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Enhancing predation of a subterranean insect pest: A conservation benefit of winter vegetation in agroecosystems

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ABSTRACT

Generalist predator communities are abundant and diverse in agroecosystems, but pests often persist nevertheless. Winter vegetation (e.g., cover crops) provides an agronomically sound opportunity to conserve predator communities and promote their impact on pests. We evaluate whether winter vegetation increases predation of *Diabrotica virgifera*, a key subterranean pest of maize. Fields of maize were preceded by a winter cover crop (slender wheatgrass) or a fallow period (bare soil) over two years. Pest populations and root damage were measured in each field, from which the gut contents of predators aspirated from the soil surface, or extracted from the soil column, were analyzed using qPCR and primer sets specific to *D. virgifera* COI gene sequences. Predation intensity on restrained *D. virgifera* larvae (sentinels) was observed during the three larval stadia of the pest ($n = 400$ 3rd instars per plot per stadium). A diverse predator community consumed *D. virgifera* in maize fields, and predation was significantly greater in maize following cover crops (as measured with sentinels, but not gut content analysis). Predation was particularly intense during the 3rd stadium of the pest, especially in the cover-cropped maize. qPCR-based gut content analysis of natural populations functioned well in determining which predators consumed *D. virgifera*, but was only correlated with their impact on the pest and its damage when the relative frequency of detection, quantity of DNA calculated, and predator abundance were combined into a predation index. In support of these observations, predation intensity on sentinels was negatively correlated with *D. virgifera* populations and plant damage, but did not provide an accurate picture of the community involved. Cover crops reduced *D. virgifera* populations by increasing predation levels on this pest, which indicates that conserving predation as an ecosystem service is a mechanism for how this form of habitat diversification functions. Also, we conclude that employing diverse methods provides the best insight into trophic relationships within subterranean systems. Finally, because of the dynamic and diverse interactions between pests and their natural enemy complexes, we advocate conserving diverse predator communities within agroecosystems, rather than targeting conservation efforts at specific key predator taxa.

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1. Introduction

Trophic relationships within soil food webs have important implications for both above and belowground terrestrial ecosystem processes (Wardle et al., 2005; Fountain et al., 2008; Eisenhauer et al., 2009), yet we know very little about the key interactions within subterranean food webs (Bardgett, 2002; Coleman, 2008; van der Putten et al., 2009; Nielsen et al., 2010). Top-down factors (i.e., predation, parasitism, and disease) influence biological communities, and these processes can be conserved within a habitat to reduce pestiferous species through biological control (Symondson et al., 2002; Snyder et al., 2006; Macfadyen et al., 2009). Although predator populations are diverse and abundant even in intensively managed agroecosystems, pests persist and the question remains as to how we can promote predator services without sacrificing farm productivity. Central to understanding this question is realizing that predators evolved within natural systems that are relatively undisturbed and biodiverse compared with ephemeral cropland (Tscharntke et al., 2007; Macfadyen and Bohan, 2010). Within these natural systems, predators rely on numerous resources (prey and non-prey foods, overwintering sites, favorable microclimates, preferred oviposition sites, etc.) that are often reduced or removed in annual cropping systems (Landis et al., 2000; Lundgren, 2009). Conserving ecosystem characteristics that support predator function to cropland while maintaining farm profitability is challenging. A practice currently advocated in sustainable agriculture that has repeatedly been shown to increase predator abundance is the deployment of winter (often non-crop) vegetation, or cover cropping. In addition to the numerous agronomic benefits of cover cropping to soil health and weed

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suppression (Clark, 1998), cover crops often reduce insect pest pressure in the subsequent crop (Brust and House, 1990; Bugg and Waddington, 1994; Tillman et al., 2004). The precise mechanisms for why these patterns occur remain largely unstudied, especially in soil food webs which are likely directly affected by the additional complexity that winter cover crops and their residue provide to this habitat. Development of new tools for unraveling subterranean trophic linkages between complex predator communities and agricultural pests, and for promoting the ecosystem services of predators in cropland, will make the application of biologically based pest management more realistic for land managers.

Studying soil food web interactions is difficult without disrupting normal community processes, and the best picture of subterranean trophic dynamics will likely come from simultaneously employing several methodological approaches (Luck et al., 1988; Harwood and Obrycki, 2005; Weber and Lundgren, 2009a). Quantifying predator communities that co-occur with a target pest is important in determining which species are putative natural enemies, but population monitoring provides little information on which predators are consuming the prey of interest. Predation intensity measured with sentinel prey items (i.e., known numbers of prey emplaced in a habitat and subsequently recollected) identifies which predators find the target prey acceptable in the field, but the precise natural predator–prey dynamics are difficult to recreate using this method (Muilenburg et al., 2008; Lundgren et al., 2010). Gut content analysis of predators is useful for identifying specific trophic linkages within a food web (i.e., knowing which species are eating a target species, less the species not focused on like birds or rodents) (Juen and Traugott, 2007; Fournier et al., 2008; Kuusk et al., 2008; Harwood et al., 2009; King et al., 2010), but there remain strong concerns regarding the correlation of predation intensity on a pest and the feeding indices provided by gut content analysis (Naranjo and Hagler, 2001; Harwood and Obrycki, 2005; Greenstone et al., 2007; Weber and Lundgren, 2009b). Given that all predation metrics have caveats to their interpretation, it is currently unknown for most systems which metrics are best correlated with predator function in the sense of biological control of a given prey type.

Diabrotica virgifera virgifera (Coleoptera: Chrysomelidae) is a subterranean pest of maize roots (Vidal et al., 2005; Gray et al., 2009) whose suppression may benefit from farm management efforts that conserve its natural enemy community. The fact that this insect incurs 95–99% mortality prior to eclosion (Onstad et al., 2006; Hibbard et al., 2010) suggests that predation by the abundant predator community of this insect is intense (Lundgren et al., 2009c; Toepfer et al., 2009; Lundgren et al., 2010), and that habitat alterations to encourage this form of mortality may help reduce pest populations below economic levels. To this end, Lundgren and Fergen (2010) incorporated winter vegetation (i.e., a winter cover crop) into agroecosystems prior to planting maize and observed increases in predator abundance, decreases in pest abundance, and reductions in root damage to the crop. Here, we employ qPCR-based gut content analysis and predation on sentinel pests to test whether (1) winter vegetation increases predation on the pest, and (2) predation on the pest reduces crop damage. Additionally, we (3) establish the relative intensities of interactions between predators and life stages of *D. virgifera*.

2. Methods

2.1. Treatment establishment and sampling procedures

Research was conducted during 2007 and 2008 near Brookings, SD, USA (latitude, longitude: 44.348, −96.811). A 12.5-ha no-till field was divided evenly into annually rotated corn and soybean halves. Maize (glyphosate-tolerant DeKalb 44–92; Monsanto Company, St. Louis, MO, USA) was planted at 77,000 plants ha^{-1} (76 cm between rows) in late May. The maize was fertilized with 169 kg N ha^{-1} prior to planting, and glyphosate was applied at 3.3 L ha^{-1} (Roundup Weathermax, Monsanto Company) prior to planting. Experimental plots (18 m × 24 m each; $n = 6$, 8 in 2007, 2008, respectively) were established into the soybean half of the field in the years prior to the experiments. A randomly and evenly assigned set of the plots was fall-planted in early September with slender wheatgrass, *Elymus trachycaulus* (Link) Gould ex Shinners (Poaceae) (cv. Revenue, Milborn Seeds, Brookings, SD, USA), for use as a winter cover crop (broadcasted at 34 kg ha^{-1}) (Osborne et al., 2008). The cover crop was killed with glyphosate before planting maize, leaving only the residue behind. The remaining plots were maintained as bare soil with glyphosate. Mowed grass alleyways (6–12 m wide) separated plots.

Twenty-five days prior to planting maize, plots were infested with *D. virgifera* eggs that were produced at NCARL, USDA-ARS in Brookings (protocols discussed by Sutter and Branson, 1986). Specifically, 3000 and 3300 viable eggs m^{-1} in 2007 and 2008, respectively, were placed in the maize row using a tractor-mounted egg infester. Resultant larval populations of *D. virgifera* were sampled using weekly soil core samples (10 cm diam., 10 cm deep), collected from the soil at the bases of 10 plants $plot^{-1}$ $date^{-1}$ (four sample dates in 2007 and ten sample dates in 2008). Larvae were extracted from the soil over 7 days into 70% ethanol using Berlese funnels, and 1st, 2nd, or 3rd instars were distinguished based on their head capsule widths. Adult populations were collected weekly in emergence cages (0.61 m × 0.76 m, $n = 5$ $plot^{-1}$), which were evenly spaced along a centralized linear transect through each plot soon after when 3rd instars were detected. Herbivore damage to the roots of 15 plants per plot were assessed destructively using the 1–6 Iowa rating scale (Hills and Peters, 1971). Additional details on these experimental procedures, and the abundance and diversity of insect communities in the two treatments is published in Lundgren and Fergen (2010).

2.2. Predator collection

Predator populations were hand-collected from the soil surface (both years), and extracted from the soil column (2008 only). In both years, predators were hand-collected from quadrat samples ($n = 3$ $plot^{-1}$) beginning at approximately 09:00 on six dates between 18-May and 5-July. In 2008, quadrat samples were collected on seven dates between 21-May and 18-July (see Fig. 1 for 2007 and 2008 sample dates). For each sample, a 0.5-m square, sheet-metal quadrat (15 cm tall) was pressed into the soil at a randomly selected site (e.g., Lundgren et al., 2006). Predators within the quadrat were aspirated by mouth into vials, and were frozen at −20 °C in 70% ethanol until processing. In 2008, predators that emerged from the Berlese funnels (used for sampling pest larvae) within 24 h of collection were placed in 70% ethanol and stored at −20 °C.

2.3. Gut content analysis

Predators that consumed *D. virgifera* in the field were identified using qPCR-based gut content analysis. In 2007, all predators collected from the soil surface were analyzed (536 specimens). In 2008, the qPCR resources were split between surface- and soil column-captured predators (432 and 384 specimens, respectively). Approximately seven surface-collected predators were randomly selected from each plot on each sample date in 2008. For the predators collected in the soil column, we randomly selected approximately five predators from each treatment on each sample date. Prior to analysis, each specimen was identified to as fine a

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