ORIGINAL ARTICLE

Role of arthropod communities in bioenergy crop litter decomposition[†]

Arthur R. Zangerl[1], Saber Miresmailli[1,2,‡], Paul Nabity[3,4], Allen Lawrance[1], Alan Yanahan[1], Corey A. Mitchell[2,5], Kristina J. Anderson-Teixeira[2,4], Mark B. David[2,5], May R. Berenbaum[1,2,3,4] and Evan H. DeLucia[2,3,4]

[1]*Department of Entomology,* [2]*Energy Bioscience Institute,* [3]*Department of Plant Biology,* [4]*Institute of Genomic Biology,* and [5]*Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana, IL 61801, USA*

Abstract The extensive land use conversion expected to occur to meet demands for bioenergy feedstock production will likely have widespread impacts on agroecosystem biodiversity and ecosystem services, including carbon sequestration. Although arthropod detritivores are known to contribute to litter decomposition and thus energy flow and nutrient cycling in many plant communities, their importance in bioenergy feedstock communities has not yet been assessed. We undertook an experimental study quantifying rates of litter mass loss and nutrient cycling in the presence and absence of these organisms in three bioenergy feedstock crops—miscanthus (*Miscanthus* x *giganteus*), switchgrass (*Panicum virgatum*), and a planted prairie community. Overall arthropod abundance and litter decomposition rates were similar in all three communities. Despite effective reduction of arthropods in experimental plots via insecticide application, litter decomposition rates, inorganic nitrogen leaching, and carbon–nitrogen ratios did not differ significantly between control (with arthropods) and treatment (without arthropods) plots in any of the three community types. Our findings suggest that changes in arthropod faunal composition associated with widespread adoption of bioenergy feedstock crops may not be associated with profoundly altered arthropod-mediated litter decomposition and nutrient release.

Key words biodiversity, bioenergy, decomposition, detritivore, land use change, prairie

Introduction

Widespread adoption of bioenergy feedstock crops to meet growing demand for alternative energy sources has the potential to alter many aspects of agroecosystem

Correspondence: Evan H. DeLucia, Department of Plant Biology, 265 Morrill Hall, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA. Tel: 217 333 6177; fax: 217 244 7246; email: delucia@illinois.edu

[†]Although this project was designed primarily by ARZ, his untimely death due to illness prevented him from seeing this work published. This article is dedicated to his memory.

[‡]Current address: Sumatics LLC, 575 Madison Ave., New York, NY 10022, USA.

function. Because first-generation bioenergy crops, including corn (*Zea mays*) for ethanol production and soybean, canola, and other oilseeds for biodiesel, are associated with a number of environmental problems (Hill *et al.*, 2006; Donner & Kucharik, 2008; Smeets *et al.*, 2009; David *et al.*, 2010) and have lower yields than may be attainable from cellulosic sources (Somerville *et al.*, 2010), alternative second-generation bioenergy crops are viewed as promising sources of lignocellulose for the production of bioenergy. To meet US production targets for renewable fuel (U.S. Environmental Protection Agency, 2010) will require allocating vast quantities of agricultural land to growing bioenergy feedstocks (U.S. Department of Energy, 2011), much of which is expected to be planted in perennial nonedible grasses. Such massive land use conversion will have widespread

impacts on agroecosystem biodiversity and ecosystem services, including carbon sequestration.

Among the organisms most likely to be affected by widespread land-use conversion are arthropods. Because of their abundance and ecological diversity, changes in community composition of arthropods have implications for delivery of a wide variety of ecosystem services. Landis and Werling (2010) reviewed studies to date on arthropod community responses to expanded bioenergy crop habitats. The major focus on anticipating impacts on arthropod communities has, not surprisingly, been on identifying pest herbivores, which by consuming otherwise harvestable tissue can reduce biomass and hence energy yields. Little is known about the potential impacts on diversity and abundance of beneficial detritivorous arthropod communities, which play an important role in determining rates of litter decomposition and hence energy flow and nutrient cycling.

Ecosystem services of detritivorous arthropods have been examined in a wide range of plant communities (Seastedt, 1984). Mass losses caused by the presence of an intact soil invertebrate community have been estimated at 37% in evergreen broadleaf forest, to 25% in coniferous forest, and 12% or less in dwarf forest and alpine meadow, and reductions in the abundance of microarthropods reduced rates of mass loss in all of these communities by one third to two thirds (Wang *et al.*, 2009). Beyond rates of mass loss, the abundance of soil arthropods can directly influence rates of release of specific nutrients. In a Hawaiian rain forest, macroinvertebrates increased rates of litter decomposition by 16.9% and rates of nitrogen and manganese release by 33.2% and 30.3%, respectively (Meyer *et al.*, 2011). Very few measurements of macroinvertebrate contributions to biogeochemical cycling have been made in grassland or cropland ecosystems, however, particularly in field settings. In one of the few studies to date, Osler *et al.* (2004) reported that gross nitrogen immobilization rates are linked to mite community structure in the Australian wheat belt (Osler *et al.*, 2004). As for the impact of changes in nutrient dynamics on plants, Eisenhauer *et al.* (2010) provided indirect evidence of the importance of the detritivorous arthropod fauna to experimental grassland communities by comparing plant growth in subplots treated or untreated by insecticides. Biomass accumulation was significantly lower in insecticide-treated plots, suggesting that reductions in arthropod abundance, particularly that of Collembola, decreased nutrient mineralization and cycling and thus plant nutrition.

Detritivorous arthropods, especially collembolans, are known to be a conspicuous component of bioenergy feedstock communities and thus may contribute significantly in a direct way to nutrient cycling and an indirect way

to plant growth. Bellamy *et al.* (2009) sampled invertebrate diversity in miscanthus using pitfall traps and sweep sampling with the intent of quantifying food resources for birds and found elevated numbers of collembolans in miscanthus compared to winter wheat. Similarly, Holguin *et al.* (2010) examined arthropod diversity in switchgrass by trophic category, conducting a three-year study with pitfall traps and sweep-nets. Despite the fact that pitfall trapping revealed comparable or greater numbers of "scavengers" than herbivores (herbivores varied from 11.2 to 80.6 per sampling date whereas scavengers varied from 37.6 to 83.6 during the same sampling period), the ecosystem services provided by these arthropods were not described. Moreover, collembolans were identified as consistently abundant in pitfall traps, but their abundance was not reported and the implications of their abundance and diversity for agroecosystem dynamics were not discussed.

In the absence of substantial information relating to macroinvertebrate contributions to litter decomposition (and hence nutrient cycling) in grasslands and croplands, it is difficult a priori to predict how the arthropod contributions to litter decomposition will change with landscape conversion to bioenergy crops. These contributions are key to calculating the sustainability of bioenergy crop cultivation. The identity of bioenergy crop might well affect this important ecosystem service. High-diversity prairie, as close in composition to natural communities of the Midwestern United States, has been proposed as an ecologically sustainable biofuel source (e.g., Hill, 2007). Its high diversity should in theory provide a greater variety of habitats and ecological communities for detritivores than would be available in monoculture cropping systems. Of two grass species proposed for bioenergy production, switchgrass (*Panicum virgatum*) is native to Midwestern North America and likely maintains a diverse and well-adapted native fauna. By contrast, miscanthus (*Miscanthus* x *giganteus*) is a sterile hybrid from Asian; as a nonindigenous plant recently introduced into North America, it is less likely to have been colonized by a local detritivore fauna. In the only study to date to investigate how changes in the composition of the arthropod detritivore community may vary with crop type, Eisenhauer *et al.* (2011) examined impacts of Collembola species composition and diversity on ecosystem services according to plant functional group (grasses, forbs, and legumes). Effects of Collembola diversity on litter decomposition and plant productivity were non-linear, indicating context-dependent species interactions; grass root biomass decreased with increasing Collembola diversity, for example, whereas legume root biomass increased.

In view of the absence of comprehensive information on the role of soil arthropods in litter decomposition

in bioenergy feedstock croplands, we undertook a study designed to quantify rates of litter mass loss in the presence and absence of these organisms. Our specific objectives were to compare the detritivore communities in bioenergy crops with those of food crops and reconstructed prairie with respect to (i) their overall composition with respect to taxonomic distribution and abundance; (ii) the rates of mass loss over the growing season, relative to rates in the absence of arthropods; (iii) the rates of nitrogen leaching over the growing season, relative to rates in the absence of arthropods.

Materials and methods

To measure the impact of the detritivorous arthropod community in three different bioenergy agroecosystem, our basic approach was to use insecticides to manipulate their abundance (e.g., Endelweber *et al.*, 2006, Eisenhauer *et al.*, 2010). Three different bioenergy crop systems were compared: miscanthus (*Miscanthus* x *giganteus*), switchgrass (*Panicum virgatum*), and restored prairie (mix of 28 species, Table A1, see Appendix).

Description of field site

Experiments were conducted at the University of Illinois Energy Farm located in Urbana, IL (40° 3′ 46.209″ N, 88° 11′ 46.0212″ W, ∼220 m above sea level). Experimental trays were set up within twelve 0.7-hectare plots (4 replicated plots for each crop) of miscanthus (*Miscanthus* x *giganteus*), switchgrass (*Panicum virgatum*), and restored prairie. Plots were established in 2008. Because of poor establishment, the miscanthus plots were replanted in 2009. The soil is a Flanagan-Drummer soil series (fine-silty, mixed, mesic Typic Endoaquoll), a Mollisol typical of northern and central Illinois. The field was in continuous cultivation of arable crops prior to establishing the energy crops. According to the Illinois State Water Survey, the mean temperature was 11.1°C and the mean accumulated rainfall was 1 042 mm (averaged from 1979 to 2009, www.isws.illinois.edu/data.asp).

Experimental setup

The experiment commenced in mid-March 2010, with litter randomly collected from miscanthus, switchgrass, and prairie fields one week prior to beginning the treatments. For miscanthus litter, which retains rather high integrity through early spring, collected litter was sorted into stems, inflorescences and leaves. These components were

then weighed and the proportions of biomass determined to be in the ratio of 1 : 2 : 8 stem : inflorescence : leaf. This ratio was maintained in each of the experimental units. For switchgrass and prairie, litter collections were well mixed and subsampled to create individual samples to deploy on the soil surface. Oven-dried switchgrass, miscanthus and prairie litter was either treated with an insecticide solution (150 μL Dursban, DOW AgroScience, Indianapolis, IN–mixed with 0.5 liter of tap water), which has been shown to have season-long activity against arthropods, or with water only (control). The purpose of the insecticide treatment was to provide a mechanism for estimating the rate of litter decomposition in the absence of detritivorous arthropods.

Within each plot, six bottomless aluminum trays (50 cm × 25 cm × 5 cm) were placed on top of soil within a randomly placed 0.37 m² quadrat. A layer of surface soil (collected from the edge of the plot) devoid of litter was placed in each tray and the preweighed (∼5.5 g) presoaked treated or untreated litter was then placed on top of the soil layer (corresponding to the existing crop in the plot). The trays were covered with fiberglass mesh screens to prevent litter displacement by wind, birds, or small mammals.

To quantify inorganic nitrogen leaching, ion exchange resin lysimeters were used as in Susfalk and Johnson (2002) and Langlois *et al.* (2003). The lysimeters consisted of a 5.1-cm diameter polyvinylchloride pipe and a coupling section that measured in total 7 cm in length. A layer of ion exchange resin capable of absorbing nitrate and ammonium was placed between two layers of washed sand and held together in the lysimeter with a permeable nylon membrane. The lysimeters were placed on the soil next to trays and filled with 30 g of fine sifted homogenized soil plus 4 g of treated or untreated litter, providing the same treatment arrangement as in the aluminum trays. In addition, another lysimeter received 30 g of soil-only (no litter), as an additional control to assess N leaching. Two weeks prior to placing trays and lysimeters, the areas within the quadrats were treated with herbicide (Roundup Ready PLUS, Monsanto, St. Louis, MO).

Measurement of litter mass and chemical composition in the experimental trays

Decomposing litter material was harvested in July, August, and September from one control and one treated tray at each harvest date. The harvested litter material was thoroughly washed with tap water passing over each sample, individually placed inside a plastic bucket with mesh screens at each end to allow water flow, and dried

at 60°C in an oven for three days. Initial dry mass of each litter sample was then compared with remaining dry mass at each harvest. Carbon and nitrogen concentrations of litter material were measured at each harvest and compared with that of initial litter material. For total C and N concentration per unit dry mass (and C : N), litter material was thoroughly cleaned and dried at 100°C, ground to a fine powder inside Eppendorf tubes with a plastic bead and analyzed using an Elemental Combustion System (model 4010, Costech Analytical Technologies, Valencia, CA).

Nitrogen leaching measurement

The lysimeter units were collected 6 months after their placement with the last litter harvest. The mass of nitrate and ammonium absorbed on the resin was determined by KCl extraction. Nitrate and ammonium concentrations in the extract were analyzed colorimetrically by flow injection analysis with a Lachat QuikChem 8000 (Lachat, Loveland, CO). The mass of the nitrate and ammonium absorbed on the resin was determined by multiplying the concentrations by the extract volume.

Soil arthropod survey

At each harvest, soil samples were collected from both control and treatment trays by pushing a PVC tube (15 cm in length, 10 cm diameter) down through the soil inside the trays where litter materials were placed. The soil was then placed in a Berlese funnel for one week with a light fixture above the soil sample and the exiting arthropods were collected inside tubes filled with pure ethanol. Total arthropods were counted in each sample under the microscope and specimens were identified to order. Definitively characterizing the detritivore fauna, however, required identification at the level of genus or species, which exceeded the expertise available to us at the time of the study.

Statistical analysis

To test the hypothesis that litter with an intact detritivorous arthropod community undergoes faster biomass loss and nutrient release than litter without a detritivorous arthropod community, repeated measure multiple analysis of variance (MANOVA) with all possible combinations of factors including harvest time, plant litter type and treatment was used to analyze the decomposition rate, carbon–nitrogen (C : N) ratio and soil arthropod abundance at successive harvests over the growing season. Differences in ammonium-N and nitrate-N leaching by crop type were evaluated by general linear model, with mean differences of ammonium-N and nitrate-N within a crop type separated using least significant difference (SAS Ver. 9.2).

Results

Primarily detritivorous taxa (Collembola, Acari) formed 67%, 86%, and 91% of total arthropods collected from switchgrass, miscanthus, and prairie, respectively, over the course of the study (Fig. 1). Insecticide treatment suppressed arthropod numbers for all crops below control levels within the first two harvests (Fig. 1; $F_{1,72} = 29.296$, $P < 0.05$). By the last harvest, however, arthropod abundance in insecticide trays approached that of control trays, indicative of insecticide breakdown (Table 1). This increase in numbers suggests that late stages of decomposition may have been influenced by arthropods.

Despite effective reduction of arthropods throughout the most of the experiment (Fig. 1), neither litter decomposition rate ($F_{1,18} = 0.045$, $P > 0.05$ [0.834]) nor C : N ratio ($F_{1,18} = 2.799$, $P > 0.05$ [0.112]) differed significantly between control (with arthropods) and treatment (without arthropods) plots in all crop species (Figs. 2 and 3, Table 1).

Release rates of ammonium-N or nitrate-N were not significantly different between control and insecticide treatments (Fig. 4). There was a pattern of nitrate-N immobilization in the litter in all treatments (soil-only versus control and insecticide treatments), with only prairie having a difference that was statistically significant. For ammonium-N release, litter additions increased the amount of N leached a small amount compared to soil-only for miscanthus and switchgrass.

Discussion

As reported for other grassland ecosystems (e.g., Eisenhauer *et al.*, 2010), mites and collembolans dominated the arthropod communities as a whole. In that, these groups are in turn dominated by detritivores; our findings suggest that the litter community is essentially a community of detritivores. Mites and collembolans outnumbered presumptively predaceous taxa in some instances by one to two orders of magnitude, suggesting that predators are not likely to be responsible for ecosystem impacts on litter decomposition associated with crop type.

In these grass-dominated communities, the fact that arthropod removal had no impact on litter decay suggests that decomposition is likely driven by microbial
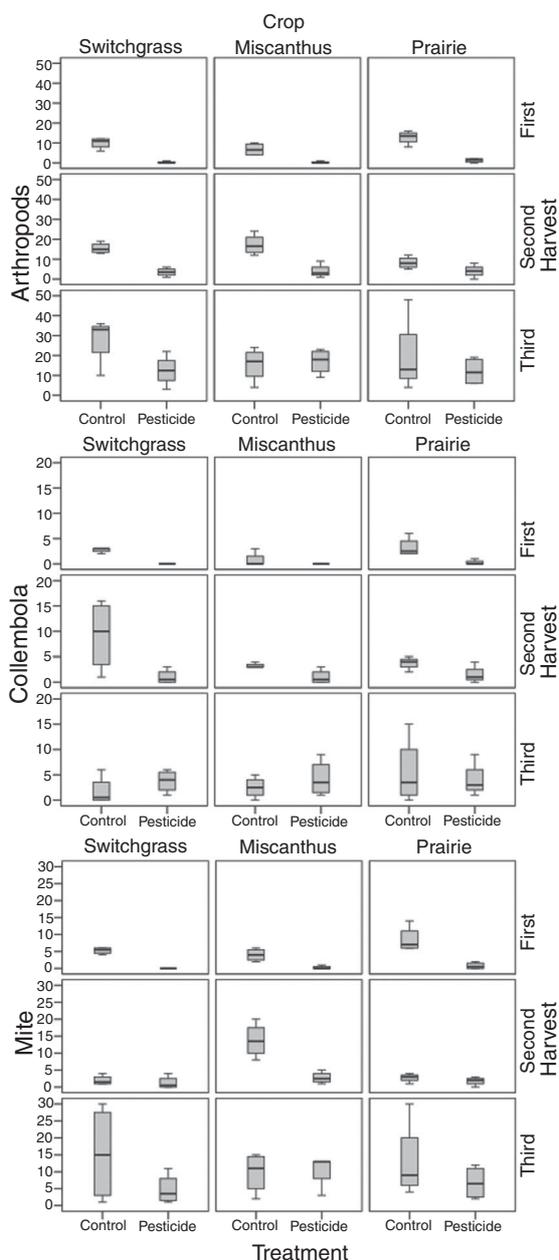
Fig. 1 Total number of arthropods, number of collembolans and number of mites ± SD in a single soil column (PVC column, 15 cm length, 10 cm diameter) collected after each litter harvest within control and treated trays.

decomposition, at least over the time scale of the experiment. In a comparable experiment (Eisenhauer *et al.*, 2010), impacts of eradicating the soil macroinvertebrate fauna on plant growth were measured over a span of 12 months (two growing seasons); it is possible that, over the course of another growing season, arthropod removal may have had a greater impact on litter decomposition.

Table 1 Results of MANOVA for the effect of harvest time, insecticide treatment, and crop type on decomposition rate, C : N ratio, and arthropod abundance, including all interaction terms. The most conservative test statisics (e.g., lowest probability (*P*) value) for the Pillai's Trace, Wilks' Lambda, or Hotelling's Trace statistic are displayed.

Effect	Value	*F*	Hypothesis df	Error df	*P*
Decomposition rate					
Harvest time	0.873	58.317	2	17	0.000
Harvest time × crop	0.424	1.695	4	32	0.176
Harvest time × treatment	0.109	1.035	2	17	0.376
Harvest time × crop × treatment	0.033	0.134	4	32	0.969

Effect	Value	*F*	Hypothesis df	Error df	Sig.
C : N					
Harvest time	0.969	16.932	4	72	0.000
Harvest time × crop	0.331	1.784	8	72	0.094
Harvest time × treatment	0.053	0.452	4	68	0.771
Harvest time × crop × treatment	0.122	0.600	8	68	0.775

Effect	Value	*F*	Hypothesis df	Error df	Sig.
Arthropod abundance					
Harvest time	0.787	5.402	12	100	0.000
Harvest time × crop	0.792	2.139	24	208	0.002
Harvest time × treatment	0.457	2.470	12	100	0.007
Harvest time × crop × treatment	0.713	1.879	24	28	0.010

Insect herbivores can greatly affect nitrogen cycling in ecosystems (Hunter, 2001; Lovett *et al.*, 2002). Inasmuch as the decomposition rate was unaffected by treatment, neither the litter C : N ratio nor the release of inorganic N as ammonium and nitrate were affected by the absence
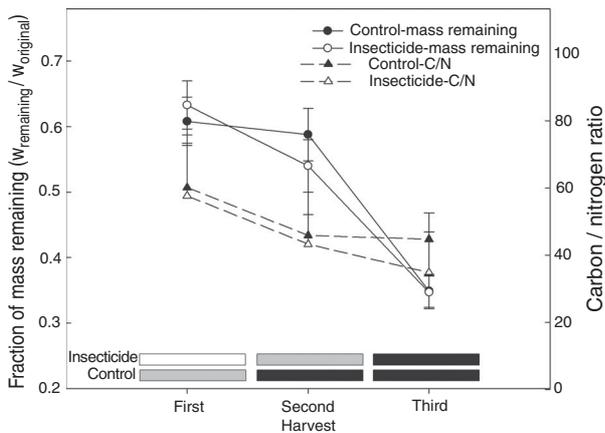
Fig. 2 Mean remaining litter fraction (remaining dry mass/ original dry mass) and C : N ratio of all three plant communities ± SE at three litter harvest time. The colored squares at the bottom of the graph represent arthropod status (white = absent; gray = emerging in low numbers; black = present).
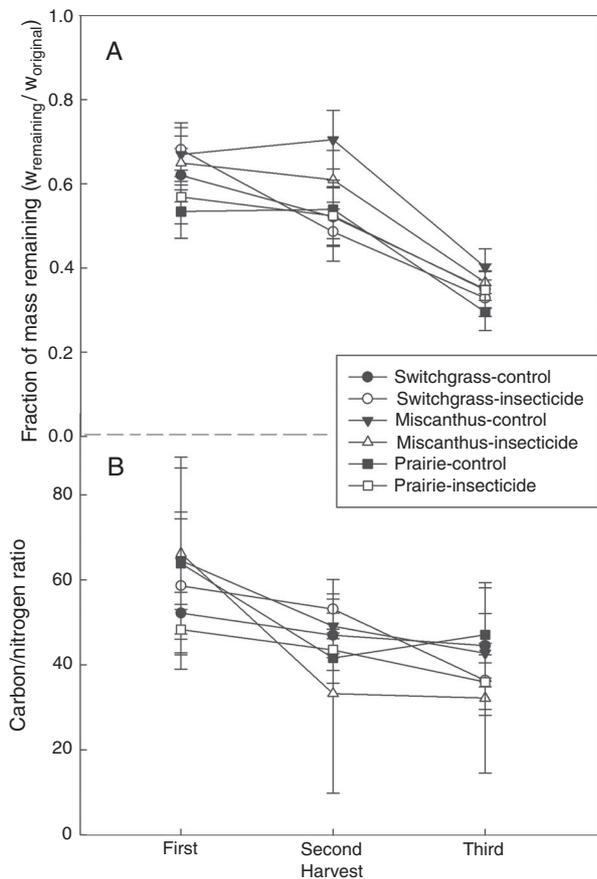
Fig. 3 (A) Mean litter fraction remaining (dry mass/original dry mass) at each harvest time, and (B) C : N ratio at each harvest time.
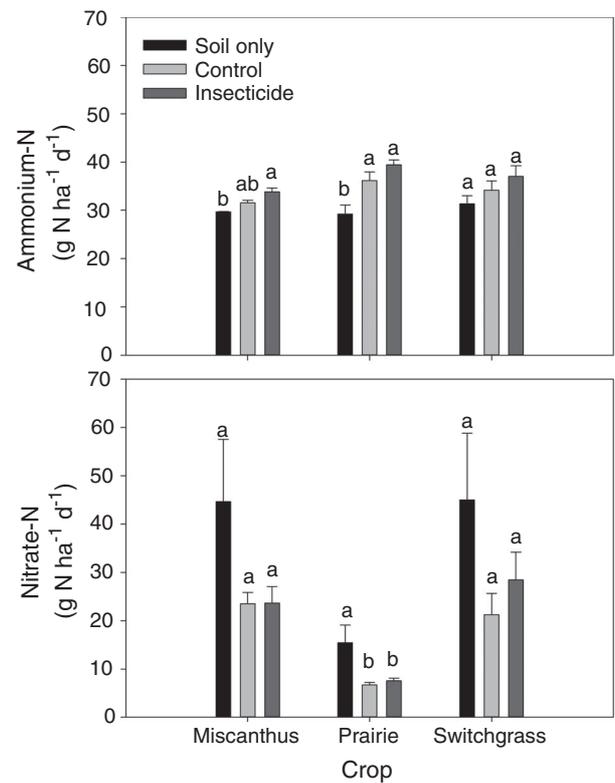
Fig. 4 Mean ammonium-N and nitrate-N leaching expressed per day of treatment period (±SE) for soil-only, control, and insecticide treatments. Means of ammonium-N or nitrate-N within a crop type with the same letter(s) are not significantly different at 0.05%.

of arthropods, and litter decomposition proceeded with a progressive narrowing of the C : N ratio. Because the C : N ratios of the litter were initially wide and between 50 and 70 (Fig. 3), more N was immobilized as microbial decomposition (presumably) occurred and C was released as CO_2. Nitrate from atmospheric deposition entering the litter in precipitation was likely immobilized by the microbial community in the litter treatments, compared to the soil-only treatment, where this nitrate was leached through the soil. Substantial inorganic N is typically not released from litter and soils until the C : N ratio is less than about 20 (Sylvia *et al.*, 2005). This low C : N ratio had not been attained by the end of the experiment (Fig. 3), explaining the low rates of nitrate leaching from plots with litter (control, insecticide treatment), relative to bare soil. Therefore, our results show the decomposition pattern of C and N and release of N in these crop systems was due primarily to microbial activity, with no effect directly attributable to differences in arthropod abundance.

Although these findings collectively suggest that arthropods did not play a dominant role in litter decomposition and associated N release in these crop systems, the rate of mass loss was higher between August and September than between July and August (Figs. 2–4)–a finding that differs from the expected pattern of decelerating mass loss over time. This increase in the rate of mass loss may have been driven by abiotic conditions or by increasing arthropod abundance at the end of the experiment (Fig. 1).

In mixed deciduous forest and grassland communities, microfauna contribute to more than ∼40% of the decay rates of foliage litter, but this contribution is highly variable among community types (Seastedt, 1984). In contrast, this study indicates that arthropods did not play a dramatic role in the decomposition of bioenergy litter material. The diversity of the soil invertebrate population is related to plant diversity (Tilman, 1982; Siemann *et al.*, 1998; Symstad *et al.*, 2000). That the bioenergy crops examined in this study, even the relative species-rich prairie, were planted on land recently in monoculture agriculture may in part explain the inability to detect a significant effect of arthropods on decomposition. The relatively small scale of this study, restricted to experimental plots, limits the extent to which results may be extrapolated to landscape scale but our findings suggest that changes in arthropod faunal composition associated with widespread adoption of bioenergy feedstock crops on land formerly used for row-crop agriculture is unlikely to alter profoundly arthropod-mediated litter decomposition and nutrient release. Concerns remain over the effects of land use changes on other ecosystem services, including pest control and pollination, but our study suggests that not all ecosystem services provided by arthropods are likely to be affected in the same way by land use changes associated with bioenergy feedstock production.

Acknowledgment

Disclosure

The authors have no conflicts of interest to disclose.

References

Bellamy, P.E., Croxton, P.J., Heard, M.S., Hinsley, S.A., Hulmes, L., Hulmes, S., Nuttall, P., Pywell, R.F. and Rothery, P. (2009) The impact of growing miscanthus for biomass on farmland bird populations. *Biomass and Bioenergy*, 33, 191–199.

David, M.B., Drinkwater, L.E. and McIsaac, G.F. (2010) Sources of nitrate yields in the Mississippi River basin. *Journal of Environmental Quality*, 39, 1657–1667.

Donner, S.D. and Kucharik, C.J. (2008) Corn-based ethanol production compromises goal of reducing nitrogen export by the Mississippi River. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 4513–4518.

Eisenhauer, N., Sabaise, A.C.W. and Scheu, S. (2011) Collembola species composition and diversity effects on ecosystem functioning vary with plant functional group identity. *Soil Biology and Biochemistry*, 43, 1697–1704.

Eisenhauer, N., Sabais, A.C.W., Schonert, F. and Scheu, S. (2010) Soil arthropods beneficially rather than detrimentally impact plant performance in experimental grassland systems of different diversity. *Soil Biology and Biochemistry*, 42, 1418–1424.

Endlweber, K., Schädler, M. and Scheu, S. (2006) Effects of foliar and soil insecticide applications on the collembolan community of an early set-aside arable field. *Applied Soil Ecology*, 31, 136–146.

Hill, J., Nelson, E., Tilman, D., Polasky, S. and Tiffany, D. (2006) Environmental, economic, and energetic costs and benefits of biodiesel and ethanol biofuels. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 11206–11210.

Hill, J. (2007) Environmental costs and benefits of transportation biofuel production from food- and lignocellulose-based energy crops. A review. *Agronomy for Sustainable Development*, 27, 1–12.

Holguin, C.M., Reay-Jones, F.P.F., Frederick, J.R., Adler, P.H., Chong, J.-H. and Savereno, A. (2010) Insect diversity in switchgrass grown for bioenergy in South Carolina. *Journal of Agricultural and Urban Entomology*, 27, 1–19.

Hunter, M.D. (2001) Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology*, 3, 77–84.

Landis, D.A. and Werling, B.P. (2010) Arthropods and biofuel production systems in North America. *Insect Science*, 17, 220–236.

Langlois, J., Johnson, D.W. and Mehuys, G.R. (2003) Adsorption and recovery of dissolved organic phosphorus and nitrogen by mixed-bed ion-exchange resin. *Soil Science Society of America Journal*, 67, 889–894.

Lovett, G.M., Christenson, L.M., Groffman, P.M., Jones, C.G., Hart, J.E. and Mitchell, M.J. (2002) Insect defoliation and nitrogen cycling in forests. *Bioscience*, 52, 335–341.

Meyer, W.M., Ostertag, R. and Cowie, R.H. (2011) Macroinvertebrates accelerate litter decomposition and nutrient release in a Hawaiian rainforest. *Soil Biology and Biochemistry*, 43, 206–211.

Osler, G.H.R., Recous, S., Fillery, I.R., Gauci, C.S., Zhu, C.Y. and Abbott, L.K. (2004) Correlation between mite community

structure and gross N fluxes. *Soil Biology and Biochemistry*, 36, 191–194.

Seastedt, T.R. (1984) The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology*, 29, 25–46.

Siemann, E. (1998) Experimental tests of the effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, 79, 2057–2070.

Siemann, E., Tilman, D., Haarstad, J. and Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist*, 152, 738–750.

Somerville, C., Youngs, H., Taylor, C., Davis, S.C. and Long, S.P. (2010) Feedstocks for lignocellulosic biofuels. *Science*, 329, 790–792.

Smeets, E.M.W., Bouwman, L.F., Stehfest, E., Vuuren, D.P.V. and Posthuma, A. (2009) Contribution of N_2O to the greenhouse gas balance of first-generation biofuels. *Global Change Biology*, 15, 1–23.

Susfalk, R.B. and Johnson, D.W. (2002) Ion exchange resin based soil solution lysimeters and snowmelt collectors. *Communications in Soil Science and Plant Analysis*, 33, 1261–1275.

Sylvia, D.M., Fuhrmann, J.J., Hartek, P.G. and Zuberer, D.A. (2005) *Principles and Applications of Soil Microbiology*, 2nd ed. Pearson Prentice Hall, Upper Saddle River, NJ.

Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

U.S. Department of Energy (2011) *U.S. Billion-Ton Update*: *Biomass Supply for a Bioenergy and Bioproducts Industry* (eds. R.D. Perlack & B.J. Stokes), pp. 227. ORNL/TM-2011/224. Oak Ridge National Laboratory, Oak Ridge, TN. Available at: http://bioenergykdf.net.

U.S. Environmental Protection Agency (2010) Renewable Fuel Standard Program (RFS2) Regulatory Impact Analysis (EPA-420-R-10–006). Assessment and Standards Division, Office of Transportation and Air Quality, United States Environmental Protection Agency, Washington, DC, USA. www.epa.gov/otaq/renewablefuels/420r10006.pdf.

Wang, S., Ruan, H. and Wang, B. (2009) Effects of soil microarthropods on plant litter decomposition across an elevation gradient in the Wuyi Mountains. *Soil Biology and Biochemistry*, 41, 891–897.

Zeri, M., Anderson-Teixeira, K.J., Hickman, G.C., Masters, M., DeLucia, E.H. and Bernacchi, C.J. (2011) Carbon exchange by establishing biofuel crops in central Illinois. *Agriculture, Ecosystems and Environment*, 144, 319–329.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table A1. Species composition and relative abundance of the restored prairie at the UIUC Energy Farm. (Zeri *et al.*, 2011)