

THE DYNAMICS OF EASTERN HARDWOOD FORESTS WITH AND WITHOUT BEECH BARK DISEASE

Jeffrey Garnas¹, Matthew Ayres¹, and Celia Evans²

¹Biological Sciences, Dartmouth College, 103 Gilman Hall, Hanover, NH 03755

²Adirondack Watershed Institute, Paul Smith's College, Paul Smiths, NY 12970

ABSTRACT

The spread of beech bark disease (BBD) through eastern North America has had a strong impact on the structure and function of the forest ecosystem, beginning some time after the introduction of the beech scale, *Cryptococcus fagisuga* Lind. (Homoptera:Eriococcidae), in 1890. Stands infected by beech scale and by one or more associated species of the ascomycete genus *Neonectria* typically exhibit adult tree mortality approaching 50% within the first 10 years post-infection (Houston 2005). Despite early predictions that beech (*Fagus grandifolia* Ehrh.) would be removed from the forest canopy, the species has maintained a strong presence throughout most of its range and has even increased in basal area in some stands (Leak 2006). A long-standing hypothesis that BBD enhances the production, growth rate, and/or survival of root sprouts provides a plausible mechanism for the persistence of the species (Held 1983, Houston 1975). We used Forest Inventory and Analysis (FIA) data to examine how the spread of BBD may interact with tree reproductive strategy to alter the size and age structure of forest stands. We analyzed stand trajectory over time with respect to expectations from the self-thinning curve (Fig. 1) and tested how the direction of change with respect to the mean size and density of trees differed in the presence versus absence of BBD, relative to the proportion of beech in the stand.

We parameterized thinning curves for each state and for all states combined using $\log_{10}$ -transformed estimates

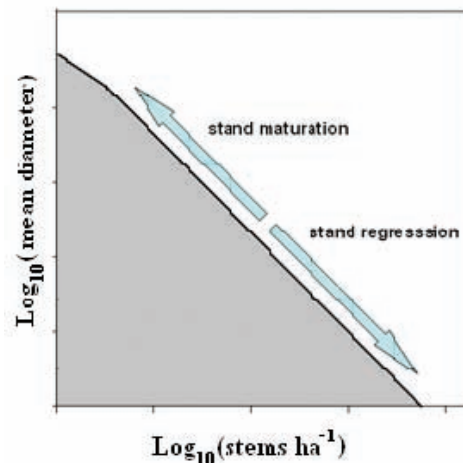


Figure 1. Theoretical representation of a self-thinning curve, showing alternate stand trajectories over time.

of mean diameter and stem density at the first measured cycle, limiting our dataset to all plots containing >1% beech basal area that were sampled two or more times in the past 25 years. We used the regression line estimate for the 95th quantile as the thinning curve boundary (slope = -0.33 ± 0.04 ; Cade and Guo 2000, Cade and Noon 2003, Koenker 2005). Boundary slopes did not differ among 20 of 22 states and approximated the theoretical expectation of $-4/9$ (corrected from $-4/3$ to reflect a linear measure on the Y-axis), widely cited in studies of self-thinning in plants (White and Harper 1970, Yoda et al. 1963). Normal stand maturation corresponds to movement either toward the thinning curve boundary (tree growth/increased mean

diameter) or along the boundary in the direction of fewer, larger stems (tree growth plus self-thinning, or a decrease in stem density due to competition for light or nutrients in a closed canopy). “Stand regression” was defined as movement along the same boundary line in the opposite direction, corresponding to a reduction in mean tree size and/or an increase in the number of stems over time. We calculated stand trajectory as the Euclidean distance between matched plots at time₁ and time₂ relative to the thinning curve boundary, assigning a positive value to stand maturation and a negative value to stand regression. To our knowledge, this is the first analysis of forest dynamics in eastern North America that takes advantage of the spatially extensive and scientifically selected study sites in FIA data. A surprising general result was that stands closest to the thinning curve boundary at time₁ were significantly more likely to move in the direction of stand regression. Because this is opposite the predicted pattern of tree growth and self-thinning in the absence of disturbance, it implies that forest disturbance of various kinds may be more widespread than expected. Mechanisms that could be contributing to this pattern include pests and pathogens, harvesting of mature and overmature stands, and changes in biogeochemistry (e.g., nitrogen deposition and calcium depletion) that tend to produce mortality of large trees in relatively mature stands.

Results were consistent with the a priori prediction that a greater proportion of stands in BBD-infected forests moved in the direction of stand regression. That is, within regions with a relatively long history of BBD, but not in regions that have lacked BBD, there was a significant increase in the variance in stand trajectory as % beech basal increase. The statistical support was that the slopes of forest maturation by BBD basal area increased from the 10th to the 90th quantiles (Koenker 2005) where BBD was present (BBD-present: $F = 10.7$, $df = 1,1719$, $P = 0.001$) but not where BBD was absent ($F = 0.9$, $df = 1,3235$, $P = 0.33$). In the spring of 2007, I will seek to conduct additional tests by including another FIA cycle in the analyses, and by explicitly considering effect of latitude and year of scale insect establishment on variation in stand trajectory. These data provide strong initial support for the role of BBD in

dramatically altering the size and age structure of stands throughout its range.

Literature Cited

- Cade, B.S.; Guo, Q.F. 2000. **Estimating effects of constraints on plant performance with regression quantiles.** *Oikos*. 91: 245-254.
- Cade, B.S.; Noon, B.R. 2003. **A gentle introduction to quantile regression for ecologists.** *Frontiers in Ecology and the Environment*. 1: 412-420.
- Held, M.E. 1983. **Pattern of beech regeneration in the East-Central United States.** *Bulletin of the Torrey Botanical Club*. 110: 55-62.
- Houston, D.R. 1975. **Beech bark disease aftermath forests are structured for a new outbreak.** *Journal of Forestry*. 73: 660-663.
- Houston, D.R. 2005. **Beech bark disease: 1934 to 2004...Or, what's new since Ehrlich?** In: *Beech bark disease: Proceedings of the beech bark disease symposium; 2004 June 16-18; Saranac Lake, NY*. Gen. Tech. Rep. NE-331. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 138-141.
- Koenker, R. 2005. **Quantile regression.** Cambridge, New York: Cambridge University Press.
- Leak, W. 2006. **Fifty-year impacts of the beech bark disease in the Bartlett Experimental Forest, New Hampshire.** *Northern Journal of Applied Forestry*. 23: 141-143.
- White, J.; Harper, J.L. 1970. **Correlated changes in plant size and number in plant populations.** *Journal of Ecology*. 58: 467-&.
- Yoda, K.; Kira, T.; Ogawa, H.; Hozumi, K. 1963. **Self-thinning in overcrowded pure stands under cultivated and natural conditions.** *Journal of Biology of Osaka City University*. 14: 107-129.