2.—Mean squared deviation of the maximum dispersal distance of the beech scale insect in North America vs. the time since release. The straight line is a least-squares fit, with the exclusion of the data point in brackets.

expected. These reduced velocity estimates could be from potential differences in insect growth rates between the advancing front and the aftermath zone. They could also result from the convergence of insect populations from multiple introduction points or, most likely, from the influence of human vectors.

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