



Environmental factors that influence the association of an earthworm (*Lumbricus terrestris* L.) and an annual weed (*Ambrosia trifida* L.) in no-till agricultural fields across the eastern U.S. Corn Belt

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ABSTRACT

The earthworm, *Lumbricus terrestris* L., caches seeds of the agricultural weed *Ambrosia trifida* L. in its burrow, providing seeds with a protected overwintering site. Seedlings subsequently emerge from the burrows, resulting in an association of the two species (hereafter “LtAt association”). Although populations of these species frequently co-exist in no-till agricultural fields in the eastern U.S. Corn Belt, an association is not always evident. To identify environmental influences on the LtAt association, 30 no-till agricultural fields were surveyed across the eastern U.S. Corn Belt during spring 2007, 2008 and 2009. The LtAt association occurred across states and soil types, but the strength of the association varied with climate differences during the previous September through March. The strongest environmental driver of LtAt association was frequency of “moderate rain day” (MRD; day that received 12.8–25.3 mm of precipitation), with a 1-day increase in MRD frequency increasing the odds of LtAt association by a factor of 1.42. Thus, the potential for *L. terrestris* to cache seeds and facilitate seedling recruitment is increased by precipitation frequency and amount during September through March. These results highlight the importance of climate variation within a region in driving trophic interactions that regulate weed population dynamics.

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1. Introduction

Ambrosia trifida is a summer annual plant species capable of both dominating plant communities (Abul-Fatih and Bazzaz, 1979) and causing significant reductions in crop yield (Webster et al., 1994; Harrison et al., 2001). In the eastern U.S. Corn Belt, *A. trifida* infestation densities often exceed economic thresholds for corn (*Zea mays* L.) and soybean (*Glycine max* [L.] Merr.) production (Gibson et al., 2006; Kruger et al., 2009) because biotypes have evolved to resist or to evade conventional control practices (Schutte et al., 2008; Heap, 2009). Although the major threat to profitable crop production from *A. trifida* currently occurs in the eastern U.S. Corn Belt, concern for this species is widespread as it populates disturbed habitats of temperate ecosystems throughout the globe (Bassett and Crompton, 1982; Rybníček and Jager, 2001; Kil et al., 2004).

Compared to many of the annual weed species of corn and soybean production, *A. trifida* produces relatively low numbers of viable seeds (Harrison et al., 2001). Moreover, on the soil surface, *A. trifida* seeds are highly susceptible to predation by vertebrate and invertebrate granivores (Harrison and Regnier, 2003), and, in the soil seedbank, *A. trifida* seeds are relatively short-lived (Davis et al., 2005; Harrison et al., 2007). These results suggest that *A. trifida* year-to-year persistence is largely dependent upon the overwinter survival of a small number of seeds. Increased knowledge of *A. trifida* seed fate in agroecosystems will clarify mechanisms by which this highly competitive weed endures, and may contribute to the development of seed predator-based control tactics (Menalled et al., 2006).

Regnier et al. (2008) observed that, shortly after dispersal from maternal plants, *A. trifida* seeds on the soil surface of no-till agricultural fields were collected and buried by the earthworm, *Lumbricus terrestris*, and germinated and emerged from the burrows the following spring. In general, surface litter caching is thought to be a deliberate action to stimulate decomposition of plant tissues that provide *L. terrestris* with a source of food (Edwards and Bohlen, 1996). For seeds, caching by *L. terrestris* may improve the probability of survival because rapid burial reduces susceptibility to

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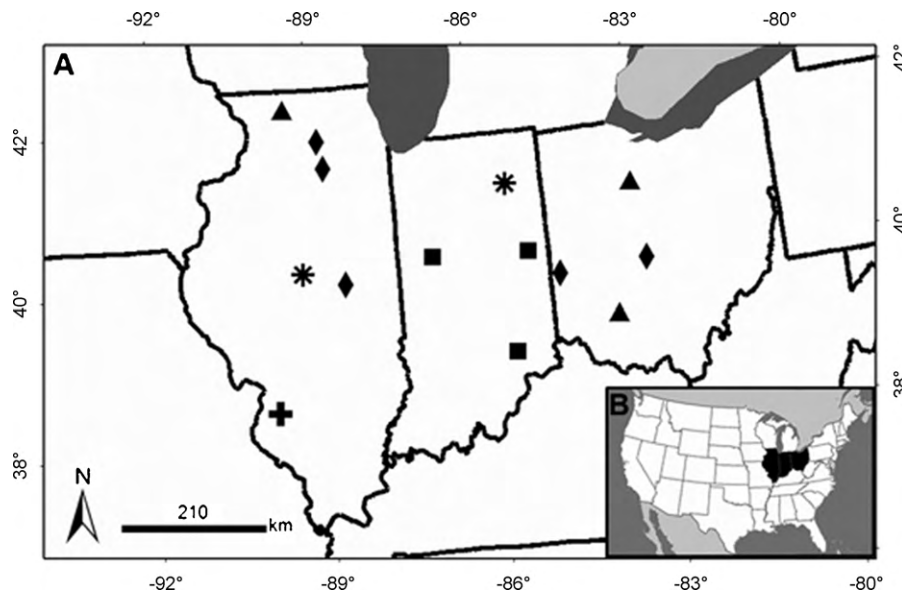


Fig. 1. (A) Locations of no-till agricultural fields surveyed in this investigation. Diamonds (◆) represent fields sampled during 2007, 2008, 2009; squares (■) represent fields sampled during 2008, 2009; triangles (▲) represent fields sampled during 2007, 2008; asterisks (*) represent fields sampled in 2009; and the cross (+) indicates a field sampled in 2008. (B) Distant view of study region, the eastern U.S. Corn Belt, indicated by filled U.S. states.

predation (White et al., 2007). The net effect of *L. terrestris* caching on *A. trifida* seedling recruitment is conditioned by the presence of post-dispersal seed predators (Regnier et al., 2008). In the absence of post-dispersal seed predators, *L. terrestris* caching reduces the proportion of annual seed rain that will produce a seedling because some seeds are buried below the optimal depth for emergence. But, in environments with high risks of post-dispersal seed predation, improved seed survival from caching increases the proportion of annual seed rain that will produce a seedling. Accordingly, the interaction of *L. terrestris* and *A. trifida* may represent a conditional mutualism (Bronstein, 1994) that influences seedling recruitment of a highly competitive agricultural weed.

Species interactions are often affected by the environment in which they occur (e.g., Kolb et al., 2007). Because *L. terrestris* behavior is highly influenced by soil temperature, soil moisture and soil physical characteristics (Daniel, 1991; Perreault and Whalen, 2006; Hawkins et al., 2008), the environment may strongly affect *L. terrestris* foraging for *A. trifida* seeds, thereby influencing the proportion of *A. trifida* seedlings associated with *L. terrestris* burrows (hereafter “LtAt association”). Although likely to occur, environmental effects on the LtAt association have yet to be determined. Previous research indicated that *L. terrestris* and *A. trifida* populations frequently co-existed in no-till agricultural fields in the eastern U.S. Corn Belt, but an association was not always evident (Davis et al., 2008). In this investigation, naturally occurring variation in the LtAt association across the eastern U.S. Corn Belt was utilized to clarify soil and climate factors that influence this species interaction. Specifically, the LtAt association was hypothesized to be influenced by site properties including: soil texture, soil pH, soil organic matter, precipitation, air temperature; and an information-theoretic approach was utilized to elucidate the environmental factor most associated with LtAt association presence.

2. Materials and methods

Previous research indicated that seeds cached by *L. terrestris* may produce seedlings that emerge from middens (mounds of coarse organic matter and *L. terrestris* castings that cap burrow openings) (Milcu et al., 2006; Regnier et al., 2008). Greater than 95% of the cumulative total emergence for an *A. trifida* seed rain dispersed

into soil occurs within 1 year of dispersal (Harrison et al., 2007), and therefore, seedling location (midden or nonmidden) reflects the mechanism of burial (*L. terrestris* caching or otherwise) for seeds dispersed into soil during the previous year. Accordingly, the percent of total seedlings within a defined area that emerge from *L. terrestris* middens is indicative of the strength of the LtAt association for the most recent seed rain. Through comparison of percent midden emergence and percent of soil surface covered by middens, the presence or absence of the LtAt association can be determined for a particular field (Regnier et al., 2008).

2.1. Study locations

Corn and soybean fields in the eastern U.S. Corn Belt were identified according to the following criteria: the presence of a reproductive *A. trifida* stand during the previous growing season, and at least 1 year removed from tillage (i.e., no-till fields). Thirty sites were included across 2007, 2008 and 2009 (Fig. 1). For several sites, changes in management prevented multiple-year sampling. Weed control and soil management practices for all site-years were typical for no-till, corn and soybean production in the region. Unwanted vegetation was eliminated both at crop planting with tank mixes of residual and non-residual herbicides and at 3–5 weeks after crop emergence with non-residual herbicides. Soil nutrient levels were manipulated with annual applications of synthetic fertilizers, and soil hydrologic conditions were altered with subsurface drainage.

2.2. Data collection

Measurement locations for the LtAt association were determined in each field by a multi-step process. First, the field was visually scouted for *A. trifida* seedlings. Then, in the area of greatest seedling density, two 23-m transects were established. This transect length was previously determined to sufficiently cover a typical *A. trifida* stand in agricultural fields (Davis, unpublished data). Along each transect at 0.9 m intervals, square quadrats (0.04 m²) were classified to one of four categories based on the presence or absence of both *A. trifida* seedlings and *L. terrestris* middens. Hereafter, quadrats containing *A. trifida* seedlings

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