

REVIEW

Arthropods and biofuel production systems in North America

Douglas A. Landis and Benjamin P. Werling

Department of Entomology, and Great Lakes Bioenergy Research Center, 204 Center for Integrated Plant Systems, Michigan State University, East Lansing, Michigan, USA

Abstract Biomass harvest may eventually be conducted on over 100 000 000 ha of US crop and forest lands to meet federally-mandated targets for renewable biofuels. Such large-scale land use changes could profoundly impact working landscapes and the arthropod communities that inhabit them. We review the literature on dedicated biofuel crops and biomass harvest from forests to look for commonalities in arthropod community responses. With expanded biofuel production, existing arthropod pests of biofuel crops will likely become more important and new pests will emerge. Beneficial arthropods will also be influenced by biofuel crop habitats, potentially altering the distribution of pollination and pest control services to the surrounding landscape. Production of biofuel crops including initial crop selection, genetic improvement, agronomic practices, and harvest regimes will also influence arthropod communities. In turn, arthropods will impact the productivity and species composition of biomass production systems. Some of these processes have the potential to cause landscape-level changes in arthropod community dynamics and insect-vectored plant diseases. Finally, changes in arthropod populations and their spatiotemporal distribution in the landscape will have impacts on consumers of insects at higher trophic levels, potentially influencing their population and community dynamics and producing feedbacks to arthropod communities. Given that dedicated biofuel crops and intensified biomass harvest from forests are still relatively uncommon in North America, as they increase, we anticipate ‘predictably unpredictable’ shifts in arthropod communities and the ecosystem services and functions they support. We suggest that research on arthropod dynamics within biofuel crops, their spillover into adjacent habitats, and implications for the sustainability of working landscapes are critical topics for both basic and applied investigations.

Key words biodiversity, land use change, pest management

Introduction

Recent interest in production of energy from plant biomass has spurred global efforts to develop dedicated biofuel crops and intensify biomass harvest from forest ecosystems. For simplicity, we hereafter refer to both sources of biomass collectively as biofuel produc-

tion systems. Arthropods are key mediators of ecosystem function in terrestrial ecosystems and as such, any changes in the way that humans appropriate plant biomass for biofuel production has immense implications. At one level, herbivorous arthropods will act as pests of biofuel crops, potentially reducing the quantity or quality of biomass harvested. Improved management systems will clearly be needed to mitigate the negative impacts of arthropods as plant pests. Alternatively, in their roles as decomposers, pollinators, predators and parasitoids, arthropods will be beneficial to biomass production systems. Moreover, beneficial arthropods may obtain resources in biofuels that increase their

Correspondence: Douglas A. Landis, Department of Entomology, 204 Center for Integrated Plant Systems, Michigan State University, East Lansing, MI 48824-1311, USA. Tel: (517) 353 1829; fax: (517) 353 5598; email: landisd@msu.edu

abundance and provision of services in the broader landscape. Increased adoption of biofuel crops may thus change the ways arthropod-mediated ecosystem services (Isaacs *et al.*, 2009) such as pollination and pest suppression are distributed in agricultural landscapes. Finally, because arthropods provide food for other organisms (e.g., birds and mammals), any changes in arthropod community structure will have indirect effects that are certain to radiate throughout terrestrial food webs (Polis *et al.*, 1997). However, it is also certain that such indirect effects are likely to be highly variable, with some being beneficial, some neutral, and others detrimental to ecosystem function. As society considers increased biofuel production systems, entomologists have a unique opportunity to examine their varied implications.

Current and future biofuel cropping systems in North America

At present, the US produces about nine billion gallons of ethanol annually (Anonymous, 2009b), primarily from the fermentation of corn grain. In addition, approximately 700 000 000 gallons of biodiesel (Anonymous, 2009a) are produced from soybean, canola and other vegetable oils. These first-generation biofuels are based on well-known technologies that use the edible portion of food crops. As such, they have been criticized for contributing to increased food prices (Naylor *et al.*, 2007; Mitchell, 2008, but see also Trostle, 2008). Second-generation biofuels are produced from lignocellulose obtained from the inedible portions of food crops (e.g., wheat straw and corn stover) or a non-food plant (Schubert, 2006). Such cellulosic biofuels can be produced from biomass harvested from forests or dedicated woody energy crops such as willow and poplar, as well as from herbaceous plants such as switchgrass, miscanthus, and mixed prairie grasses and forbs (Perlack *et al.*, 2005). The resulting biomass may be directly burned to generate electricity or co-fired with fossil fuels such as coal. Alternatively, cellulosic biomass can be processed via either thermochemical (i.e., pyrolysis) or enzymatic platforms to produce a variety of liquid fuels and other products (Ragauskas *et al.*, 2006). The US Energy Independence and Security Act of 2007 calls for an increase in renewable fuel production from 8 billion gallons in 2008 to 36 billion gallons in 2022. Cellulosic biofuels are to account for 16 billion gallons of this increase (Anonymous, 2009b). Meeting these targets is anticipated to require harvesting biomass from over 100 000 000 ha of US land (Graham *et al.*, 2007; Perlack *et al.*, 2005; Schmer *et al.*, 2008).

In this review we explore what is known about the role of arthropods in biofuel cropping systems. Our goal is to provide an entry into the relevant literature. In exploring this literature, we highlight the major phenomena (Table 1) that have emerged with increased production of existing biofuel crops and draw on research that provides lessons for future biofuel production systems (Table 2). In doing so, we also suggest key areas for future research. Our specific focus is on current and proposed biofuel production systems in North America. However, we draw on research from other regions when it can inform the future development of biofuels in North America. Although specific biofuel crops will differ throughout the world, the processes and concepts we explore here should prove widely applicable. For example, data from existing biofuel cropping systems from northern Europe provide a wealth of information that can be applied to North America. We also move beyond the borders of biofuel crops to discuss the landscape-level implications of increased biofuel production for arthropod communities and the ecosystem services that they provide (Losey & Vaughan, 2006). It is important to note that we do not focus on the use of arthropods for improved biomass processing, as this is the focus of other contributions in this special issue. In addition, for many of the traditional food crops, pest management aspects have been previously reviewed. In these cases we simply refer to the relevant reviews and focus on more recent literature and on novel aspects encountered when the crop is used for biofuel production.

Arthropods and herbaceous biofuel crops

Use of existing food crops for biofuel production

A number of existing crops are already used, or could be used, for biofuel production in North America. These include soybean (*Glycine max* (L.) Merr.) and the oilseed Brassicas (*B. rapa* L. (*campestris*), *B. juncea* (L.) Czern., and *B. napus* L.) for biodiesel production and corn (*Zea mays* L.), sweet sorghum (*Sorghum bicolor* (L.) Moench), sugar beet (*Beta vulgaris* L.) and sugarcane (*Saccharum* spp.) for ethanol production. Much of the relevant pest management literature for these crops has been previously reviewed: soybean (Kogan & Turnipseed, 1987; Turnipseed & Kogan, 1976), oilseed brassicas (Lamb, 1989), sorghum (Young & Teetes, 1977), sugar beet (Lange, 1987), sugar cane (Long & Hensley, 1972) and corn (Brindley *et al.*, 1975; Chiang, 1978; Levine & Oloumi-Sadeghi, 1991; Gray *et al.*, 2009).

Table 1 Examples of the major ways in which arthropods are known to interact with biofuel production systems. References indicate selected examples from the text.

Arthropod/biofuel crop interaction	Selected example(s)
Arthropods as pests of biofuel crops	
Increased importance of existing pests	Coyle, 2002; Hansen, 2003; Mattson <i>et al.</i> , 2001
Emergence of new pests	Dimou <i>et al.</i> , 2007; Ward <i>et al.</i> , 2007
Arthropods cause shifts in biofuel crop community composition or productivity	Schmitz, 2008
Biofuel crops alter arthropod pest dynamics in surrounding landscape	
Potential to increase insecticide resistance	Hansen, 2003
Potential for pest build-up and spillover into surrounding crops	Ahmad <i>et al.</i> , 1984; Semere & Slater, 2007
Biofuel crops act as reservoirs for insect-transmitted diseases	Huggett <i>et al.</i> , 1999
Impacts on beneficial arthropods	
Biofuel crop provides resources (shelter, food etc.) for beneficials	Carmona <i>et al.</i> , 1999; Menalled <i>et al.</i> , 2001; Gardiner <i>et al.</i> , 2010
Biofuel crops alter spatial or temporal distribution of beneficials	Frank <i>et al.</i> , 2008
Biofuel crops impact pollination/pest control services to surrounding landscape	Reddersen, 2001; Landis <i>et al.</i> , 2008
Biomass harvest patterns impact arthropod habitat	
Community shifts	Nitterus & Gunnarsson, 2006; Ulyshen & Hanula, 2009
Food web shifts	Hedgren, 2007
Alter habitat for rare species	Jonsell <i>et al.</i> , 2007
Change physical structure of habitat	Kortello & Ham, 2010
Biofuel crop influences other trophic levels via arthropod subsidies	
Bird nesting success	Sage & Tucker, 1997, 1998

Pest complexes attacking widely-used crops can change over time and space, suggesting that new pests will continue to challenge entomologists in established pest management systems. For example, the recent introduction of sweet sorghum into Greece for experimental biofuel production revealed heavy infestations of the stalk borer, *Sesamia nonagrioides* Lefebvre (Dimou *et al.*, 2007). This was the first report of a stalk-boring insect in sorghum in this country. Similarly, Ward *et al.* (2007) studied canola insect pests in Alabama in anticipation of increased production for biodiesel. They reported the first known occurrence of the North American endemic clover stem weevil, *Languria mozardi* Latreille, on canola. These examples suggest that host shifts onto biofuel crops by existing insect fauna are likely to be an ongoing process, creating new pest management challenges as production of existing crops expands to new areas.

Existing crops might also expand in acreage as they are increasingly used for biofuels, potentially increasing the availability of pest habitat and exacerbating control problems. Specifically, demand for biofuels that are also produced for food could pressure farmers to reduce rotation intervals, double crop within years, or even move

to continuous cultivation. In Denmark, oilseed rape production has expanded and is anticipated to grow further as demand for biodiesel increases. This has led to production of winter- and spring-sown crops, extending the period of bud availability for the pollen beetle, *Meligethes aeneus* F. and forcing increased insecticide use. As a result, *M. aeneus* is now highly resistant to pyrethroids and partially resistant to dimethoate, the two main groups of insecticides used to control it (Hansen, 2003). Similarly, increases in the extent of canola production in Australia over time are correlated with increased densities of diamondback moth, *Plutella xylostella* (L.) a key pest of brassicas (Schellhorn *et al.*, 2008). Although not strictly a result of biofuel crop production, these examples illustrate the type of land use pressures that are likely to impact insect management practices in the future. More generally, expanding production of existing crops can profoundly influence pest problems if these crops are more suitable for pests than the crops they replace or if they provide resources at key points in the pest's life cycle (Kennedy & Storer, 2000).

The expansion of biofuel crops might also indirectly influence pest problems by affecting natural enemy

Table 2 Ecological lessons and critical research avenues derived from examination of existing studies on arthropods in biofuel production systems.

1. New pests of biofuel crops will continue to emerge. Endemic herbivores could include biofuels in their host range as production expands to new areas.
2. Changes in the extent of biofuel production in existing production areas could alter the availability of habitat for existing pests, exacerbating pest problems.
3. Expansion of biofuel production could negatively affect biocontrol if biofuel crops are unsuitable for natural enemies or replace habitats that are critical for their persistence. Alternatively, some biofuel crops may be more suitable for natural enemies than the crops they replace. These could provide habitat for natural enemies that contribute to control of pests, both in biofuel crops and the broader landscape.
4. Existing data gives hints about the taxa that will become pests of biofuel crops. However, data should be collected across wider geographic areas and the impact of pests on biomass yield should be quantified.
5. Biofuel crops show genetic variation in insect resistance. This variation could be mined to produce resistant cultivars.
6. Direct pests are not the only problem. Biofuels could also act as perennial reservoirs of viruses that can be transmitted to other crops via mobile insect vectors.
7. It will be crucial to design and execute experiments that compare arthropod communities between candidate biofuel crops. Existing data largely come from experiments that are not designed for this purpose.
8. The conservation benefits of biomass crops to arthropods and the organisms that use them as food have only received preliminary attention.
9. Conservation benefits will not be uniform, but will be impacted by landscape context, within-site management and plant diversity.
10. The final impact of herbivores on biofuel productivity will depend on the full suite of interactions that occur between pests and other members of the arthropod community. Abstracting these interactions from their community-context could lead to misleading predictions about pests and biofuels.

populations. In the US, increased demand for corn as a biofuel feedstock has led to increases in corn production with negative impacts on biocontrol services in surrounding crops. Landis *et al.* (2008) reported that biocontrol of the invasive soybean aphid decreased in soybean grown in areas with increased corn acreage, costing growers a minimum of US\$58 million per year in lost yield and increased pest management costs. This could occur because corn is unsuitable for natural enemies, or because increases in corn production result in the loss of other key habitats. For example, non-crop habitats (e.g., forests and grasslands) appear to provide critical habitat for natural enemies (Bianchi *et al.*, 2006), and cultivating these habitats to increase crop production could reduce biological control.

Switchgrass

The US Department of Energy has been developing switchgrass, *Panicum virgatum* L. as a biomass crop since the early 1990s (McLaughlin & Kszos, 2005). Literature on switchgrass production provides an excellent example of the type of arthropod pest data that is, and is not, available for relatively novel biofuel crops.

Existing data suggests that pests can affect the establishment of switchgrass, but may cause only minor damage once established (Wolf & Fiske, 1995). Parrish *et al.* (1999) reported that in Virginia newly emerged switchgrass seedlings were susceptible to grasshoppers, crickets, corn flea beetle, *Chaetocnema pulicaria* Melsheimer and other insects, particularly when these insects inhabited pre-existing vegetation killed for switchgrass establishment. They reported that while not labeled at the time, an in-furrow soil insecticide (carbofuran) provided consistent advantages in establishment (Fike *et al.*, 2006). In addition, a report from Nebraska suggested that switchgrass seedlings were susceptible to chinch bug, *Blissus leucopterus leucopterus* (Say) and showed characteristic reddening of the leaves in the greenhouse; however, neither nymphal infestations nor damage was observed in the field (Ahmad *et al.*, 1984). These data provide hints on the types of pests that will challenge switchgrass. However, these data have been collected over a limited geographic area and yield losses due to pests have not been quantified. Collecting these data will enable potential pest problems to be compared between different biofuel crops across varying geographic contexts.

Switchgrass genotypes show considerable variability in insect susceptibility, suggesting the opportunity to breed

for resistance or discover resistance genes that may be useful in molecular-based breeding programs. In Hawaii, the 'Alamo' cultivar of switchgrass proved among the most resistant of all grass species tested to the yellow sugarcane aphid, *Sipha flava* (Forbes) (Miyasaka *et al.*, 2007). Dowd and Johnson (2009) report that seedlings of 'Trailblazer' and older 'Blackwell' plants were among the most resistant to feeding by the fall armyworm, *Spodoptera frugiperda* (J.E. Smith). Switchgrass accessions collected from the field proved widely divergent, with some readily fed upon by *S. frugiperda* and others causing high mortality in 2 days. Thus, both cultivated and wild populations may contain a genetic variation that can be mined for desirable traits.

Biofuel crops may also provide habitat for natural enemies. For example, tussock-forming grasses such as switchgrass are known to improve habitat for a variety of beneficial insects (Thomas *et al.*, 1991). Frank *et al.* (2008) tested the attractiveness of switchgrass and other native plants to foliar and ground-dwelling insect natural enemies, planting them in conservation strips on golf courses (Frank & Shrewsbury, 2004). These conservation strips increased predator, parasitoid and alternate prey numbers versus controls, primarily within 4 m of the strip. Predation of black cutworm larvae, *Agrotis ipsilon* (Hufnagel) was also higher in treatments containing conservation strips. Similarly, plantings of other native, tussock-forming grasses including big bluestem, *Andropogon gerardii* Vitman and Indiangrass, *Sorghastrum nutans* Nash, enhanced natural enemy abundance and predation of pests in potato over short distances (Werling, 2009). In a 2-year study examining carabid communities in switchgrass, corn and sweetgum, *Liquidambar styraciflua* L. plantations, Ward and Ward (2001) consistently captured more carabids in corn and switchgrass. However, switchgrass had the highest mean species richness (12.1 and 6.5 species/year) and greatest mean diversity (product of richness and evenness) of carabids with 29 species in total collected. Most of these were common agricultural species; communities were dominated by *Harpalus pennsylvanicus* Dej. in one year and *Anisodactylus furvus* LeConte in another. Menalled *et al.* (2001) studied the carabid community in switchgrass and mixed alfalfa, *Medicago sativa* L. and timothy, *Phleum pratense* L. filter strips adjacent to soybean. Overall, carabids were more abundant and diverse in switchgrass. Moreover, weed seed removal was significantly higher in the switchgrass filter strips and was positively correlated with an increased abundance of seed-feeding carabids in this habitat. In a concurrent study, Carmona *et al.* (1999) reported significantly greater abundance of the seed-feeding field cricket, *Gryllus pennsylvanicus* Burmeister in the switchgrass

versus alfalfa/timothy strips or soybean. Overall, multiple studies suggest that switchgrass may support abundant populations of some natural enemies that could potentially reduce biomass losses to pests.

Most of the above studies were not constructed to compare arthropod communities between biofuel crops; hence, comparisons relevant to making choices among candidate biofuel crops are often not made. To address this, Gardiner *et al.* (2010) contrasted the beneficial arthropod communities in three biofuel crops (corn, switchgrass and mixed prairie) to test the hypothesis that more diverse plant communities would support increased levels of beneficial arthropods. They found that most generalist predators and bees were either more abundant or diverse in the perennial and floristically more diverse grasslands than in corn. Bee communities were more species-rich in switchgrass ($n = 55$ spp.) and significantly more abundant in switchgrass than corn in early- to mid-season samples. This approach allowed the arthropod communities inhabiting different biofuel crops to be directly compared, suggesting that perennial grass systems may favor a variety of beneficial arthropods over annual crops like corn.

Miscanthus

Miscanthus × giganteus (hereafter miscanthus) is a hybrid grass that has been used for bioenergy production in Europe since the 1960s and was recently introduced to the US (Lewandowski *et al.*, 2003). It is a triploid (3×) hybrid produced by crossing *M. sinensis* (Thunb.) (2×) with *M. sacchariflorus* (4×). *Miscanthus* provides an example of the role that insect-vectored plant viruses might play in influencing biomass production and production of other crops. In Europe, few pests have been reported that directly damage miscanthus; however, Huggett *et al.* (1999) reported that the corn leaf aphid, *Rhopalosiphum maidis* Fitch was able to colonize miscanthus in the greenhouse and was most fecund on established plants. In addition, *R. maidis* successfully transmitted Barley Yellow Dwarf Virus (BYDV) to miscanthus and symptoms were expressed. In contrast, the bird cherry-oat aphid, *Rhopalosiphum padi* L. was unable to complete development on miscanthus and BYDV transmission was not demonstrated. They conclude that widespread production of miscanthus may result in a large reservoir of BYDV in the landscape and pose a threat to other sensitive crops, particularly as the perennial miscanthus could represent a bridging host for *R. maidis* from the time they leave cereal crops in mid-summer and colonize newly planted cereals in the fall.

Preliminary investigations have also examined the potential conservation value of miscanthus for arthropods. A wide variety of invertebrates inhabit miscanthus stands. In one of the few studies on the arthropod community of miscanthus, Semere and Slater (2007) sampled ground beetles, butterflies and arboreal invertebrates in re-establishing miscanthus stands following rhizome harvest in England. In these 2–3-year-old, open canopy stands, the miscanthus was only 53–265 cm tall and weed cover was high (41%–96%). In contrast, established miscanthus stands may reach 4 m in height (Lewandowski *et al.*, 2003) and have closed canopies. As such, they noted that the insect community was as much influenced by the weed cover as the crop. Ground beetles were about as abundant in miscanthus as in uncropped field margins, while butterflies were three-fold more abundant in field margins. The abundance of arboreal invertebrates varied by taxa, but was generally greater in field margins than in miscanthus (Semere & Slater, 2007). Bellamy *et al.* (2009) studied the bird community of miscanthus and winter wheat in England and sampled the invertebrate community as a potential food source using pitfall and sweep sampling. These were also relatively young miscanthus stands in their first to fifth growing seasons. In winter pitfall samples, overall invertebrate abundance did not differ between the crops. In the spring samples, there was a significantly greater abundance of foliar insects in wheat. The abundance of other taxa was generally similar between the crops, with the notable exception that Collembola were more abundant in miscanthus. These studies suggest that newly establishing miscanthus (with its open canopy and weedy understory) may support relatively abundant populations of some (e.g., carabids and Collembola) but not all, arthropod taxa. These studies also highlight the importance of expanding experimental treatments so that the conservation benefits of competing biofuel crops can be compared.

Relatively little has been reported regarding the use of miscanthus by beneficial insects. In Japan, *M. sinensis* has been used to provide overwintering and summer aestivating sites for lady beetles in an attempt to enhance their activity in nearby alfalfa fields (Takahashi, 1997). In the eastern US, ornamental *M. sinensis* is attacked by the miscanthus mealybug, *Miscanthioccocus miscanthi* (Takahashi). Gordon and Davidson (2008) reported *M. miscanthi* as a new prey record for the coccinellid *Hyperaspis paludicola* Schwarz and range expansion of the coccinellid feeding on mealybug as far north as Washington, DC. This scarcity of information on natural enemies and miscanthus points to a need to collect more data. This will enable entomologists to evaluate the potential impacts of this crop on biocontrol in agricultural landscapes.

Reed canary grass

Reed canary grass, *Phalaris arundinacea* L. is a Eurasian and North American native plant that is used as a forage and biomass crop in parts of Europe (Landstrom *et al.*, 1996). In the US, only a few populations from Ontario are known to predate European settlement and are considered native and non-invasive (Lavergne & Molofsky, 2004). In contrast, non-native invasive genotypes of reed canary grass now occur throughout much of the US and Canada, likely as the result of multiple introductions of European genotypes as a forage crop plant and more recently for phytoremediation and wastewater treatment (Lavergne & Molofsky, 2004). Reed canary grass is being considered as a potential biomass crop in the US (Perlack *et al.*, 2005); however, others have questioned its use given its invasive status (Raghu *et al.*, 2006).

Reed canary grass hosts a variety of pests and beneficial insects, suggesting that comparing different biofuel crops will require an accounting of both costs (e.g., pest damage) and benefits (e.g., natural pest suppression) produced by the arthropods they support. In Europe, reed canary grass and other forage crops are reported to be attacked by a variety of insects including the larvae of chafer beetles, *Melolontha melolontha* L., wireworms, *Agriotes* spp., and leather jackets *Tipula* spp. (Tscharrntke & Greiler, 1995). Semere and Slater (2007) also reported that reed canary grass was infested by green peach aphid, *Myzus persicae* (Sulz.) in England, with infestation levels reaching 20%. No yield losses were noted and BYDV symptoms were absent. They also sampled ground beetles, butterflies and arboreal invertebrates in reed canary grass fields and compared abundance and diversity to that found in miscanthus. Reed canary grass harbored marginally lower numbers of carabids, and butterfly abundance was two-fold less than in miscanthus. There was no difference in the diversity of butterflies between the two crops. Arboreal taxa were generally less abundant in reed canary grass with the exception of Hemiptera populations, which were more abundant (Semere & Slater, 2007).

Insect herbivores can use multiple host plants, creating the opportunity for pests from one habitat to spill over into other crops. For example, in the US, cereal leaf beetle, *Oulema melanopus* L. is a pest of small grains. Cereal leaf beetle larvae are known to feed on reed canary grass (Wilson & Shade, 1966) and both cereal leaf beetle and the frit fly, *Oscinella frit* L. have been reported as pests of reed canary grass where it is used in wastewater treatment facilities (Byers & Zeiders, 1976), suggesting the potential for increased production of reed canary grass to cause pest spillover onto grain crops. Thus, biofuels could provide

habitats for mobile pests that can move into other crops and cause damage.

Reed canary grass is an invasive species that can spread from plantings to other habitats, out-competing native plants and reducing the diversity of associated arthropods. For example, wetlands that are invaded by reed canary grass show decreased plant diversity (Schooler *et al.*, 2006). This in turn has been related to a decrease in moth species richness (Schooler *et al.*, 2009). If production of reed canary grass as a biofuel crop causes increased invasion into natural wetlands, there could be negative implications for native biodiversity. This example suggests that if not responsibly used, novel biofuel plants could become invasive and degrade native plant communities and the arthropods that depend on them.

Mixed prairie

Tilman *et al.* (2006) proposed that a high-diversity, low-input biofuel cropping system based on native US tallgrass prairies may have a series of benefits over so-called low-diversity high-input systems such as corn. Specifically, these systems could be grown on marginal soils with minimal inputs of fertilizer. As a result, little carbon would be expended in their production, making these feedstocks carbon-negative. Consequently, on low-fertility soils, high-diversity low-input systems may have nearly the same energy output as low-diversity high-input systems and may be more economical to produce (Zhou *et al.*, 2009).

A complete review of insects in native prairie systems is beyond the scope of this manuscript. Rangeland entomology has been previously reviewed by Watts *et al.* (1982), and Whiles and Charlton (2006) provide an excellent review of the ecological significance of arthropods in tallgrass prairies. Here we focus on insect communities in reconstructed grasslands, specifically on management factors relevant to their utility as biofuel crops.

Mixed prairie could produce conservation benefits for multiple arthropod taxa. In nearly all cases, biofuel crops based on prairie communities would represent prairie reconstructions not restorations, as they would be planted on lands previously cleared for agriculture or forestry. A number of studies have compared the insect fauna of remnant and reconstructed prairies. Arthropod species richness, diversity, or both are frequently higher in remnant versus reconstructed prairies. This has been shown for butterflies (Debinski & Babbitt, 1997; Shepherd & Debinski, 2005), grasshoppers (Bomar, 2009), Collembolla (Brand & Dunn, 1998), and mixed taxa (Panzer *et al.*, 1995). Larsen & Work (2003) showed

that carabid abundance and species richness was significantly higher in reconstructed versus remnant prairies.

Other studies have compared arthropod communities between prairies and other habitats. For example, Larsen *et al.* (2003) showed that carabid beetles were more abundant, species-rich and diverse in either reconstructed or remnant prairies when compared to woodlands or agricultural croplands, and that prairies contained a higher percentage of specialist species. Hopwood (2008) showed that roadsides restored with native grassland plants supported a significantly greater abundance and species richness of bees compared to weedy unrestored roadsides. Finally, Gardiner *et al.* (2010) found that bees were significantly more abundant in mixed prairie than corn in early-mid season samples. Overall, it can be concluded that a variety of arthropod taxa readily use reconstructed prairies.

Research suggests that the conservation benefits of prairie are contingent on other factors, including landscape context and site management. Stoner and Joren (2004) showed that insect communities in remnant prairies were strongly affected by land management practices and to a lesser degree by landscape factors. In general, plant species richness declined with increasing intensity of management from hay production to moderate- and high-intensity grazing. In turn, plant community composition explained the greatest amount of variation in Orthoptera and Lepidoptera communities. In contrast, curculinoid communities were equally influenced by blooming flower density (which was only slightly influenced by management) and landscape factors, while predator communities were primarily influenced by landscape variables. Other studies highlight the impact of site-scale variables on arthropod communities. For example, Larsen and Work (2003) found that carabid diversity in prairies declined with time since burning, and Gardiner *et al.* (2010) found that coccinellid diversity was positively correlated with floristic diversity in reconstructed mixed prairies. These studies demonstrate that the community-level impacts of prairie-based biofuel production are likely to be very complex and influenced by both within-site management and landscape structure. Thus, the conservation benefits of biofuels will vary between differently managed fields of the same crop and in different landscapes.

Arthropod communities can in turn interact to influence the structure and productivity of grasslands via complex, indirect interactions. Schmitz (2008) showed that predators could influence the long-term biomass productivity of grassland mesocosms by causing changes in herbivore behavior. Specifically, the presence of sit-and-wait predators changed grasshopper behavior, forcing them to feed on non-preferred plants. This resulted in slightly increased

plant diversity but significantly less overall biomass, perhaps due to decreased N mineralization rates driven by changes in litter input. This study shows that long-term productivity of grassland-based biofuel crops is likely to strongly depend on how arthropod communities interact with plant diversity and overall management practices. Furthermore, indirect interactions among insect species could produce impacts on biomass that are not predictable from studies that focus on individual insect herbivores and plants. Thus, it will be important to complement lab studies of biofuel pests with field studies where herbivory of biofuels is examined in its community context.

Arthropods and woody biofuel crops

Short-rotation woody crops

Use of short-rotation willow, *Salix* spp. and poplar, *Populus* spp. plantations for biomass production, and more recently phytoremediation, has a long history in northern Europe (Perttu, 1995, 1999; Rowe *et al.*, 2009). In the US, clones of poplar (Dickmann *et al.*, 2001) and willow (Abrahamson *et al.*, 1998; Volk *et al.*, 2006) selected for fast growth are planted at high densities and periodically harvested (coppiced) promoting regrowth. The resulting biomass can be used for direct energy generation in a co-firing facility or used in production of liquid biofuel.

The biology and management of insect pests in North American short-rotation hardwood systems were recently reviewed by Coyle *et al.* (2005). They provide detailed life histories for 32 insects attacking poplar, willow, sweetgum and sycamore plantations in North America. They also suggest general guidelines for reducing insect damage in intensive plantations which include: (i) use of resistant cultivars; (ii) using polycultures of different cultivars; (iii) creating landscape mosaics of smaller plantings rather than large monocultures; and (iv) maintaining high natural enemy-to-pest ratios.

Both poplar and willow are attacked by a wide variety of species and guilds of herbivorous insects. The cottonwood leaf beetle, *Chrysomela scripta* (Fabricius) is the most widespread and significant of the more than 300 insects and mites known to feed on poplar in the US (Mattson *et al.*, 2001). It is particularly damaging to young trees. Poplar is also attacked by several other important defoliators, sap feeders, and stem borers (Coyle *et al.*, 2005). Planting low-susceptibility clones is a primary tactic to avoid insect damage in poplar. Mattson *et al.* (2001) provide information on the susceptibility of over 90 clones to *C. scripta*, spotted poplar aphid, *Aphis maculatae* Oestlund, forest tent caterpillar, *Mal-*

cosoma disstria Hübner and tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois). As cottonwood production expands, new arthropod pests are still emerging. For example, the cottonwood leafcurl mite, *Tetra lobulifera* (Keifer) was only recently reported as a significant pest of cottonwood (Coyle, 2002).

Willow is attacked by a variety of herbivores, and research with willow herbivores provides an example of how experiments can be used to streamline efforts to screen for resistance. The imported willow leaf beetle, *Plagioderma versicolora* (Laicharting) is the most economically damaging pest of willow in the eastern US (Wade & Breden, 1986) and is capable of causing complete defoliation. Willow is also attacked by a variety of Saliaceae specialist and generalist defoliators (Coyle *et al.*, 2005). Nordman *et al.* (2005) screened 19 willow and 6 poplar clones for resistance to defoliating insects and used multivariate statistical approaches to analyze patterns of resistance. They found significant correlations in the feeding patterns among insects that could speed screening programs. For example, they report that nearly all the differences among clones of the seven insects could have been inferred from the feeding patterns of just three generalist species: *Popillia japonica* Newman adults, *Nymphalis antiopa* L. larvae, and adults of either specialist, *Polydrusus impresifrons* (Gyllenhal) or *Crepidodera nana* Say.

Labrecque and Teodorescu (2005) compared the field performance of 10 willow and 2 poplar clones against insect and disease attack in Quebec, Canada. They observed *P. versicolora*, *Disonychia alternata* Illiger, *Calligrapha multipunctata bigsbyana* Kirby, *Empoasca fabae* Harris, *Janus abbreviatus* (Say) and *Tuberolachnus salignus* Gemelin feeding on selected willow clones. In addition, *P. versicolora*, *D. alternata* and *Chaitophorus populicola* Thomas were occasionally observed on poplar clones. In US tests, willow varieties with *S. viminalis* in their background have been severely damaged by potato leafhopper, *Empoasca fabae* Harris (Volk *et al.*, 2006).

Willows and poplars may also support beneficial arthropod communities and provide food for birds. Reddersen (2001) suggested that the early and copious blooming of willow may be important for flower-visiting insects in Denmark. Sage and Tucker (1998) recorded over 120 invertebrate species in the canopy of willows and poplar in Europe and 45 species of ground-dwelling carabid and staphylinid beetles. Cunningham *et al.* (2004) reported greater species richness and diversity of butterflies at the boundary of willow plantations versus arable land controls. Sage *et al.* (1994) recorded 14 species of butterflies in the margins of short-rotation plantations, with most representing relatively common and widespread species (Rowe *et al.*, 2009). In studies of bird use of short-rotation

willow, Sage *et al.* (2006) characterized the plantings as often weedy and insect-rich habitats. They found that nesting birds used the willows as foraging sites and insect remains were found in the feces of nestlings (Sage & Tucker, 1997; Sage & Tucker, 1998).

Biomass harvest from forests

In the US, woody biomass can be harvested from forests in a variety of forms. Primary sources include logging residues from conventional harvesting or land clearing operations and removal of excess biomass in thinning or fuel reduction operations. Secondary sources include mill residues and pulping liquors, with tertiary sources being urban wood residues from tree-trimming and harvest or construction materials (Perlack *et al.*, 2005). Here we focus on the implications of the harvest of primary woody biomass for bioenergy on arthropod communities. This literature provides examples of how within-site management can alter habitat structure to affect arthropod communities.

Dead wood, including both coarse and fine woody debris, is an essential resource that supports insect biodiversity in forest systems (Hanula *et al.*, 2006). Removing this debris for biofuels could affect species that depend on this resource. For example, in Europe saproxylic insects that feed on dead and decaying wood are a highly threatened group (Davies *et al.*, 2008). Invertebrates make up nearly half (433/985) of the rare to endangered plant, animal and fungi species in Sweden and many of these depend on the presence of dead wood (Berg *et al.*, 1994). However, due to changes in forest management, dead wood has declined in many forest ecosystems (Fridman & Walheim, 2000; Norden *et al.*, 2004). Jonsell *et al.* (2007) showed that as many as 22 European red-listed species utilize fine woody debris as their primary habitat. They found large differences among wood species and some among debris size classes. Overall, they conclude that the fine woody debris from some species, for example spruce, could be harvested for bioenergy with less impact on invertebrate biodiversity than other species.

Other studies suggest that the way in which trees are harvested could affect biocontrol of tree pests. Specifically, Hedgren (2007) showed that in Sweden stumps serve as habitat for a diversity of mostly harmless bark beetles as well as their predators and parasitoids. In contrast to normal low-cut stumps, high-cut stumps intended for insect conservation purposes were favored by parasitoids with the density of three species significantly increased in their presence. By conserving habitat for natural ene-

mies, high-cut stumps may favor biocontrol of destructive bark beetles.

The treatment of remaining wood residues following harvest also impacts forest arthropod communities. Removal of slash from clear-cut areas reduced carabid beetle but not lycosid spider abundance in the short-term (Nitterus & Gunnarsson, 2006); however, 5–7 years after harvest the abundance and diversity of carabid beetles was higher in slash-removal versus slash-remaining sites (Nitterus *et al.*, 2007). Slash-removal sites had increased abundance of generalist species and a decline in forest species. Finally, the spatial arrangement of harvested and unharvested areas can affect forest insects. In a study of forest in which wood fuel was removed to reduce fire risk, the damselfly, *Argia vivida* (Hagen) preferred cleared fuel treatment areas during the day but roosted in trees at night (Kortello & Ham, 2010). They suggest that maintaining unmodified stands next to fuel management areas would provide the best mix of habitats to conserve this species. In contrast, a study manipulating coarse woody debris in southeastern US loblolly pine, *Pinus taeda* L. forests showed no significant differences in abundance, species richness or diversity of saproxylic beetles (Ulyshen & Hanula, 2009). However, carabid beetles were more species-rich and diverse in plots with log inputs.

Genetic improvement of biofuel crops

Genetic improvement of biofuel crops will impact arthropods in a variety of direct and indirect ways. Efforts are underway to genetically improve many biofuel crops (Vermerris, 2008) using techniques ranging from conventional and molecular crop breeding to transgenic modification. Indeed, much of the corn currently grown in the US includes transgenes from *Bacillus thuringiensis* (Bt) (e.g. Pilcher *et al.*, 2002) conferring resistance to lepidopteran and coleopteran pests (Kozziel *et al.*, 1993; Moellenbeck *et al.*, 2001). Bt toxins have also been incorporated into some *Populus* varieties to protect against coleopteran pests (Mattson *et al.*, 2001). While questions remain about the potential for transgenic plants to cause insecticide resistance, secondary pest outbreaks and non-target effects, if developed and deployed wisely they also have potential to reduce insecticide use while promoting beneficial natural enemies and pollinators (Kos *et al.*, 2009).

Improvement of biofuel crops to enhance processing characteristics and energy yield could also cause a variety of direct and indirect effects. For example, the lignin content of plant cell walls reduces the efficiency of

cellulose breakdown during processing (Hisano *et al.*, 2009); low-lignin biofuels are thus considered a desirable target for transgenic technology. Lignin is a product of the shikimic acid pathway and modification of lignin quality or quantity could alter production of other products of the pathway, which include alkaloids and tannins important in plant defense against insects (Bennett & Wallsgrove, 1994). Finally, even seemingly unrelated improvements to biofuel crops such as incorporation of herbicide resistance may alter insects and their management. For example, several current biofuel crops (corn, soybean and canola) include transgenes that confer herbicide resistance. This alteration changes the ecology and management of these crops in subtle ways that can be of significant importance to arthropods. For example, soybean producers that grow glyphosate-resistant crops incur fixed costs (labor, fuel, machinery etc.) to spray the herbicide. As such, the relatively small additional cost to add an insecticide to these applications may be seen as inexpensive “insurance” against future insect attack. This situation has resulted in an increase in insecticide applications against the soybean aphid, *Aphis glycines* in midwestern US soybeans (Olson *et al.*, 2008) with potentially negative impacts on natural enemies (Ohnesorg *et al.*, 2009). While many impacts of crop genetic improvement may be similarly difficult to anticipate, by collaborating with biofuel crop developers, entomologists can help direct development of sustainable biofuel cropping systems.

Landscape considerations

Meeting mandated targets for renewable ethanol in the US will require harvesting biofuel feedstocks from agricultural, grazing and forest lands (Perlack *et al.*, 2005). This will likely include increased production of traditional biofuel crops, addition of new crops into the landscape and increased harvest of biomass feedstocks from existing forest and rangelands. Doing so will cause changes in landscape structure and landscape diversity that are likely to have profound impacts on arthropods that are both harmful and beneficial from a human standpoint.

Increasing monocultures?

Expansion of biofuel production could reduce landscape and plant diversity, creating monocultures that disrupt predator–prey interactions. Specifically, pressures to produce biomass could result in the production of one or a few crops across entire agricultural landscapes, reducing landscape diversity and biocontrol. For example, Landis *et al.* (2008) showed that increased corn produc-

tion for biofuels from 2005–2006 to 2007 in the US led to a decline in agricultural landscape diversity in their study area, resulting in reductions in predator abundance and a loss of pest control services to neighboring crops. Alternatively, Gardiner *et al.* (2009) suggest that increasing grasslands in the same landscapes (thereby increasing landscape diversity) could counter this effect and restore biocontrol services. Similarly, a broad array of studies in multiple regions suggest that natural enemy abundance, diversity and pest control is greater in landscapes that contain a mix of crop and non-crop habitats compared to landscapes containing only annual crops (Bianchi *et al.*, 2006).

At the scale of a single crop, a wide variety of studies similarly suggest that planting polycultures can reduce pest problems and increase predator populations compared to monocultures, although there are important exceptions (Andow, 1991). Accordingly, studies in mixed prairie have shown that predator-to-prey ratios increase with plant diversity (Haddad *et al.*, 2009). Similar processes may occur in forested landscapes. In a study comparing willow plantations to natural willow stands, Dalin *et al.* (2009) found that while average density of the blue willow leaf beetle, *Phratora vulgatissima* L. did not vary between the habitat types during the 7-year study period, the plantations showed greater temporal variation, resulting in outbreaks that were not observed in natural stands. They suggest that generalist predators may reduce the potential for outbreaks in mixed stands, and that larvae may have a more difficult time finding a new host plant to feed on after defoliating an individual tree in a mixed stand.

Implications for insect-vectored plant diseases

Increased cultivation of some biofuel crops is likely to be associated with changes in the patterns of insect-vectored plant diseases. For example, switchgrass stands are reported to be attacked by the corn flea beetle, *C. pulicaria* (Parrish *et al.*, 1999) a vector of the bacterial disease Stewart’s wilt, *Erwinia stewartii* raising the question: will increased production of switchgrass alter the epidemiology of this disease? Moreover, several potential biofuel crops including switchgrass and miscanthus have been shown to be hosts for the Barley Yellow Dwarf Viruses (BYDVs) (Garrett *et al.*, 2004; Huggett *et al.*, 1999), a group of plant viruses vectored by a number of grass-feeding aphids (Irwin & Thresh, 1990). As perennial grasses, switchgrass and miscanthus may serve as persistent reservoirs of virus, intensifying BYDV pressure on annual small grains (A. Schrottenboer & C. Malmstrom, personal communication). Insect vectors and viruses

harbored by biofuel crops may have important consequences for natural communities as well. In California, BYDV is now believed to have facilitated the invasion and domination of perennial grasslands by exotic annual grasses (Malmstrom *et al.*, 2005). Healthy perennial grasses are rarely invaded by healthy annual grasses; however, the presence of BYDV and aphid vectors reverses the competitive relationship, allowing invasion and dominance by annuals (Borer *et al.*, 2007).

New landscape elements could influence beneficial insects

The increase of any biofuel crop in the landscape will almost undoubtedly change established patterns of arthropod overwintering, movement, and their interaction with host plants and each other. While North American studies do not yet exist, it is easy to imagine that the addition of perennial grasses as biofuel crops will provide overwintering sites for many arthropods due to their perennial nature and well-developed litter layer. These characteristics will likely alter arthropod decomposer communities in the soil as well as influence their natural enemies at higher trophic levels. Repeated harvest of perennial crops without tillage may also alter soil structure, creating other impacts on soil arthropods. Inclusion of woody biomass crops in formerly annual crop landscapes will also change predator communities in agricultural landscapes. For example, Maredia *et al.* (1992b) showed that five species of coccinellid beetles immediately adopted poplar plantations when they were added to a research station as a short-rotation biomass crop in a long-term experiment. Within 1 year, poplar treatments harbored the highest abundance of the exotic seven-spotted lady beetle, *Coccinella septempunctata* L. (Maredia *et al.*, 1992a) a common predator in annual crop habitats. Colunga-Garcia and Gage (1998) also showed that poplar habitats were readily utilized by the multicolored lady beetle, *Harmonia axyridis* (Pallas) which they implicated in the decline of several species of native coccinellids. It seems clear from this single example that the inclusion of new biofuel crop types in agricultural landscapes will inevitably alter beneficial arthropod communities in unexpected ways.

Other impacts of biofuels

Because arthropods are consumed by higher trophic levels we can also expect significant shifts in the dynamics of their consumers as well. Birds have already been studied in biofuel crops to some degree; they respond to both changes in habitat physical structure as well as to

changes in food sources provided by arthropods (Sage *et al.*, 2006). A recent meta-analysis comparing vertebrate (bird and mammal) abundance and diversity in biofuel crops versus reference habitats shows consistent declines when seminatural habitats are converted to biofuel crops (Fletcher *et al.*, 2010). Alternatively, the conversion of current or former croplands to biofuel grasslands (switchgrass or mixed prairie) has the potential to greatly increase wildlife habitat in managed landscapes (Fargione *et al.*, 2009; Fletcher *et al.*, 2010). Finally, the interaction of arthropods and humans will undoubtedly be altered by biofuel production. One could imagine landscapes where biofuel crops increase landscape diversity to favor pollinators and butterflies. Alternatively, if biofuel crops reduce landscape diversity they may reduce these vital and aesthetically desirable amenities. Some of these impacts may be so large that documenting them could help shape US policy toward biofuels. For example, Landis *et al.* (2008) have suggested that the design of future biorefineries is likely to be a key decision point structuring future landscapes. If biorefineries are optimized for a single feedstock it is almost inevitable for that crop to increase dramatically within the supply zone of such a facility. They suggest that biorefineries optimized to process multiple feedstocks have the opportunity to help foster more diverse landscapes and resulting ecosystem services and amenities.

Summary and conclusions

Our review suggests that expansion of biofuel cropping systems in North America is likely to have extensive and in many cases complex impacts on arthropod communities in North American landscapes. Some of these impacts will be beneficial, others harmful, and many will take years to be fully realized. With expanded biofuel crop production, existing arthropod pests of biofuel crops will become more important and new pests will emerge. This will require applied entomologists to develop novel integrated pest management (IPM) systems for biofuel crop pests. Management of biofuel crops, including crop selection, agronomic practices, and harvest regimes will all influence arthropod communities. In turn, arthropods will impact the productivity and species composition of biofuel cropping systems. Some of these processes have the potential to produce landscape-level changes in arthropod community dynamics and insect-vector plant diseases. In some cases, biofuel crops may harbor plant diseases or insect vectors, potentially increasing damage to other crops and even natural plant communities. Because of the potential for long-range dispersal of insect vectors, such

impacts could have far-reaching effects and should be used to inform selection of regionally appropriate biofuel crops.

Beneficial arthropods will also be influenced by biofuel crop habitats, altering the distribution of ecosystem services they provide to the surrounding landscape. Insect natural enemies may be favored or disfavored by biofuel crop choice. In landscapes currently dominated by annual crops, the inclusion of new perennial biofuel crops has the potential to increase natural enemy abundance and diversity. Similarly, pollinators may be favored by the addition of biofuel crops that provide food and overwintering resources. In both cases careful selection and addition of biofuel crops into agricultural landscapes could increase the services these taxa provide. Arthropods of conservation concern may be particularly vulnerable to habitat alteration and thus should be carefully considered in selection of biofuel crops and in harvest methods.

Finally, changes in arthropod abundance and their spatial or temporal distribution in the landscape will have impacts on consumers of insects at higher trophic levels, potentially influencing their population and community dynamics and producing feedbacks to arthropod communities. One might imagine a situation where introduction of a biofuel crop increases insect abundance, which in turn alters bird foraging and nesting success. This may in turn increase avian predation of insects in the biofuel crop or nearby habitats with effects that ramify through a variety of food webs. Given that biofuel crops are still relatively uncommon in North America, as they increase, we can anticipate 'predictably unpredictable' shifts in arthropod communities and the ecosystem services and functions they support. We suggest that research on arthropod dynamics within biofuel crops, their spillover into adjacent habitats, and implications for the sustainability of working landscapes are critical topics for both basic and applied investigations.

The research opportunities posed by novel biofuel production systems are nearly endless and many could be exceedingly important, perhaps to the point that the results of this research could alter the deployment of biofuel crop technologies across the landscape. Given that biofuel production systems are still being developed in North America, entomologists have a unique opportunity to consider how biofuel production may impact arthropods, and may be able to initiate studies to document these effects. Research is particularly needed to address the potential impact of biofuel cropping on insects of conservation concern, the provision of key ecosystem services such as pollination and pest suppression, and the landscape level impacts of biofuel cropping on arthropod

communities and the organisms and ecosystem functions they support.

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