2015

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Published in *Journal of Applied Entomology* (2015), 12pp; doi: 10.1111/jen.12276

Submitted April 22, 2015; accepted September 15, 2015.

Estimation of efficacy functions for products used to manage corn rootworm larval injury

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Abstract

Maize, *Zea mays* L., is an economically important crop grown throughout the world. Corn rootworm, *Diabrotica* spp. (Coleoptera: Chrysomelidae), larvae constitute a significant economic threat to maize production in the United States, where yield losses and management costs associated with corn rootworm species exceed $1 billion annually. Furthermore, the introduction of the western corn rootworm, *D. virgifera virgifera* LeConte, into maize-producing regions of Europe has made managing corn rootworm larval injury an international concern. Larvae injure maize plants by feeding on root tissue and are the primary target of management activities. Products commonly used to protect root systems from injury include chemical insecticides (seed or soil applied) and genetically modified maize hybrids expressing toxins derived from *Bacillus thuringiensis* Berliner (Bt). The confirmation of field-evolved resistance to various Bt toxins in populations of the western corn rootworm presents a significant management challenge. We performed a meta-analysis to provide a broad understanding of the relative efficacy of the primary products currently being used to manage corn rootworm larval injury, including insecticidal seed treatments, soil insecticides and Bt hybrids (with and without the addition of soil insecticide). Our analysis is unique in the breadth of locations and years included — we analyzed 135 individual trials conducted from 2003 through 2014 at multiple sites in both Illinois and Nebraska. Panel data were produced by pairing the mean node-injury rating for each treatment of a given trial with the mean node-injury rating for untreated maize. Linear regression models were developed to estimate the relationship between the potential for corn rootworm larval injury and product performance. For a given level of injury potential, the parameters estimated reveal differences in the degree of root protection offered by the various product categories analysed. Implications for developing long-term, integrated, and sustainable practices for managing this important pest of maize are discussed.

Keywords: *Diabrotica barberi* Smith & Lawrence, *Diabrotica virgifera virgifera* LeConte, maize, northern corn rootworm, western corn rootworm, *Zea mays* L

Introduction

Maize, *Zea mays* L., is an economically important crop grown throughout the world. An estimated 177 million ha of maize were planted in 2013; the United States accounted for approximately 20% of this area (USDA NASS 2013). Corn rootworm larvae, *Diabrotica* spp., represent a significant and widespread economic threat to maize production in the United States (Gray et al. 2009). In the Midwest, the corn rootworm complex is dominated by two species: the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, and the northern corn rootworm, *Diabrotica barberi* Smith & Lawrence (Spencer et al. 2009). Metcalf (1986) estimated that yield losses and management costs associated with corn rootworm species exceed $1 billion annually in the United States, although Dun et al. (2010) suggested that an updated estimate may be significantly greater.

Although corn rootworm adults feed on silk tissue and may interfere with pollination at high densities, larval feeding activity is the primary target of management activities (Levine and Oloumi-Sadeghi 1991). Larvae injure maize plants by feeding on root tissue, which can reduce photosynthetic activity (Godfrey et al. 1993; Riedell and Reese 1999; Urías-López et al. 2000); inhibit the utilization of soil moisture (Godfrey et al. 1993) and nitrogen (Spike and Tollefson 1989); and lead to colonization by phytopathogenic or saprophytic fungi (Bryson et al. 1953; Kurtz et al. 2010). Environmental factors (e.g. moisture stress or soil compaction) play a role in determining the severity of root injury (Spike and Tollefson 1988; Ellsbury et al. 1994). When root injury is severe, plants may become lodged and difficult to harvest, reducing yield by up to 34% (Spike and Tollefson 1991). Gray and Steffey (1998) noted that yield loss due to root injury and lodging is variable and influenced by a host of biological or environmental factors. For every node (i.e. circle of roots) consumed, a yield loss of approximately 15–18% can be expected (Dun et al. 2010; Tinsley et al. 2013b).

Chemical insecticides have played a critical role in managing corn rootworm larval injury (van Rozen and Ester 2010). Soil insecticides are applied while planting and include granular or liquid formulations. The efficacy of soil insecticides can be affected by various environmental and operational factors (e.g. Musick and Fairchild 1967; Mayo 1980; Sutter et al. 1989; Levine and Oloumi-Sadeghi 1991). In the United States, maize hybrids are commonly treated with a low rate (e.g. 0.25 mg active ingredient/seed) of a neonicotinoid insecticidal seed treatment to prevent injury from so-called secondary pests (Gray 2011); examples include wireworm, Elateridae spp. or grape colaspis, *Colaspis brunnea* (F.) larvae. However, when applied at a higher rate (e.g. 1.25 mg active ingredient/ seed), insecticidal seed treatments do provide marginal protection against corn rootworm larval injury (Cox et al. 2007).

Genetically modified maize hybrids that express insecticidal proteins derived from the soil-borne bacterium *Bacillus thuringiensis* Berliner (Bt) were first commercialized in 1996 to manage damage caused by the European corn borer, *Ostrinia nubilalis* (H€ubner) (Head and Ward 2009). Since 2003, maize hybrids expressing one or two corn rootworm-active Bt toxin(s) have been commercialized (Head and Ward 2009). These toxins have been described in much detail (Moellenbeck et al. 2001; Ellis et al. 2002; Schnepf et al. 2005; Vaughn et al. 2005; Raybould et al. 2007; Walters et al. 2008, 2010). Bt maize has been widely adopted (Fernandez-Cornejo and Wechsler 2012) and is associated with substantial income benefits for maize producers in the United States (Brookes and Barfoot 2013). However, in many areas of the Corn Belt, western corn rootworm populations have evolved resistance to multiple Bt toxins, which has been associated with severe injury to Bt maize (Gassmann et al. 2011, 2014; Wangila et al. 2015). The confirmation of Bt resistance presents a potentially significant challenge for managing corn rootworm larvae and has resulted in a renewed focus on implementing long-term, integrated and sustainable management practices (Cullen et al. 2013). A robust understanding of the relative efficacy provided by the primary tactics currently being used to manage corn rootworm larval injury is therefore necessary. Here, we present results from a meta-analysis conducted to address this need.

Materials and Methods

Data preparation

Data used for this analysis were obtained from small-plot research trials conducted by personnel in the Department of Crop Sciences at the University of Illinois at Urbana-Champaign and in the Department of Entomology at the University of Nebraska–Lincoln. A common objective of these experiments was to evaluate the efficacy of various products for managing corn rootworm larval injury. We analyzed 135 individual trials that were conducted from 2003 through 2014. The trials were conducted predominantly at university research and education centers in Champaign, DeKalb, Pike, and Warren counties in Illinois and in Clay, Dixon, and Saunders counties in Nebraska. Three exceptions were trials conducted in grower fields in Whiteside County (Illinois) and in Cedar and Wayne counties (Nebraska). All trials in Illinois were conducted under rain-fed conditions; trials in Nebraska were conducted primarily under irrigated conditions. A general summary of trial design and data collection is presented below; consult the references listed in Table S1 for specific information about individual trials.

The experimental design for all trials was a randomized complete block with between 2 and 10 replications.

Planting dates ranged from mid-April through late June, although 99% of the trials were planted during April or May. Previous crops for the trial sites included maize, late-planted maize, or late-planted maize interplanted with pumpkins (*Cucurbita pepo* L.). The latter two cropping situations are considered trap crops, which are routinely used to attract corn rootworm adults and increase the likelihood of oviposition for efficacy trials conducted during the subsequent year. Plot dimensions varied depending on the individual trial, ranging from 1 to 8 rows in width and from 5.3 to 149.4 m in length; between-row spacing was always 0.76 m (30 in). Individual plots for a given trial experienced similar agronomic conditions (e.g. fertilization, tillage, weed management). Although a number of response variables were evaluated during each trial, the primary interest of our analysis was corn rootworm larval injury. Methods used to evaluate injury were highly consistent across trials. Between 5 and 10 root systems were evaluated per plot for each treatment present in a given trial. Root systems were washed and rated for injury using the 0–3 node-injury scale developed by Oleson et al. (2005). Root evaluation dates ranged from early July through early August.

Panel data were produced by pairing the mean node-injury rating for each treatment of a given trial with the mean node-injury rating for the untreated check. Each observation therefore consisted of a value for the potential for corn rootworm larval injury (i.e. the predictor variable) and a value for product performance (i.e. the dependent variable). When more than a single untreated check occurred in a trial, mean node-injury ratings for the multiple untreated checks were averaged to produce a single value for injury potential. Depending on the identity of the product being evaluated, observations were grouped into four categories: seed treatment, soil insecticide, single-toxin Bt maize (± soil insecticide) or dual-toxin (i.e. pyramided) Bt maize (± soil insecticide). For the seed treatment and soil insecticide categories, treatments were included in our analysis only when commercially available and evaluated at rates specifically labelled for managing corn rootworm larval injury. All seed treatments were neonicotinoids, while soil insecticides included organophosphates, phenylpyrazoles, pyrethroids or a combination thereof. Single-toxin Bt maize expressed one of the following insecticidal toxins: Cry34/35Ab1, Cry3Bb1, or mCry3A. Dual-toxin Bt maize expressed the combinations Cry34/35Ab1+ Cry3Bb1, Cry34/35Ab1+ mCry3A, or eCry3.1Ab1+ mCry3A. All Bt maize hybrids included in this analysis were treated with a low rate of neonicotinoid seed treatment (0.25–0.50 mg active ingredient/seed).

Statistical analysis

We used the regression procedure (PROC REG) of SAS 9.3 (SAS Institute Inc., Cary, NC) to perform all analyses. Models for each treatment category were prepared independently. For example, the model estimated for the seed treatment category included only those observations for which a seed treatment was used to prevent corn rootworm larval injury. The form of each model can be represented in matrix notation as $\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \boldsymbol{\varepsilon}$ where $\mathbf{Y}$ is the known vector of values for product performance (Y_i), $\mathbf{X}$ is the known design matrix of values for injury potential (X_i), $\boldsymbol{\beta}$ is the unknown vector of parameter estimates (β_k), and $\boldsymbol{\varepsilon}$ is the unknown vector of observational errors (ε_i). Stated simply, each model can be represented as a line in two-dimensional space with injury potential (Xi) used to predict product performance (Yi).

Parameter estimates were initially obtained using ordinary least squares. Because the Y-intercept (β_0) for each model was not significant (see Results for further details), β_0 was omitted from future steps. From a logical perspective, a node-injury rating of zero (i.e. $Y_i = 0.00$) would be expected for any product used to manage corn rootworm larval injury when the potential for such injury is null (i.e. $X_i = 0.00$). A commonly used diagnostic tool for describing the fit of a regression model is the coefficient of determination (R^2): a model with a large R^2 value can be described as accounting for more variation in the response variable than one with a smaller R^2 value. However, R^2 values lose their traditional interpretation when β_0 is omitted (Kutner et al. 2004). We therefore calculated pseudo-R^2 values for each model using the formula $R^2 = \sum\hat{Y}_i^2/\sum Y_i^2$ where $\hat{Y}_i$ is the predicted value for each observation (Eisenhauer 2003).

Residuals (ε_i) from initial models were assessed visually and determined to be heteroscedastic: values for ε_i increased with X_i. When non-constant error variance is detected, Kutner et al. (2004) recommend using weighted least squares for parameter estimation. Because $|\varepsilon_i|$ for each observation serves as an estimator for the standard deviation (σ_i), regressing $|\varepsilon_i|$ against X_i produces a simple linear standard deviation function that can be used to assign a weight (w_i) to each observation. Weights are assigned so that observations with less variability have a greater influence on parameter estimation than those with more variability. The formula for calculating each weight was $w_i = 1/(\hat{s}_i)^2$ where is the estimated value for σ_i from the standard deviation function.

Models for the seed treatment and soil insecticide categories included a single parameter (β_1) representing the slope of the relationship between injury potential and product performance. For both Bt maize categories, we were interested in determining if the slope of the relationship was altered when soil insecticide was added. This was achieved by redefining injury potential as X_{i1}, adding a qualitative indicator variable (X_{i2}), and estimating two parameters (β_1 and β_2). The indicator variable had two levels: 1 if soil insecticide was added to Bt maize and 0 if left untreated. The slope of the relationship for the Bt maize categories was therefore β_1 when left untreated and β_1 + β_2 when soil insecticide was added.

Results

1204 observations, representing a wide range of injury potential, were analyzed (seed treatment: N = 64, X_i range = 0.11–3.00; soil insecticide: N = 510, X_i range = 0.01–3.00; single-toxin Bt maize: N = 484, X_i range = 0.01–3.00; dual-toxin Bt maize: N = 146, X_i range = 0.02–2.36). Because the maximum value for injury potential was 2.36 for the dual-toxin Bt maize model, any inferences for this treatment category should be restricted to this value or less. For each model, the parameter estimate for the intercept was not statistically significant (seed treatment: β_0 = –0.17, t = –1.21, P = 0.23; soil insecticide: β_0 = 0.02, t = 0.52, P = 0.60; single-toxin Bt maize: β_0 = –0.01, t = –0.57, P = 0.57; dual-toxin Bt maize: β_0 = –0.01, t = –0.65, P = 0.52). As a result, the decision to exclude the intercept from the final models was justifiable. Overall tests of significance for the models analyzed were statistically significant, and pseudo-R^2 values were moderate to high (Table 1). Weighted least squares parameter estimates, standard errors and significance tests are located in Table 2. Parameters estimated for the various models suggest that, if untreated maize had a node-injury score of 1.00, the following node-injury scores would be expected: seed treatment = 0.52, soil insecticide = 0.28, single-toxin Bt maize = 0.22, single- toxin Bt maize with soil insecticide = 0.10, dual-toxin Bt maize = 0.10 and dual-toxin Bt maize with soil insecticide = 0.03. The regression relationship for each model is represented graphically in Figure 1.

Table 1. Significance tests and pseudo-R^2 values for models analyzed

Model	d.f.$_N$	d.f.$_D$	F value	P value	Pseudo-R^2
Seed treatment	1	63	269.8	<0.01	0.73
Soil insecticide	1	509	583.6	<0.01	0.70
Single-toxin Bt maize (± soil insecticide)	2	482	136.5	<0.01	0.54
Dual-toxin Bt maize (± soil insecticide)	2	144	61.8	<0.01	0.55

Statistical tests were performed using PROC REG of SAS 9.3. Models were declared significant at P < 0.05. See text for an explanation of the calculation and interpretation of pseudo-R^2 values.

Table 2. Weighted least squares parameter estimates, standard errors and significance tests

Model	Parameter	Estimate	SE	t value	P value
Seed treatment	β_1	0.52	0.032	16.4	<0.01
Soil insecticide	β_1	0.28	0.011	24.2	<0.01
Single-toxin Bt maize (± soil insecticide)	β_1	0.22	0.015	14.9	<0.01
	β_2	–0.12	0.020	–6.1	<0.01
Dual-toxin Bt maize (± soil insecticide)	β_1	0.10	0.009	10.7	<0.01
	β_2	–0.07	0.014	–4.9	<0.01

Statistical tests were performed using PROC REG of SAS 9.3. For all t-tests, d.f. = 1. Parameters were declared significant at P < 0.05.

Discussion

The analysis we present is unique in the breadth of locations and years included. Many experiments have evaluated products for managing corn rootworm larval injury at relatively few sites during a short period of time (e.g. Petzold-Maxwell et al. 2013; Tinsley et al. 2015). Our analysis, however, included multiple sites from two principal maize-producing states (USDA NASS 2013) and used data representing over a decade of research. Although the pseudo-R^2 values reported for the various models were moderate to high (Table 1), between 27 and 46% of variability in the data remained unexplained. Apart from environmental variation occurring across years and sites, the primary factor contributing to unexplained variability was likely the diversity of products analyzed for each model. Because our analysis describes the relationship between injury potential and product performance for the various management tactics in general, differences in efficacy among unique products within a category would contribute to unexplained variability. Furthermore, variability in efficacy may even occur for different formulations or hybrids of a single insecticidal active ingredient or Bt event, respectively. For example, Gray et al. (2007) demonstrated the potential variability in efficacy among

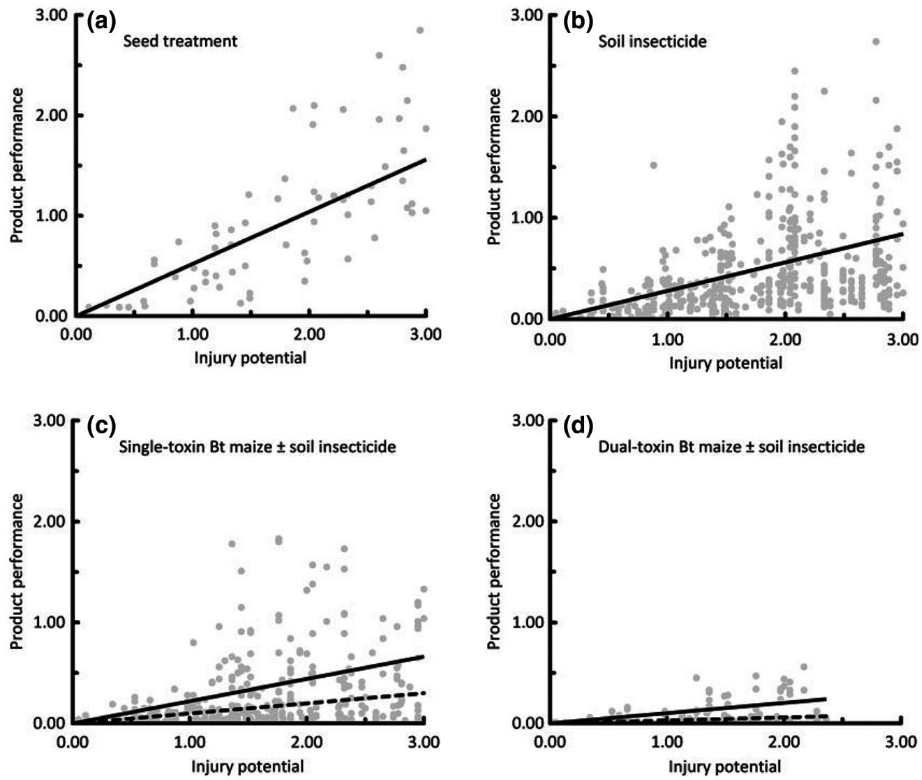

Figure 1. Regression relationship between product performance and injury potential for the various products analyzed. Both axes represent the 0–3 node-injury scale (Oleson et al. 2005). For (c) and (d), the relationships for Bt maize both with (dashed) and without (solid) soil insecticide are presented.

different Bt maize hybrids modified using the same transgenic event (MON 863, Cry3Bb1).

Our primary goal was to produce efficacy functions for describing the relative performance of currently available tactics for managing corn rootworm larval injury. Although labelled for corn rootworm larval control, our analysis indicates that seed treatments are unlikely to protect against larval injury as effectively as the other tactics analyzed (Figure 1). For a given level of injury potential, injury for maize protected by a seed treatment is expected to be 86, 136, and 420% greater than if soil insecticide, single-toxin Bt maize or dual-toxin Bt maize was used, respectively (calculated using the values reported in Table 2). As noted by van Rozen and Ester (2010), our results suggest that the value of seed treatments for managing injury may be of limited value where larval densities are substantial (i.e. injury potential is high).

The relationship between injury potential and product performance for the soil insecticide and single-toxin Bt maize models did not differ substantially (Figure 1). Using conventional maize (or Bt maize expressing lepidopteran-specific toxins only) with soil insecticide has been suggested as an option to delay potentially the development of Bt resistance (Cullen et al. 2013). A strong correlation between the development of Bt resistance and the cultivation of maize expressing the same Bt toxin over successive years has been reported (Gassmann et al. 2011; Wangila et al. 2015). Our results suggest that substituting conventional maize with soil insecticide for single-toxin Bt maize could represent a practical choice when incorporated into a long-term, integrated approach for managing corn rootworm larval injury. Such a substitution would help delay the development of resistance by interrupting the selection pressure imposed by Bt maize. However, growers have reported limited access to conventional maize with yield potential similar to that of transgenic maize (Gray 2011; Cullen et al. 2013). Furthermore, the efficacy of soil insecticides may be diminished when associated with early planting (Musick and Fairchild 1967; Mayo 1980), poor calibration (Levine and Oloumi-Sadeghi 1991), dry soil conditions (Sutter et al. 1989) or lack of insecticide incorporation (Levine and Oloumi-Sadeghi 1991). These factors, combined with the putative environmental and human health benefits associated with reduced insecticide use, were cited during the initial registration of Bt maize targeting corn rootworm larvae (USEPA 2003).

For a given level of injury potential, our results suggest that single-toxin Bt maize will experience 120% more corn rootworm larval injury than dual-toxin Bt maize (calculated using the values reported in table 2). This finding supports those of previous experiments that have documented improved root protection for dual-toxin Bt maize over maize protected by a single toxin (Prasifka et al. 2013; Head et al. 2014). Using pyramided

Bt maize with multiple corn rootworm-specific toxins over single-toxin Bt maize has been hypothesized to delay the development of Bt resistance (Onstad and Meinke 2010) and has been recommended previously (Cullen et al. 2013). The enhanced efficacy per unit of injury potential we observed for dual-toxin Bt maize will likely increase its adoption over single-toxin Bt maize, assuming that cost is not prohibitive.

Another goal of our analysis was to determine whether adding soil insecticide to Bt maize significantly altered the relationship between injury potential and product performance. We determined that using soil insecticide with single- or dual-toxin Bt maize significantly decreased the slope of the relationship; and this observation was more noticeable for single-toxin Bt maize (Table 2). For a given level of injury potential, our results suggest that single- and dual-toxin Bt maize with soil insecticide is expected to experience 55 and 70% less injury than when untreated, respectively (calculated using the values reported in Table 2). However, the magnitude of improvement in efficacy (and potentially yield) depends on the injury potential at a given location and may or may not represent a significant economic benefit. Clearly, where injury potential is minimal (e.g. 0.10), investing in soil insecticide in addition to a Bt maize hybrid will not improve efficacy to a noticeable extent. Yet even when injury potential is substantial (e.g. 2.00), the predicted difference in product performance when treated or not treated with soil insecticide is only 0.26 and 0.14 for single- and dual-toxin Bt maize, respectively. Furthermore, Petzold-Maxwell et al. (2013) questioned the value of using soil insecticide in conjunction with Bt maize from a resistance management standpoint and noted that benefits related to reduced insecticide use associated with planting Bt maize would be diminished if such a combination approach is used.

This analysis provides a robust evaluation of the primary tactics currently being used to manage corn rootworm larval injury in the United States. One potential deficiency is the lack of included information related to product performance at locations where Bt resistance is suspected or confirmed. Performance issues associated with field-evolved resistance to Bt maize in populations of the western corn rootworm have been reported since at least 2009 (Gassmann et al. 2011); however, a reliable assessment of the proportion of US maize fields subject to resistant populations has yet to be estimated. The performance of Bt maize expressing the toxin to which resistance has been confirmed will likely be reduced when compared with the values our analysis predicts. We hypothesize that Bt resistance will have implications for the utility of both single-toxin Bt maize (e.g. performing similarly to untreated maize) and dual-toxin Bt maize (e.g. performing similarly to single-toxin Bt maize, depending on the specific toxins present in the pyramided trait). Finally, combining the information in our analysis with corn rootworm damage functions (e.g. Dun et al. 2010; Tinsley et al. 2013b) and a comprehensive estimation of product adoption and injury potential would allow for a more precise estimate of the annual cost of corn rootworm species to maize.

Acknowledgments — We thank Kevin Steffey and Tom Hunt for providing leadership for many of the trials included in this analysis. Many technicians deserve credit for trial management, including Jim Brown, Logan Dana, Terry DeVries, Gerald Echtenkamp, Josh Heeren, Keith Jarvi, Bill McCormick and Jared Schroeder. We acknowledge the many undergraduate interns and graduate research assistants who participated in data collection. We are grateful for the helpful contributions of employees of the various university research centers where these trials were conducted. We extend our gratitude to many industry cooperators for providing funding, seed, and insecticide to conduct the trials used for our analysis, including Adama USA, AMVAC Chemical Corporation, BASF SE, Bayer CropScience AG, Cheminova A/S, Dow AgroSciences LLC, DuPont Pioneer, FMC Corporation, Helena Chemical Company, Monsanto Company, Syngenta AG, and Valent USA Corporation.

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Supporting Information

Table S1. References for all trials included in this analysis

Year	State	County	Reference(s)
2003	Nebraska	Clay (3)	DeVries and Wright 2004a,b,c
		Dixon	Jarvi et al. 2004
		Saunders	Meinke et al. 2003
2004	Illinois	Champaign (4)	Estes et al. 2004a,b,c,d
		DeKalb	Estes et al. 2004c
		Warren	Estes et al. 2004c
	Nebraska	Clay (3)	DeVries and Wright 2005a,b,c
		Dixon	Jarvi et al. 2005
		Saunders (2)	Meinke et al. 2004a,b
2005	Illinois	Champaign (4)	Estes et al. 2005a,b,c,d
		DeKalb	Estes et al. 2005d
		Warren	Estes et al. 2005d
	Nebraska	Clay	DeVries and Wright 2006
		Saunders (2)	Meinke et al. 2005a,b
2006	Illinois	Champaign (4)	Estes et al. 2006a,b,c; Gray et al. 2006
		DeKalb	Estes et al. 2006c
		Pike	Estes et al. 2006c
		Warren	Estes et al. 2006c
	Nebraska	Clay (2)	DeVries and Wright 2007a,b
		Dixon	Jarvi et al. 2007
		Saunders (3)	Meinke et al. 2006a,b,c
2007	Illinois	Champaign (3)	Estes et al. 2007a,b,c
		DeKalb	Estes et al. 2007c
		Pike	Estes et al. 2007c
		Warren	Estes et al. 2007c
	Nebraska	Clay (2)	DeVries and Wright 2007c, 2008
		Saunders (4)	Meinke et al. 2007a,b,c,d
2008	Illinois	Champaign (4)	Estes et al. 2008a,b,c,d
		DeKalb	Estes et al. 2008d
		Pike	Estes et al. 2008d
		Warren	Estes et al. 2008d
	Nebraska	Clay (2)	DeVries and Wright 2009b,c

When more than a single trial was conducted in a specific county during a particular year, the number of unique trials is listed in parentheses.