

Andrew Liebhold · Joseph Elkinton

Oak mast seeding as a direct cause of gypsy moth outbreaks?

A response to Selås

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In our paper (Liebhold et al. 2000) we reviewed the literature on the dynamics of the gypsy moth (*Lymantria dispar* L.) populations in North America. This paper highlighted a previously developed hypothesis, namely that gypsy moth outbreaks are caused by decreased rates of predation by small mammal predators as a result of diminished predator populations following years of low mast production by oaks. We further developed this theory by hypothesizing that spatial synchrony in gypsy moth populations may result, in part, due to spatial synchrony in mast seeding by oaks. Furthermore, we presented historical time series on gypsy moth outbreaks and mast seeding as further evidence of the mast / small mammal / gypsy moth causal dependency.

In this issue Selås (2003) presents an interesting alternative mechanism to explain the relationship between mast seeding in oaks and gypsy moth outbreaks; he hypothesizes that in years of high mast production, the chemical composition of host foliage is more favorable for gypsy moth development and this results in greater population growth and ultimately in outbreaks. He argues that the lag 1 cross-correlation between gypsy moth defoliation and acorn abundance shown in Fig. 4 of Liebhold et al. (2000), though weak, was positive and should be interpreted as evidence for this direct relationship between oak foliage quality and gypsy moth outbreaks.

While we feel that the hypothesis presented by Selås is interesting, there is very little evidence to support it. First, there is a tremendous body of literature that indicates that predation by small mammals is the largest and most important source of mortality affecting low-density gypsy moth populations. As long ago as the 1940s (Bess et al. 1947) the critical role of small mammals was identified and this has been confirmed many times later in detailed life table studies (Campbell and Sloan 1977; Elkinton and Liebhold 1990; Elkinton et al. 1996). It has only been relatively recently that any relationship between mast seeding and gypsy moth dynamics was even considered but experimental manipulations of mast and small mammal abundance have provided tremendous support for this tri-trophic interaction (Elkinton et al. 1996; Jones et al. 1998). In contrast there is little evidence indicating that foliage quality plays an important role in gypsy moth dynamics. While there have been claims of important host plant effects on population processes such as virus transmission (Hunter and Schultz 1993) and induced defenses causing delayed impacts via maternal effects (Rossiter 1991), further studies have not confirmed the presence of these effects in natural populations (D'Amico et al. 1998; Myers et al. 1998; Erelli and Elkinton 2000). Specifically, there has never been any documentation that gypsy moth larvae perform better on trees during years of mast seeding. Additionally, life table studies (e.g., Campbell 1967) do not indicate that the increase of gypsy moth populations from low to high levels is associated with, or preceded by, increased fecundity as would be expected under Selås's hypothesis. Thus, the vast literature on gypsy moth population biology all points towards the role of small mammal predators as the dominant factor behind fluctuations in low density populations, rather than mast-induced increases in foliage quality.

There are several other reasons why the hypothesis of Selås must be questioned. The positive lag 1 cross correlation that he identified in our cross correlograms is very weak compared to the values for lags of -2, -1 and 3 ($\rho_1 = 0.11$, $\rho_3 = -0.49$, $\rho_{-1} = -0.50$, $\rho_{-2} = -0.25$) and is

A. Liebhold (✉)
Northeastern Research Station,
USDA Forest Service,
180 Canfield St.,
Morgantown, WV 26505, USA
E-mail: aliebhold@fs.fed.us
Tel.: +1-304-2851512
Fax: +1-304-2851505

J. Elkinton
Department of Entomology & Graduate Program
in Organismic and Evolutionary Biology,
University of Massachusetts,
Amherst, MA 01003, USA

thus not a dominant cross-correlation. Furthermore, it would be virtually impossible for gypsy moths to change from low-densities (e.g., <5 egg masses / ha) to outbreak levels (e.g., >500 egg masses / ha) in one generation. As Selås points out, gypsy moth females are capable of laying many (ca. 500) eggs, but survival in virtually every population that has been sampled never exceeds 20% and adult sex ratios are typically male biased (Campbell 1967; Elkinton and Liebhold 1990). Thus the transition from low to high densities in a single generation as hypothesized by Selås would be highly unlikely.

Selås presents several other studies where lagged correlations have been observed between outbreaks of herbivore populations and mast seeding in their hosts (Selås 1997, 2000a, 2000b; Selås et al. 2001). Each of these studies documents the existence of lagged correlations between oscillations in mast and herbivore abundance. The existence of these lagged correlations is interesting but we suggest that more caution should be used in interpreting their cause. Though the theory advanced in these papers is that mast directly influences herbivore abundance via changes in host plant chemistry, little if any data are provided to document such a relationship. It seems equally possible that these lagged relationships could instead be due to herbivore feeding affecting the mast cycles rather than *visa versa*. Several other explanations, such as the influence of mast on predator populations, may be possible as well. The existence of lagged interspecific synchrony among trophic levels is a fascinating phenomenon but in order to understand its causes, more work is needed on specific mechanisms rather than relying on population correlations alone.

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