

Indirect effects of deer on insect pests and soybean plants

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- Abstract**
- 1 White-tailed deer (*Odocoileus virginianus* Zimmermann) and insect pests negatively affect soybean production; however, little is known about how these herbivores potentially interact to affect soybean yield. Previous studies have shown deer browse on non-crop plants affects insect density and insect-mediated leaf damage, which together reduce plant reproductive output. In soybeans, reproductive output is influenced by direct and indirect interactions of different herbivores.
 - 2 Here, we quantified indirect interactions between two groups of herbivores (mammals and insects) and their effects on soybean growth and yield. We examined responses of insect pest communities along a gradient of deer herbivory (29% to 49% browsed stems) in soybean monocultures.
 - 3 Structural equation models showed that deer browse had direct negative effects on soybean plant height and yield. Deer browse indirectly decreased insect-mediated leaf damage by reducing plant height. Deer browse also indirectly increased pest insect abundance through reductions in plant height. Similarly, deer herbivory had an indirect positive effect on leaf carbon: nitrogen ratios through changes in plant height, thereby decreasing leaf nutrition.
 - 4 These results suggest that pest insect abundance may be greater on soybean plants in areas of higher deer browse, but deer browse may reduce insect herbivory through reduced leaf nutrition.

Keywords crop damage, crop pests, *Glycine max*, species interactions, white-tailed deer.

Introduction

Large mammalian herbivores alter ecosystem processes by restructuring interactions among plant and animal communities (Wardle *et al.*, 2004). Long-term grazing of large mammalian herbivores can cause shifts in dominant plant species and reduces plant regeneration (Den Herder *et al.*, 2004; Kitt *et al.*, 2009; Nakahama *et al.*, 2016). The changes in these plant communities often create cascades that affect other herbivores, such as insects (Suominen *et al.*, 1999; Feber *et al.*, 2001; Greenwald *et al.*, 2008). Generally, large mammal grazing affects both density and diversity of herbivorous insects, but may have little effect on insect herbivory (Takagi & Miyashita, 2014; van Klink *et al.*, 2015). In agroecosystems, which are typically monocultures of a single crop plant species, indirect effects of mammalian herbivory on insect herbivores are likely mediated through changes in the physical and chemical characteristics of

plants, rather than shifts in plant communities (Shimazaki & Miyashita, 2002; Colligan *et al.*, 2011; Rogerson *et al.*, 2014).

Mammalian herbivores directly and indirectly change insect herbivore communities (Wardle *et al.*, 2004). Directly, mammalian herbivores may alter insect communities through competition for food or accidental predation (Stewart, 2001). Indirectly, herbivory may cause changes in plant growth rates, secondary defence chemicals, or nutrition that prevent secondary herbivory (Nykänen & Koricheva, 2004; Ohgushi, 2008). Nonetheless, ungulate herbivory may stimulate plant regrowth that may increase the abundance of later insect herbivores (Hjältén & Price, 1996; Vandegehuchte *et al.*, 2018). Additionally, herbivory may alter plant tissue nutritional value (Chen, 2008), such as leaf C : N ratio. Herbivore-induced plant defences including secondary chemical compounds increase leaf carbon content (increase leaf C : N ratio; less palatable leaves), while younger tissue and herbivore-induced increases in amino-acids in tissue increase nitrogen content of leaves (decrease leaf C : N ratio; more palatable leaves). Specifically, ungulate herbivory

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has been shown to increase nitrogen and crude protein content of leaves, resulting in increased insect herbivore abundance (Barrett & Stiling, 2007; Gann *et al.*, 2016). Conversely, internal secondary compounds may also increase with prior herbivory (Jing *et al.*, 2015), causing the plant to become unpalatable to later herbivores (Shimazaki & Miyashita, 2002; Machado *et al.*, 2016). In a meta-analysis of prior insect herbivore damage on later plant and insect responses, carbohydrates decreased, and phenolic compounds increased after damage (Nykänen & Koricheva, 2004). Changes in plant compounds can reduce the growth rate of later insect herbivores (Nykänen & Koricheva, 2004). In crop systems, these herbivory-induced defences may be effective at preventing colonization and damage by insect herbivores (Karban *et al.*, 1997; Agrawal, 1998).

The impact of large mammalian herbivores on insect herbivores may vary by functional or taxonomic groups and whether the insects are generalists or specialists (Tabuchi *et al.*, 2010; Lind *et al.*, 2012; Zhou *et al.*, 2015). Previous research has found the greatest change in community composition following grazing herbivore exclusion in arachnid, leafhopper, and true bug communities with less drastic changes in dung and click beetle communities (van Klink *et al.* 2016). Similarly, the exclusion of ungulate herbivory has shown significant but variable increases in abundance (more than twice that of control plots) of four guilds of insect herbivores – stem borers, seed predators, sap suckers, and gall makers (Gómez & González-Megías, 2007). Additionally, mammalian herbivore browse may affect insects with sucking mouthparts but not chewing mouthparts (Den Herder *et al.*, 2004; Allombert *et al.*, 2005) or *vice versa* (Barrett & Stiling, 2007), which may be related to induced changes in xylem and phloem properties associated with insect herbivore preferences (Romero & Bolker, 2008; Ebert *et al.*, 2018). Furthermore, these changes and their subsequent impacts on the insect herbivores are dependent on the plant species and how and to what extent it reacts to damage (Nykänen & Koricheva, 2004).

A major mammalian herbivore in eastern North American agricultural systems is the white-tailed deer (*Odocoileus virginianus* Zimmermann), which can be overabundant in Midwestern and Northeastern states due to increased forage availability, changes in land use, and lack of natural and human predation (Côté *et al.*, 2004). White-tailed deer browse pressure alters understory plant communities, vegetation structure, and microclimate conditions of forests (Rooney & Waller, 2003). Within agroecosystems, crops such as soybeans comprise upwards of 76–88% of white-tailed deer diet (Colligan *et al.*, 2011). Deer browse in soybean fields can reduce plant height, aboveground biomass, and yield (Rogerson *et al.*, 2014; Begley-Miller & Cady, 2015). Fields surrounded by forest may experience exacerbated deer damage, particularly when crop plants are young (deCalesta & Schwendeman, 1978; Garrison & Lewis, 1987). However, deer effects on final crop yield are not always significant despite plant damage (Rogerson *et al.*, 2014; Hinton *et al.*, 2017).

The changes in crop plant characteristics following deer herbivory may result in cascading changes in insect pest communities. Deer browse on non-crop vegetation can increase leaf hardness and decrease both insect herbivore diversity and insect herbivore-mediated leaf damage (Shimazaki & Miyashita, 2002; Allombert *et al.*, 2005). Other mechanisms may include plant damage that attracts arthropod predators, leading to decreased

pest abundance (Zhu & Park, 2005; Mallinger *et al.*, 2011). Deer browse may also increase the structural complexity of plants giving rise to greater numbers of flowering stems and increased soybean yields (Colligan *et al.*, 2011). New regrowth may be more nutritious and palatable in insect pests (Board & Tan, 1995).

Deer-induced plant changes in row-crop agroecosystems are short-term as crop fields are replanted annually, in contrast to forest or perennial crop ecosystems where there may be long-term population- and community-level change in plant and insect communities. However, there may be an immediate trade-off between plant defences and growth when recovering from herbivory. Soybeans readily regrow following deer browse (Hanley *et al.*, 2007), but it is unknown whether soybean plants alter leaf nutritional content in response to deer browse. In the case of crop plants like soybean, it is important to understand how plant response to both indirect and direct competitive interactions of different herbivores may influence final crop yield.

The primary goal of this study was to determine whether deer browse influenced insect pest abundance and insect-mediated leaf damage in soybean plants. Since accidental consumption of insects by deer is expected to be minor and since soybean plants readily regrow following mammalian herbivory, we hypothesized deer browse would influence insect pest abundance and herbivory on soybeans through indirect effects on plant height and plant nutritional quality (C : N ratio). Since we expected deer browse to reduce plant height (Begley-Miller & Cady, 2015) and plant height to be positively related to insect abundance, we predicted an indirect negative effect of deer browse on both chewing and sucking insect abundance. Alternatively, if ungulate herbivory induced plant defences and increased leaf nutritional content (lower C : N ratio; Barrett & Stiling, 2007; Gann *et al.*, 2016), this reduction in C : N ratio in leaves may attract insect herbivores (indirect positive effect of deer browse on insect abundance). Therefore, while we expect the potential for both positive and negative indirect effects of deer on insect abundance, it is not possible to predict, *a priori*, which of the two effects are stronger. Further, because of conflicting results in previous studies on mammal herbivory effects on chewing and sucking insects (Den Herder *et al.*, 2004; Barrett & Stiling, 2007), it was unclear whether chewing and sucking insects would have similar or diverging responses to deer browse. Finally, we expected total herbivory (chewing insects and deer) to affect plant reproductive output (crop yield) in an additive manner, because of possible opposing indirect effects of deer herbivory on insect herbivores (Stephens *et al.*, 2013).

Materials and methods

Field sites

Our study was conducted in six conventionally managed, no-till soybean (*Glycine max* (L.) Merr.) monoculture fields, 60 × 70 m in size (0.4 ha), that were part of a multi-year corn-soy rotation at the Miami University Ecology Research Center, Oxford, Ohio (39.525963, -84.722171). Half of each field (30 × 70-m plots) was planted in winter radish the previous winter and removed before soybean planting as part of a separate study, but had no effect on our study (see Supporting information, Fig S1). Fields ranged from 12 to 85 m from a forested edge where deer were

likely present; thus, all fields were equally accessible by deer. All fields were planted (6 June 2018) at a rate of 7900 seeds ha⁻¹ with fungicide-treated (metalaxyl, prothioconazole, and penflufen), round-up ready seeds (Variety P36T14R2, Pioneer, Johnston, Iowa). Fields were pre-treated with glyphosate (Cornerstone Plus, Winfield, Ames, Iowa) and 2,4-D (Shredder, Winfield, Ames, Iowa) then post-treated with glyphosate (Extreme, BASF, Ludwigshafen, Germany) and fomesafen (Flexstar, Syngenta, Basel, Switzerland).

Estimation of deer browse, insect herbivory, and plant metrics

Insect pest and plant samples were collected along six 10-m transects per field, located 7.5 m apart, centered in each field, for a total of 36 transects (6 transects × 6 fields = 36 transects; see Supporting information, Fig S1). All samples except for estimated yield were collected during four sampling periods in summer 2018 (July 11–13 July 25–26 August 9–10 August 22–24). First, insects were sampled using sweep net sampling along each transect using 10 figure-8 sweeps along each 10-m transect. Insects were stored in 95% ethanol until individuals were sorted and common pests were counted and identified to species. Insect abundance was quantified as the number of individuals per 10 sweeps. Plant height and stem count (each stem classified as browsed and undamaged) for the first 50 plants along each transect were used to estimate deer browse intensity (Colligan *et al.*, 2011). To determine chewing insect herbivore damage and leaf C : N ratio estimates, one leaf was randomly selected every 2 m along the 10-m transect for a total of six leaves per transect per sampling period. Of these six leaves, three were pressed to estimate insect herbivore damage; the missing area relative to the total leaf area was measured using ImageJ software (Martin *et al.*, 2013; Schindelin *et al.*, 2015). The remaining three leaves were stored at -30 °C for later nutrient analysis. Leaves were dried to constant mass at 60 °C; leaves from each transect were homogenized and ground to a fine texture with a coffee grinder (Krupps, Solingen, Germany), and analysed for total carbon (C) and nitrogen (N) using a Fisher Scientific Flash 2000 NC Soil Analyser (Waltham, Massachusetts). Soybean crop yield (a measure of plant reproductive output) for each plot was assessed on 19 February 2019, using the standard seed count appraisal method (USDA, 2019). In short, the number of live plants in a 3.05-m sample row were recorded, and five representative plants were selected from the sample row. We counted the number of harvestable seeds on the selected plants, and calculated plants per m and seeds per plant. We then scaled this to bushels per acre adjusting for the average row width (USDA, 2019). Two yield estimates were assessed for each field. All other data were pooled at the transect level.

Statistical analysis

All statistical analyses were conducted in R version 3.5.0 (Core Team, 2018). We used structural equation modelling (SEM; the piecewiseSEM package in R, Lefcheck, 2016), to test our hypotheses of both direct and indirect effects of deer browse on chewing and sucking insect pest abundance mediated through

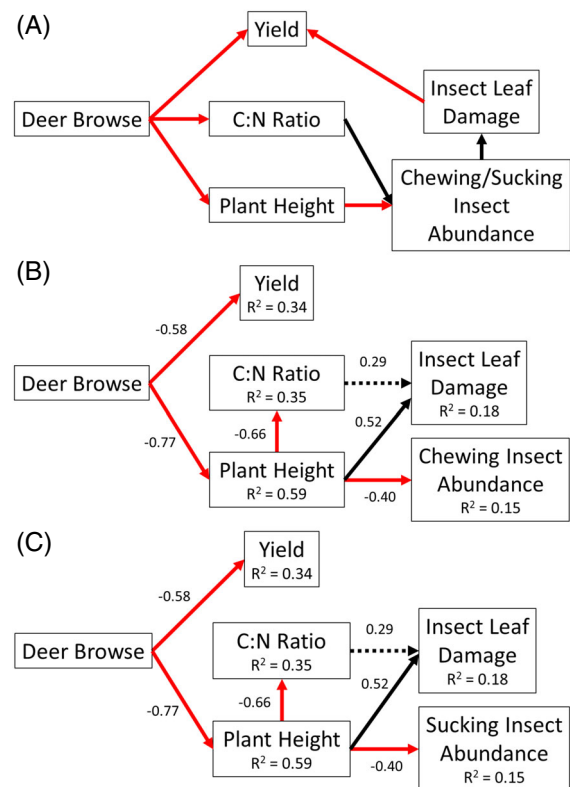


Figure 1 (A) Hypothesised structural equation model of deer influences on insect herbivory and subsequent plant yield. (B) and (C) Final structural equation model for chewing and sucking pest insect abundance, respectively. Significant paths are solid lines, nonsignificant paths are dashed. Positive relationships are in black, negative relationships are in red. Standardised coefficients are presented. Models for all responses were linear mixed effects models with field as a random term, except for soybean yield, which was a simple linear model. All predictor variables in the presented structural equation models were fixed effects. R^2 values are marginal R^2 (fixed effects only) for all paths except soybean yield ← deer browse, which is the multiple R^2 from a simple linear model. [Colour figure can be viewed at wileyonlinelibrary.com].

plant characteristics (plant height and leaf C : N ratio) and soybean yield. SEMs allow for testing of direct and indirect causal relationships among variables (Lefcheck, 2016). In a SEM, arrows represent direct, causal relationships, with the variable (boxes) at the end of the arrow representing the directional effect of one variable on the other. For all SEMs, only data from sampling period 4 were used, because this sampling coincided with soybean growth stages R1-R3, which are the growth stages that are most sensitive to herbivory. Additionally, this sampling period represented expected peak insect pest abundance and leaf damage (Pedigo & Zeiss, 1996; Penn, 2018). Initial SEMs were based on previous knowledge and hypothesized relationships among insect pests, plant characteristics, deer browse, and soybean yield (see ‘Introduction’ for predicted relationships; Fig. 1(A)). In the SEMs, linear models for endpoints of plant height, leaf C : N ratio, insect pest abundance, and insect leaf damage were fit as linear mixed effects models with soybean field as a random effect, and all other variables as fixed effects

(lme function, nlme package, R; Pinheiro *et al.*, 2019). Models for soybean yield were fit with linear models (lm function, stats package, R; R Core Team, 2018), as preliminary analyses indicated stronger among-site variation (Null model conditional $R^2 = 0.89$) than within-site variation and general patterns were more ecologically relevant than within site patterns. Model fits were assessed using Fisher's C for conditional independence ($P > 0.05$ indicates no missing paths among variables and satisfactory model fit) and model comparisons with Akaike Information Criterion (AIC); we present the model with the lowest AIC (Lefcheck, 2016). Our initial, *a priori* model was improved based on these model indices, but only scientifically valid relationships were considered.

Results

Evidence of deer browse was found on all plants, but deer browse – as a percentage of the total plant stems – decreased over the four sampling periods while leaf area damage increased (see Supporting information, Table S1). In the final sampling period, mean deer browse intensity ranged from 29% to 48%. Across all sampling periods, we collected 500 insect pests (see Supporting information, Table S1). Pest insects collected were mainly comprised of bean leaf beetles [*Cerotoma trifurcata* (Förster), Coleoptera: Chrysomelidae, 34.2%], potato leafhoppers [*Empoasca fabae* (Harris), Hemiptera: Cicadellidae, 25.6%], green cloverworms [*Hypena scabra* (Fabricius), Lepidoptera: Erebididae, 18.6%], and spotted cucumber beetles [*Dia-brotica undecimpunctata* (Barber), Coleoptera: Chrysomelidae, 10.2%]. In the final sampling period, mean soybean plant height varied from 37.5 to 60 cm; mean soybean leaf C : N ratios ranged from 7.16 to 9.56; and mean soybean yield was 13.99 bushels/acre with a range of 1.53 to 31.95 bushels/acre. Yield was lower than typical for the study area (USDA NASS, 2020), since it was estimated in February 2019 due to weather-related delays in harvesting during November 2018.

The initial hypothesized model (Fig. 1(A)) fit the data well for both chewing (Fisher's $C_{16} = 23.365$, $P = 0.104$, AIC = 65.365) and sucking insect SEMs (Fisher's $C_{16} = 21.853$, $P = 0.148$, AIC = 63.853). However, our initial model was improved with several modifications that resulted in the best fitting model with the lowest AIC for both chewing (Fisher's $C_{18} = 15.878$, $P = 0.601$, AIC = 55.878; Table 1; Fig. 1) and sucking insects (Fisher's $C_{18} = 14.987$, $P = 0.663$, AIC = 54.987;

Table 1; Fig. 1). Modifications indicated by AIC model selection included removing paths from leaf C : N ratio to chewing pest insect abundance, from insect-mediated leaf damage to soybean yield, and from deer browse to leaf C : N ratio; additions included paths from plant height to leaf C : N ratio, plant height to insect-mediated leaf damage, and leaf C : N ratio to insect-mediated leaf damage. Overall, the best-fitting model explained 34% of the variation in soybean yield, 59% variation in plant height, 15% variation in chewing pest insect abundance, 15% variation in sucking pest insect abundance, 35% variation in C : N ratios, and 18% variation in insect-mediated leaf damage. Deer browse had strong negative effects on soybean yield (Fig. 2(A)) and soybean plant height (Fig. 2(B)). Soybean yield was only influenced by deer browse (Fig. 2(A)). Leaf C : N ratio was strongly negatively influenced by soybean plant height, meaning that leaf nutritional value increased with plant height (Fig. 2(D)). Insect-mediated leaf damage responded positively to soybean plant height (Fig. 2(C)) and to leaf C : N ratio ($P = 0.125$), although the latter was a weaker effect (Fig. 1). Chewing (Fig. 2(E)) and sucking (Fig. 2(F)) pest insect abundance was negatively related to soybean plant height (Fig. 2(D)).

Deer browse also had indirect effects (products of direct paths) on chewing and sucking pest insect abundance, leaf C : N ratio, and chewing insect leaf damage, mediated through soybean plant height (Figs 1 and 2). Deer browse indirectly increased chewing and sucking pest insect abundance by reducing plant height (indirect path coef. = 0.31 for both chewing and sucking insects). Deer browse also indirectly increased leaf C : N ratios (reduced leaf nutritional value) by reducing plant height (indirect path coef. = 0.51). Finally, deer browse indirectly decreased insect leaf damage by reducing plant height (indirect path coef. = -0.40). Indirect paths of deer browse on insect leaf damage through leaf C : N ratio were weak due to weak direct effect of leaf C : N ratio on insect leaf damage.

Discussion

Our study found that deer herbivory reduced plant height and final plant yield. While areas of low deer browse were slightly below expected yields for the study region (USDA NASS, 2020), areas of mean and higher deer browse had yield estimates that were nearly 10 times less than expected for the study region. Previous studies have found variable results when investigating

Table 1 Structural equation model unstandardized path coefficients, critical values, and P values for the best model in Fig. 1(B, C)

Path	Estimate	SE	Critical value	P value
Plant height ← deer browse	-75.706	10.903	-6.943	<0.001
Leaf C : N ratio ← plant height	-0.060	0.015	-4.011	<0.001
(ln)Chewing insect abun ← plant height	-0.408	0.172	-2.367	0.025
(ln)Sucking insect abun ← plant height	-0.531	0.211	-2.523	0.017
(ln)Leaf damage ← plant height	0.003	0.001	2.814	0.009
(ln)Leaf damage ← leaf C : N ratio	0.019	0.012	1.580	0.125
Soybean yield ← deer browse	-106.639	25.412	-4.197	<0.001

All non-insect abundance paths are constant between Fig. 1(B), (C). Chewing insect abundance path is from Fig. 1(B) and sucking insect abundance path is from Fig. 1(C). Arrows represent directionality of the relationship between variables, such that the arrow is pointing towards the response and away from the predictor (response ← predictor). Note: Chewing insect abundance model was fit with a Poisson distribution.

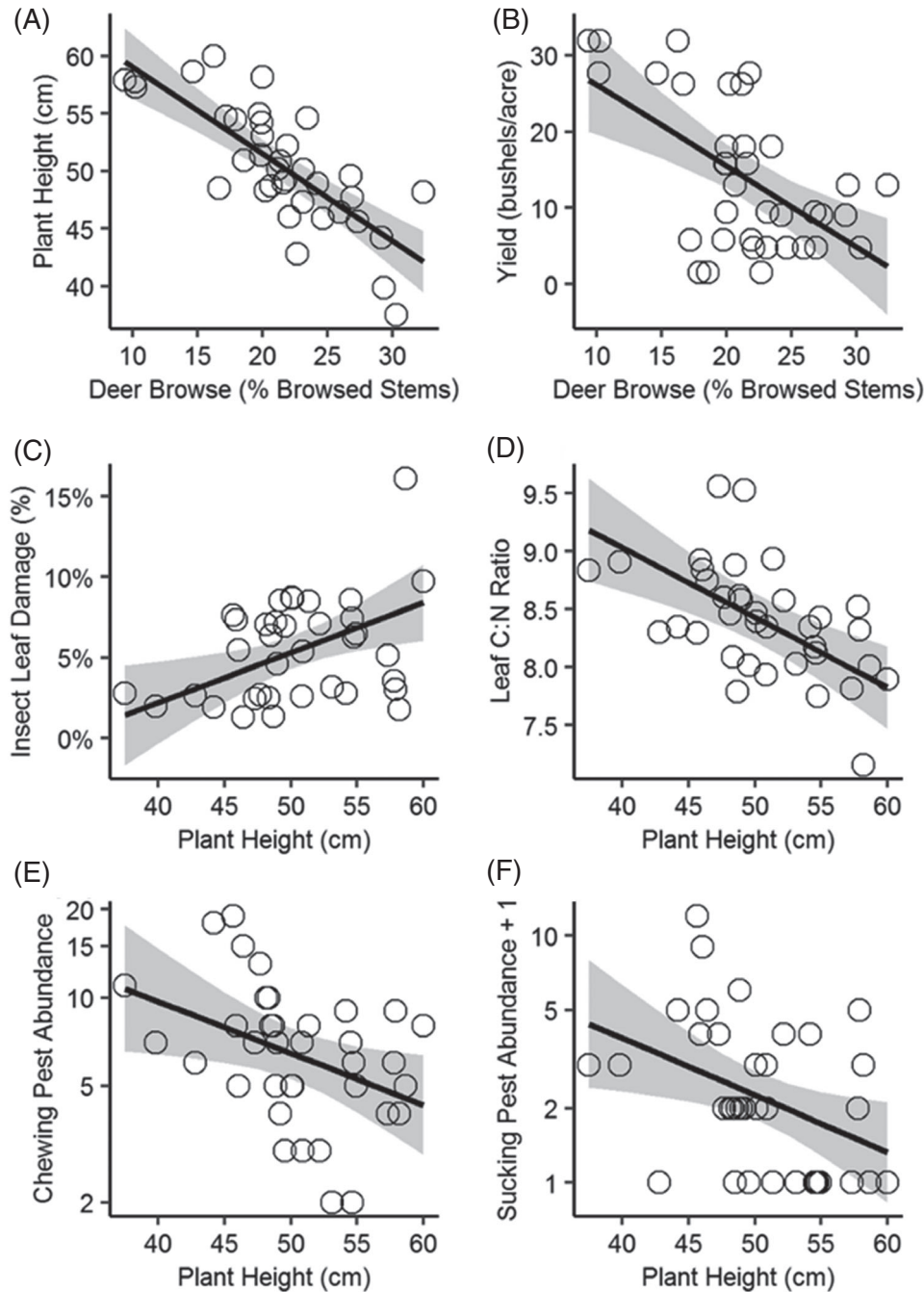


Figure 2 Relationships among (A) deer browse and soybean yield; (B) deer browse and plant height; (C) plant height and insect-mediated leaf damage; (D) plant height and leaf C:N ratio; (E) plant height and chewing pest abundance; (F) plant height and insect-mediated leaf damage. Lines for (A) are linear regression coefficients and lines for (B–F) are fixed effects coefficients from linear mixed effects regressions. Ribbons on all represent model indicated standard error. Note: y -axis of (E) and (F) are natural-log transformed.

deer browse on yields, including high deer herbivory near field edges, but no loss of yield due to deer browse (Rogerson *et al.*, 2014; Hinton *et al.*, 2017). Garrison and Lewis (1987) found that only 100% defoliation by deer before early growth of soybeans before vegetative stage with 5 nodes (V5) resulted in yield loss, but not lower levels of deer damage or simulated damage. Our results may differ from these studies because

deer damage in our study was found throughout the field sites (potentially as a function of small field size) and was not concentrated along field edges (see Supporting information, Fig S3). Variation between studies in tested soybean varieties may also explain some of the differences among studies in terms of deer herbivory on plant compensatory growth, structure, and

yield, but this should be investigated further (Powers *et al.*, 2006, Simonsen & Stinchcombe, 2007).

We did not find support for our *a priori* hypothesis that deer browse effects on soybean leaf C : N ratios would translate into changes in pest abundance. Further, chewing pest abundance was not related to insect-mediated leaf damage, perhaps because insect-caused leaf damage was a measure of cumulative insect damage whereas abundance samples were snapshots in time. This mismatch in temporal scales may have limited our ability to detect a relationship between insect abundance and insect-caused leaf damage. However, we found that deer browse mediated both insect pest abundance and damage to plants indirectly *via* plant height and C : N ratios of leaves. With an increase in deer browse, plants were shorter and had higher abundances of insect herbivores, which is consistent with previous studies (Barrett & Stiling, 2007). Insect-mediated plant damage decreased with deer browse, potentially in response to increasing C : N ratios (decreasing leaf nutrition). This result is also consistent with previous research showing antagonistic interactions between herbivores feeding on the same plant (Stephens *et al.*, 2013). Leaf C : N ratios, together with a weak relationship between insect herbivore abundance and leaf damage, indicate that browsed soybeans may be less nutritious (Yang & Joern, 1994; Lee *et al.*, 2004). In a study of soybean loopers [*Chrysodeixis includens* (Walker)] raised on plants with variable levels of nitrogen fertilization and subsequent foliage N, larval development time and consumption rates increased with lower levels of N in the foliage (Wier & Boethel, 1995). Thus, changes in leaf nutrition (C : N ratio or changes in relative abundance of carbon compounds) likely altered insect feeding, but differences between single-point estimates of insect abundance and cumulative measures of leaf damage likely limited our ability to detect a direct relationship between insect abundance and leaf damage.

Relatively little of the variation in insect herbivore abundance (marginal $R^2 = 15\%$ for both chewing and sucking insects) and damage (marginal $R^2 = 18\%$) was explained by the SEM model. Given that few natural predators of these pests were collected, this variation may be due to unmeasured aspects such as micro-site preferences, parasitoid presence, or plant interactions with environmental conditions such as soil, wind, and humidity (Wang & Mopper, 2008; Leonard *et al.*, 2016; Diepenbrock & Burack, 2017). Additionally, while unmeasured, deer browse likely increased soybean plant structural complexity with increased numbers of lateral meristems following removal of apical meristems (Begley-Miller & Cady, 2015). In turn, increased plant complexity provides more and younger foliage for insect pests (Board & Tan, 1995; Colligan *et al.*, 2011). Finally, changes in insect herbivore abundance and plant damage may have been mediated by changes in plant defences that were unmeasured (e.g. trichomes, tannins, phenols). These deer-insect interactions may change given soybean variety-differences in plant responses (i.e. C : N ratios, defence upregulation).

Insect pest populations did not reach economic thresholds (foliage loss >15% during soybean reproductive growth stage; Hammond *et al.*, 2014), resulting in relatively little insect-mediated leaf damage, and ultimately having little impact on final yield (Higley & Boethel, 1994). In years where pests are more damaging or transmit diseases to plants, possible synergy between deer and insect herbivory would be of greater

management concern. While our results indicate antagonistic effects of deer browse on insect feeding (insect-mediated leaf damage), future studies should consider indirect damage caused by insects, such as crop diseases, that also have broad economic impact on crops (Musser *et al.*, 2018).

We investigated whether deer browse mediated insect pest pressure in conventional soybean fields. We found that deer damage facilitated a higher abundance of insect herbivores, but lower levels of insect damage, as such, herbivore damage to plants was antagonistic rather than additive, as expected, likely due to reductions in leaf nutrition (increased leaf C : N ratio; Stephens *et al.*, 2013). Further, we found that deer and insect herbivory do not interact to affect soybean yield; rather, deer browse alone strongly reduced soybean yield. Economic threshold of deer browse appears to be approximately 20% mean browsed stems in soybeans, as deer browse levels above 20% had a strongly negative effect on soybean yield (Fig. 2(A)). Thus, while there is a potential for deer browse to act as a preventative measure against pest insect-caused herbivory (Karban *et al.*, 1997; Agrawal, 1998), the negative impacts of deer on soybean yield greatly outweigh any possible biocontrol benefits. Given the indirect beneficial impacts of deer browse on insect abundance and strong direct negative effects of deer browse on soybean yield, limiting deer browse in soybean fields may reduce the risk of insect infestation while preventing yield loss from deer.

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Author contributions

All authors contributed to the development and design of the study; AEV and MBM collected and processed samples; MBM and TOC performed statistical analyses; and all authors contributed to the writing of the manuscript.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Diagram of experimental design. A total of six fields were sampled, each 60 m × 70 m. Half of each field (30 m × 70 m plots)

was planted under winter radish (not part of this study). In each plot, three 10-m transects for sweep sampling were equidistant (7.5 m) from each other and the edges of each plot.

Fig. S2. Structural equation model (SEM) of deer browse influences on sucking insect pests and subsequent plant yield. Significant paths are solid lines; nonsignificant paths are dashed. Positive relationships are in black, negative relationships are in red. Standardised coefficients are presented. R^2 values are marginal R^2 (fixed effects only) for all paths except Soybean Yield \leftarrow Deer Browse, which is the multiple R^2 from a simple linear model. Differences between SEMs for chewing insects (Fig. 1) and sucking insects (this figure) are non-significant paths of Insect Leaf Damage \leftarrow Deer Browse and Insect Leaf Damage \leftarrow Sucking Insect Abundance. Fit statistics for this model: Fisher's $C_{14} = 8.069$, $P = 0.886$, AIC = 52.069.

Fig. S3. Relationship between distance into soybean field and deer browse (percent browsed stems) across sampling periods. In sampling periods 1 and 3, there is slightly more deer browse in the center of the fields; while in sampling periods 2 and 4, there is no difference in deer browse among distances into field.

Table S1. Mean (SE) chewing pest abundance, insect-mediated leaf damage (% damage), soybean plant height (cm), and deer browse (% browsed stems) across transects for each sampling period.

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