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Plant diversity increases herbivore movement and vulnerability to predation

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Abstract

Understanding how changes in plant diversity affect agroecosystem functioning remains a key challenge. We examined how intercropping alfalfa, *Medicago sativa*, with orchardgrass, *Dactylis glomerata*, affects the potato leafhopper, *Empoasca fabae*, its host plant (alfalfa), and the efficiency of a leafhopper predator, *Nabis americoferus*. In a field experiment, intercropping reduced the reproductive efficiency of the leafhopper. *Nabis* was more effective at reducing leafhopper abundance, and protecting alfalfa from hopperburn, in the polyculture than in the monoculture of alfalfa. In a series of laboratory experiments, we investigated mechanisms by which intercropping could enhance the efficiency of *Nabis*. Intercropping resulted in changes in vegetation structure and the spatial distribution of leafhoppers, but there was little evidence that these factors influenced the efficiency of *Nabis*. Instead, orchardgrass, a nonhost for leafhoppers, increased leafhopper movement, and *Nabis* captured leafhoppers more efficiently when the herbivores were more mobile. These results indicate that intercropping with nonhost plants promotes leafhopper movement and vulnerability to predation, and reveal a novel mechanism by which plant diversity can reduce herbivory.

Zusammenfassung

Zu verstehen, wie Änderungen der Pflanzendiversität die Funktion von Agrarökosystemen beeinflusst, bleibt eine wichtige Aufgabe. Wir untersuchten wie die Mischkultur von Alfalfa (*Medicago sativa*) und Wiesen-Knäuelgras (*Dactylis glomerata*) die Amerikanische Kartoffelzikade (*Empoasca fabae*), ihre Wirtspflanze und die Effizienz eines Zikadenräubers (*Nabis americoferus*) beeinflusst. In einem Freilandexperiment, reduzierte die Mischkultur die Fortpflanzungseffizienz der Kartoffelzikade. In der Mischkultur reduzierte *Nabis* die Zikadenabundanz und den Zikadenbrand auf Alfalfa mit größerer Effizienz als in der Reinkultur. In einer Reihe von Laborexperimenten untersuchten wir die Mechanismen, durch die die Mischkultur die Effizienz von *Nabis* steigern könnte. Mischkultur resultierte in Veränderungen der Vegetationsstruktur und der räumlichen Verteilung der Zikade, aber es gab kaum Hinweise, dass diese Faktoren die Effizienz von *Nabis* beeinflussten. Vielmehr verstärkte das Knäuelgras, das von den Zikaden nicht genutzt werden kann, die Bewegungen der Zikaden, und *Nabis* fing Zikaden mit höherer Effizienz, wenn diese mobiler waren. Diese Ergebnisse zeigen, dass Mischkultur mit Nicht-Wirten die Bewegungsaktivität der Zikaden erhöht und damit ihre Anfälligkeit für Prädation, und sie enthüllen einen neue Mechanismus, durch den die Pflanzendiversität den Herbivorendruck verringern kann.

Keywords: Biodiversity; Agriculture; Intercropping; Biological control; Resource concentration; Enemies hypothesis; Leafhopper

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Introduction

Understanding how changes in plant diversity affect agroecosystem functioning remains a key challenge for sustainable agriculture. Agricultural ecologists have long suspected that pest outbreaks, and the need for pesticides that threaten environmental and human health, may be reduced by increasing plant diversity within agricultural fields (Pimentel 1961). Numerous studies have investigated this possibility, and reviews of these studies have come to a similar conclusion – most of the time plant diversity reduces herbivore abundance and damage to crops (Andow 1991; Russell 1989; Letourneau et al. 2011; but see Bommarco & Banks 2003 for an important caveat). In the most recent of these reviews, the authors concluded that while crop diversification is generally effective in reducing herbivory, a mechanistic understanding for why these schemes work is often missing. This limits our ability to engineer, in a directed way, diversification schemes that will effectively control particular pest species (Letourneau et al. 2011).

Explanations for how plant diversity reduces herbivore abundance and damage include the 'resource concentration' and 'enemies' hypotheses. The resource concentration hypothesis states that insect herbivores are more likely to find and remain on their host plants in monocultures, where their host plants are concentrated, than in polycultures, where their host plants are dispersed among nonhost plant species (Root 1973). Under the resource concentration hypothesis, plant diversity reduces herbivory by reducing the relative abundance of herbivores' host plants. This, in turn, reduces herbivores' encounter rate with, or residence time on, host plants (Fig. 1, upper pathway). The enemies hypothesis states that natural enemies are less abundant and/or effective in monocultures than in polycultures, because polycultures include plant species that provide enemies with alternative prey, shelter, or a favorable microclimate (Root 1973). Under the enemies hypothesis, plant diversity reduces herbivory by providing resources to enemies that control herbivore populations (Fig. 1, lower pathway). Diversification schemes that promote both the resource concentration and enemies hypotheses will be more effective than schemes that promote only one of them. However, these mechanisms are not always compatible. For example, increasing plant diversity may reduce herbivore abundance via a resource concentration effect, but may simultaneously reduce the foraging efficiency of natural enemies (Smith 1976; Sheehan 1986).

The potato leafhopper, *Empoasca fabae*, provides an excellent opportunity to explore the mechanisms by which plant diversity reduces herbivory. Numerous studies have shown that increasing plant diversity can reduce the abundance of the potato leafhopper on focal crops (Oloumi-Sadeghi, Zavaleta, Lamp, Armbrust, & Kapusta 1987; Roltsch & Gage 1990; Lamp 1991; Andow 1992; Roda, Landis, & Miller 1997). Grass intercrops may be particularly effective, because potato leafhoppers cannot develop or reproduce on them (Lamp, Nielson, & Danielson 1994). The specific mechanism(s) by which grass intercrops reduce leafhopper abundance are not fully understood, but it seems likely that a resource concentration effect contributes. Roda et al. (1997) showed that leafhoppers do not discriminate between their host plants and grasses until after contact, and that intercropping alfalfa with grasses causes them to emigrate from plant patches. Thus, grass intercrops could reduce leafhopper foraging efficiency and could potentially "push" leafhoppers out of intercropped fields if they repeatedly encounter grass intercrops. Pushing pests with nonhost intercrops is often more effective if they eventually encounter and remain on an attractive trap crop, as occurs in push-pull systems (Cook, Khan, & Pickett 2007). Pushing pests with nonhost plants could also be more effective if it increased their encounters with natural enemies, although this possibility has not been rigorously evaluated.

In a previous study, we found that weedy grasses reduce leafhopper abundance and damage to alfalfa (Straub et al. 2013). The resource concentration effect likely contributed to this finding (Fig. 1), but there was also evidence for the enemies hypothesis. Specifically, the predator:prey ratio was higher in the weedy plots, and one predator, *Nabis americoferus*, was more effective in a microcosm experiment when grasses were present. Thus, this system appears to be one in which the resource concentration and enemies hypotheses are complementary, but the exact mechanism by which the enemies hypothesis operates remains unknown. In the earlier study, we hypothesized that the grasses reduced leafhoppers' host plant encounter rate, and that leafhoppers compensated for this by increasing their host searching behavior. As a consequence, leafhoppers were more likely to encounter and be killed by predators. We call this the 'movement-risk hypothesis' (Fig. 1, dashed arrows).

The purpose of the present study was to attempt to replicate the earlier finding that *Nabis* is more effective in polyculture, and to more rigorously examine the movement-risk hypothesis. In addition, the previous study (Straub et al. 2013) had two limitations: it was conducted in a laboratory setting, and fava bean was used as a surrogate for the focal crop, alfalfa. To address these issues, the present study was conducted in the field with alfalfa. Following the field experiment, we conducted a series of laboratory experiments to test assumptions of the movement-risk hypothesis and to evaluate an alternative hypothesis.

Materials and methods

Field experiment

An enclosure experiment was conducted in an alfalfa field intercropped with orchardgrass at Northern Star Farm in Trappe, PA, USA. The alfalfa (Harvestar^{TM} 504VP) and orchardgrass ('Potomac') were seeded together at 20 and 4.5 kg/ha, respectively. The field was planted three years prior to the experiment, in late summer 2007, and the experiment took place from 30 June to 12 July 2010. Enclosures were