

Addition of a new resource in agroecosystems: Do cover crops alter the trophic positions of generalist predators?

Pierre-François Duyck^{a,*}, Anaïs Lavigne^a, Fabrice Vinatier^a, Raphaël Achard^a, Justin N. Okolle^b, Philippe Tixier^a

^aCIRAD, UPR 26 « Systèmes Bananes et Ananas », Pôle de Recherche Agro-environnementale de la Martinique, BP. 214, 97285 Le Lamentin Cedex 2, Martinique

^bLaboratory of Nematology/Entomology, African Research Centre on Bananas and Plantains (CARBAP), BP 832, Doula, Cameroon

Received 2 July 2010; accepted 29 November 2010

Abstract

Generalist predators can play an important role in agroecosystems by controlling herbivores via top-down effects. As cover crops are increasingly used in agroecosystems, the effects of this resource on generalist predator diet need to be evaluated. We studied the effect of adding a cover crop, *Brachiaria decumbens*, on trophic niches of generalist predators in a banana agroecosystem by analysing stable isotope variation in C and N for *Cosmopolites sordidus*, a major banana pest, and its potential predators (spiders, ants, centipedes, and earwigs). While addition of the new resource did not change the trophic niche of the banana pest *C. sordidus*, the trophic position of the generalist predators was changed as indicated by $\delta^{13}\text{C}$ signature. Cover crop provided resources that are likely to support a community of insect herbivores, which are alternative preys for generalist predators. The failure of the cover crop to increase $\delta^{15}\text{N}$ signature is inconsistent with the hypothesis that the cover crop would increase intraguild predation. By providing alternative preys, the addition of a new resource in agroecosystems has the potential to increase populations of generalist predators and therefore pest control.

Zusammenfassung

Generalistische Prädatoren können in Agrarökosystemen eine wichtige Rolle spielen, indem sie eine top-down-Kontrolle auf Pflanzenfresser ausüben. Da zunehmend Gründungspflanzen in Agrarökosystemen angebaut werden, müssen die Effekte dieser Ressource auf die Nahrung der generalistischen Prädatoren bewertet werden.

Wir untersuchten den Effekt der Gründungspflanze *Brachiaria decumbens* auf die trophischen Nischen von generalistischen Prädatoren in einem Bananen-Agroökosystem. Hierzu analysierten wir die Variation der stabilen Isotope von Kohlen- und Stickstoff bei *Cosmopolites sordidus*, einem bedeutenden Bananenschädling, und seinen potentiellen Prädatoren (Spinnen, Ameisen, Hundertfüßer und Ohrwürmer).

Während die angebaute Gründung die trophische Position von *C. sordidus* nicht veränderte, änderten sich die $\delta^{13}\text{C}$ -Signaturen bei den generalistischen Prädatoren. Die Gründungspflanze bot Ressourcen, von denen vermutlich eine Gemeinschaft von herbivoren Insekten leben kann, die als alternative Beute für generalistische Prädatoren können. Deren $\delta^{15}\text{N}$ -Signatur

*Corresponding author. Tel.: +596 596 423 047; fax: +596 596 423 001.
E-mail address: duyck@cirad.fr (P.-F. Duyck).

wurde durch den Anbau der Gründüngung nicht erhöht. Dies widerspricht der Hypothese, dass der Gründüngungsanbau zu erhöhter 'intraguild predation' führen sollte.

Indem alternative Beuteorganismen unterstützt werden, hat die Hinzufügung einer neuen Ressource in Agroökosystemen das Potential, die Populationen von generalistischen Prädatoren zu erhöhen und damit die Schädlingskontrolle zu stärken.

© 2010 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Cover crops; *Cosmopolites sordidus*; Food web; *Musa* spp.; Pest control; Stable isotopes

Introduction

Generalist predators can play an important role in agroecosystems by controlling herbivores via top-down effects (Cardinale, Harvey, Gross, & Ives 2003; Bell, King, Bohan, & Symondson 2010). The population densities of such generalist predators can be increased by modifying the environment of agroecosystems to increase the numbers of alternative, non-pest prey (Wise, Moldenhauer, & Halaj 2006). Agroecosystems can be modified by management practices such as rotations, mixed cropping, and cover crops, resulting in an increase in biodiversity (Moonen & Bàrberi 2008; Dornelas, Moonen, Magurran, & Barberi 2009). For example, organic farms have significantly greater biodiversity than conventional farms (Schmidt, Roschewitz, Thies, & Tschamtko 2005; Macfadyen et al. 2009). Habitat diversity has also been shown to be positively related with biocontrol by generalist predators in agroecosystems (Landis, Gardiner, van der Werf, & Swinton 2008).

Cover crops are increasingly used in agroecosystems, and although some studies have evaluated their effect on generalist predators (Costello & Daane 2003; Hooks & Johnson 2004), no study has evaluated the effect of cover crop on the trophic niches of generalist predators. Adding a cover crop increases the quantity of primary resource for herbivorous insects. One risk of adding cover plants in agroecosystems is that this new resource may be consumed by the same herbivorous species and may thus increase pest populations. However, when the entire community, including predators and other species that suppress herbivorous populations, benefits from this new resource and their numbers are increased, peaks in pest numbers may be better controlled by top-down effects (Chen & Wise 1999). Another risk is that changes in trophic structure could allow some generalist predators to participate in more intraguild predation and thus reduce predation on pests. Indeed, intraguild predation is common among generalist predators (Arim & Marquet 2004; Rickers, Langel, & Scheu 2006), and an increase in productivity by addition of a cover crop may increase intraguild predation (Post & Takimoto 2007; Rosenheim 2007).

Because of their relatively simple food webs, agroecosystems, including banana plantations, can be good biological models for studying how the addition of a new basal food source affects top-down suppression of herbivores. Until now, most of the dessert bananas (*Musa* spp., AAA group, cv. Cavendish Grande Naine) grown for export have been cultivated intensively in monocultures on bare soil. To limit

erosion and control weeds while reducing herbicide applications, however, plantation managers are increasingly planting cover crops between banana rows. One of the candidate species for cover crops in bananas is the Signal grass *Brachiaria decumbens* (Poaceae).

The banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae) (Germar. 1825), is the most serious insect pest of banana and plantain in most production areas (Gold, Pena, & Karamura 2001) including the West Indies. *C. sordidus* is a narrowly oligophagous pest, attacking wild and cultivated clones in the related genera *Musa* (banana, plantain, and abaca) and *Ensete* (Gold et al. 2001). Adult weevils usually disperse by walking on the soil during the night (Vinatier, Tixier, Le Page, Duyck, & Lescouret 2009; Vinatier et al. 2010). After eggs have been laid on the corm of banana, larvae hatch and bore galleries inside the corm for feeding (Koppenhofer 1993b). The litter is inhabited by a number of generalist predators such as ants, earwigs, and ground beetles (Koppenhofer, Reddy, Madel, & Lubega 1992; Koppenhofer 1993a; Abera-Kalibata, Hasyim, Gold, & Van Driesche 2006). These species are potential regulators of banana weevils; for instance, Abera-Kalibata, Gold, and Van Driesche (2008) showed that ants are important predators of banana weevil eggs. Insect parasitoids of banana weevils are scarce, and classical biological control of banana weevils has so far been unsuccessful (Gold et al. 2001).

The current study uses stable isotopes of C and N to understand how a cover crop changes the food web in a banana agroecosystem. As demonstrated by Ponsard and Arditi (2000), variations in the natural abundance of stable isotopes of C and N can reveal the trophic structure of generalist predators. Stable isotopes are particularly useful when polyphagous feeders predominate, as they do in litter and soil (Oelbermann & Scheu 2002) and in our banana system. Animal tissues of consumers are weakly enriched in ^{13}C compared to their food source. Isotopic trophic enrichment Δ_{C} is the difference between $\delta^{13}\text{C}$ of an organism and $\delta^{13}\text{C}$ of its food source (see "Materials and methods" section for details about δ notation): mean $\Delta_{\text{C}} = 0.4 \pm 1.4\text{‰}$ (Gearing, Gearing, Rudnick, Requejo, & Hutchins 1984). Therefore, ^{13}C values provide information regarding the identity of the primary producer, especially if the primary producers in the system differ in ^{13}C value. Our biological model consists of a C4 cover crop (*B. decumbens*) and a C3 banana plant, which differ substantially in ^{13}C values. Relative to reference values, the $\delta^{13}\text{C}$ deviation of banana is about -26.5‰ (Yakir & Israeli 1995) and that of C4 plants ranges from

–17.0‰ to –9.0‰ (Staddon 2004). The $\delta^{13}\text{C}$ values of the herbivores and predators will therefore indicate whether the primary producer at the base of the trophic web was banana or *B. decumbens*.

While $\delta^{13}\text{C}$ is useful for determining the identity of the primary producer at the base of the food web, $\delta^{15}\text{N}$ is useful for indicating the trophic level of organisms in a food web. Isotopic trophic enrichment Δ_N is the difference between $\delta^{15}\text{N}$ of an organism and $\delta^{15}\text{N}$ of its food source: mean $\Delta_N = 3.3 \pm 1.5\%$ (Minagawa & Wada 1984). Because $\delta^{15}\text{N}$ is substantially enriched with each transfer, organisms that feed near the base of the food web will be less enriched than those that feed near the top of the food web. Thus, an organism's isotopic signature in nitrogen indicates its trophic level (Vander Zanden & Rasmussen 1999; Ponsard & Arditì 2000).

The objective of the current paper is to determine whether the addition of a cover crop in a banana agroecosystem changes the trophic niche of generalist predators. By analyzing stable isotopes of C and N, we attempted to answer the following specific questions: (i) Does the trophic position (as indicated by ^{13}C and ^{15}N values) of generalist predators change with addition of a cover crop? (ii) Does the addition of the cover crop increase the ^{15}N signature of generalist predators, suggesting an increase in intraguild predation?

Materials and methods

Study site and sampling

Our study site was located in Martinique (French West Indies, 14°N, 61°W). We compared two situations: banana (*Musa* sp.) crops grown on bare soil (obtained using the herbicide glyphosate) and banana crops intercropped with *B. decumbens* Stapf. (Signal grass, Poaceae). This perennial herbaceous grass has several advantages as a cover crop: it competes efficiently with weeds, it can be controlled mechanically, and it does not require reseeding. The banana plants were planted in February 2006 and produced about two crops a year. In banana fields, plant stages become unsynchronized over time (Tixier, Malezieux, & Dorel 2004). By 2008, therefore, our plot produced biomass regularly. The cover crop (*B. decumbens*), which had been seeded 3 months before the bananas were planted, was cut every 2 months; its biomass varied between 0.15 kg m⁻² and 0.40 kg m⁻². Although herbicide was applied to the plots with bare soil, some herbaceous weed species (*Paspalum conjugatum*, *Digitaria horizontalis*, *Axonopus compressus*, *Kyllinga brevifolia*) persisted but with very low biomass. No woody weeds were present.

We used a blocked design containing four plots (230 m² per plot) of banana trees. These plots were randomly located in the banana plantation. Each of the four blocks was separated in two plots of similar size corresponding to each treatment (bare soil or cover crop). None of these plots had

been treated with insecticide or nematicide for at least 4 years. In June 2008, litter was collected from two 625-cm² areas in each plot. This litter was then spread on a plastic sheet, and ants, earwigs, centipedes, ground beetles, and spiders were collected using forceps or aspirators. Furthermore, banana weevils and predators were collected from two pitfall traps per plot that were left in each plot for 2 days in June 2008. The last mowing was done 2 months before sampling. We choose this particular period for sampling, because the cover crop reached a maximal biomass and before the next mowing as this probably causes a diminution of arthropod populations. Because the study takes place in a wet tropical environment, there were not contrasting seasons, with relatively constant rainfall and temperature over the years. We also collected *Musa* sp. and *B. decumbens* leaves to assess the isotopic baseline of the food web. Generalist predators were identified with entomological keys or were sent to specialists for identification.

Feeding behaviour of potential predators of the banana weevil

The trap-jaw ant (*Odontomachus* spp. Fam. Poneridae) fed on and reduced the number of banana weevils in Uganda (Abera-Kalibata et al. 2008), and adults of *O. bauri* were observed attacking banana weevil larvae in crop residues in Martinique (Duyck, P.F. pers. observation). In Cameroon, *Odontomachus* spp. is commonly found associated with banana/plantain stumps and adults have been seen eating immature stages of the weevils in the field (J. Okolle, pers. comm.). In Cuba, Perfecto and Casteñeras (1998) showed that ant predation reduced banana weevil numbers by 60–70%. *Odontomachus* spp. were strongly attracted to banana weevil stages deployed as baits in the field and were able to remove banana weevil eggs from either artificially or naturally infested corm pieces (Abera-Kalibata, Gold, Van Driesche, & Ragama 2007). *Odontomachus bauri* is known to use its large mandibles to crush and stun chemically defended prey before they can emit noxious or toxic secretions (Patek, Baio, Fisher, & Suarez 2006). Consequently, this species can be an efficient predator of many litter-dwelling insect taxa (Ehmer & Hölldobler 1995; Raimundo, Freitas, & Oliveira 2009). *O. bauri* is therefore able to change its prey consumption according to which prey species are abundant.

Earwigs of the genus *Euborellia* have previously been shown to be abundant and efficient predators of banana weevils in the field in Kenya, where they reduced *C. cosmopolites* numbers in field cages by 28% (Koppenhofer 1993a). Other earwig species of the suborder Forficulina have also been shown to be predators of the banana weevil in Indonesia (Abera-Kalibata et al. 2006). Lycosid spiders are typical generalist predators that feed on many prey species including many insect herbivores that inhabit the litter (Oelbermann & Scheu 2002). While predation by Lycosidae on the banana weevil has not been reported in the litera-

ture, lycosid predation on adults of other Coleoptera species has been documented. For example, Snyder and Wise (1999) demonstrated that wolf spiders can significantly reduce numbers of the cucumber beetle, *Diabrotica undecimpunctata*.

Carabid beetles are an important group of generalist predator commonly found in agroecosystems. These ground beetles have been reported to consume a wide range of agricultural pest species including invertebrates and weed seeds (Lövei & Sunderland 1996; O'Rourke, Liebman, & Rice 2008).

Centipedes have been reported to be predators of large arthropods including beetles (Kupfer, Langel, Scheu, Himstedt, & Maraun 2006). To our knowledge, however, no studies have described centipede predation of the banana weevil.

Sample preparation and stable isotope measurements

After taxonomic description, all individuals were lyophilized for 48 h. Banana, *B. decumbens*, and animal bodies were ground into a fine powder. One milligram of each individual of the collected taxa was placed in a tin capsule for analysis. When the biomass of one animal was sufficient to constitute one sample (≥ 1 mg), animals were analysed individually. If the biomass of individual animals was too small (< 1 mg), the powder from multiple individuals of the same species was pooled to obtain the minimal sample size of 1 mg. Isotope ratios were determined by an isotope ratio mass spectrometer SerCon 20/20 coupled to an ANCA-GSL elemental analyser at the Scottish Crop Research Institute laboratory for stable isotope analysis (Dundee, Scotland). All stable-isotope values are reported in the δ notation: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Standards were PeeDee Belemnite (Peterson & Fry 1987) and atmospheric air (Mariotti 1984) for C and N, respectively.

To evaluate the reliability of isotopic measurements, five replicates of the same sample were analysed. This was done for one sample of *C. sordidus*, one sample of banana, and one sample of *B. decumbens*.

Statistical analysis

Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analysed using a linear mixed effect model for blocked design (Pinheiro & Bates 2004) where species, treatment (bare soil or cover crop) and interactions between these two factors are fitted as fixed effects and where block is fitted as a random effect. We performed this analysis in R (R Development Core Team 2004) using *lme* function in the *nlme* package (Pinheiro & Bates 2004). While the number of collected individuals may differ depending on species, treatments or block, *lme* function is robust to unbalanced designs (Pinheiro & Bates 2004). Before statistical analysis, the data were transformed to achieve nor-

malinity using the Boxcox transformation when necessary (Box & Cox 1964).

To test the hypothesis of a directional change in taxa isotopic abundance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which would indicate a change in trophic position, we also used circular statistics (Schmidt, Olden, Solomon, & Vander Zanden 2007). Length and direction of vectors of change (from bare soil to cover crop) in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ trophic space were calculated for each taxon using mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as coordinates. Mean and standard deviation of absolute and relative angles were calculated assuming von Mises distributions. Watson test was used to confirm that these distributions were appropriate while Rayleigh's test for circular uniformity was used to test the significance of mean vector direction of the community (Schmidt et al. 2007). Circular statistics were performed in R version 2.4.1 (R Development Core Team 2004) using *CircStats*, *geometry*, and *chplot* packages.

Results

We analysed 12 samples of banana weevils and 130 samples of generalist predators classified into five general taxa: ants, earwigs, centipedes, ground beetles, and spiders (Table 1). Specimens of ants, earwigs, and ground beetles were identified to species but spiders and centipedes were identified only to family because the species collected for these two taxa did not correspond to species already described.

The $\delta^{13}\text{C}$ value was $-12.4 \pm 0.1\text{‰}$ for *B. decumbens* and $-25.1 \pm 0.7\text{‰}$ for banana (Fig. 1B), and the values for all the other taxa were between these two $\delta^{13}\text{C}$ values, except for ground beetles in the cover crop treatment. Taxon and treatment greatly affected the $\delta^{13}\text{C}$ values of the entire community (Table 2). Interactions between taxa and treatment were also significant, indicating different effects of treatment among the taxa. In plots with bare soil, values of $\delta^{13}\text{C}$ ranged from -12.6‰ to -24.7‰ and were in the following order: ground beetles \gg ants $>$ spiders $>$ centipedes $>$ earwigs $>$ *C. sordidus*. In plots with the cover crop, values of $\delta^{13}\text{C}$ ranged from -11.7‰ to -24.5‰ and were in the following order: ground beetles \gg spiders $>$ ants $>$ centipedes $>$ earwigs $>$ *C. sordidus*.

Values of $\delta^{13}\text{C}$ for *C. sordidus* were $-24.7 \pm 0.2\text{‰}$ with bare soil and $-24.5 \pm 0.4\text{‰}$ with *B. decumbens* (Fig. 1), and the difference was not statistically significant ($P > 0.05$). The $\delta^{13}\text{C}$ values were significantly higher (i.e., less negative) with the cover crop than with bare soil for all taxa of generalist predator except for ground beetles ($P < 0.05$, Fig. 1). The $\delta^{13}\text{C}$ value of ground beetles was similar to that of *B. decumbens*.

The $\delta^{15}\text{N}$ values of *B. decumbens* and banana were not significantly different ($0.7 \pm 0.1\text{‰}$ and $1.7 \pm 0.8\text{‰}$, respectively, $P > 0.05$, Fig. 1), and we could therefore use a $\delta^{15}\text{N}$ value of 1.2 as an approximate baseline.

Table 1. Taxa collected from the field and number of samples (*N*) analysed by stable isotopes.

Taxa	Trophic group	Class	Order	Family	Species	<i>N</i>
Banana weevil	Herbivore (pest)	Hexapoda	Coleoptera	Curculionidae	<i>Cosmopolites sordidus</i>	12
Ants	Generalist predator	Hexapoda	Hymenoptera	Ponerinae	<i>Ondotomachus bauri</i>	59
Centipedes	Generalist predator	Chilopoda	Scolopendromorpha	Cryptopidae		6
Earwigs	Generalist predator	Hexapoda	Dermaptera	Carcinophoridae	<i>Euborellia caraibea</i>	12
Ground beetles	Generalist predator	Hexapoda	Coleoptera	Carabidae	<i>Galerita tristis</i>	34
Spiders	Generalist predator	Arachnida	Araneae	Lycosidae		19

Table 2. Effect of taxon, treatment (with or without cover crop), and interactions on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of banana weevil and its generalist predators in a linear mixed effect model.

	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
	d.f.	<i>F</i> value	<i>P</i> value	d.f.	<i>F</i> value	<i>P</i> value
Taxon	5, 127	62.55	<0.0001	5, 127	73.28	<0.0001
Treatment	1, 127	48.06	<0.0001	1, 127	3.35	0.070
Taxon \times treatment	5, 127	2.92	0.015	5, 127	1.308	0.264

$\delta^{15}\text{N}$ values for all taxa collected were greater than those for banana and *B. decumbens*. In plots with bare soil, $\delta^{15}\text{N}$ values ranged from 4.0‰ to 10.0‰ and were in the following order: *C. sordidus* < ground bee-

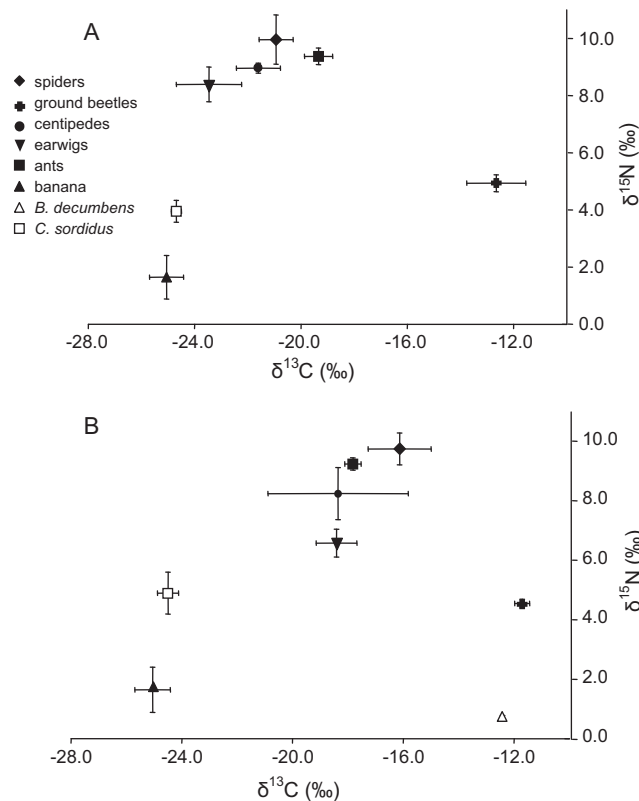


Fig. 1. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of banana, *Brachiaria decumbens* (the cover crop), *Cosmopolites sordidus* (the banana weevil), and generalist predators in the litter of a banana agroecosystem collected in plots (A) without a cover crop or (B) with a cover crop. Values are means \pm SE.

tlas << earwigs < centipedes < ants < spiders. In plots with the cover crop, $\delta^{15}\text{N}$ values ranged from 4.6‰ to 9.7‰ and were in the following order: ground beetles < *C. sordidus* < earwigs < centipedes < ants < spiders. $\delta^{15}\text{N}$ values were significantly affected by taxa but were not affected by treatment or the interaction between taxa and treatment (Table 2). A marginally significant difference ($P = 0.052$) in $\delta^{15}\text{N}$ values was observed for earwigs in plots with bare soil ($8.4 \pm 0.5\%$) vs. in plots with the cover crop ($6.6 \pm 0.6\%$).

The mean $\delta^{15}\text{N}$ value was 2.8‰ greater for *C. sordidus* than for banana. In plots with bare soil, the mean $\delta^{15}\text{N}$ values for earwigs, centipedes, ants, and spiders were, respectively, 4.0, 4.2, 5.0, and 5.5‰ higher than for *C. sordidus*. In plots with the cover crop, the mean $\delta^{15}\text{N}$ values of earwigs, centipedes, ants, and spiders were, respectively, 2.2, 3.8, 4.8, and 5.3‰ higher than for *C. sordidus*. The $\delta^{15}\text{N}$ values of ground beetles were very similar to those of *C. sordidus* (on average, the values from the beetles were only 0.3‰ above those from *C. sordidus*) in both kinds of plots.

Circular statistics showed that mean directions of vectors (from bare soil to cover crop) in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ trophic space for ants, spiders, centipedes, and earwigs ranged from 95 to 110 degrees, indicating shift from banana to cover crop signature (Fig. 2). For the entire community, the mean direction was 99.9 degrees and the mean length was 3.76‰ (Rayleigh test: $P = 0.007$).

Discussion

Effect of cover crop on trophic position of banana weevil

The use of a C4 cover crop (*B. decumbens*) in this study facilitated the determination of how that cover crop affected

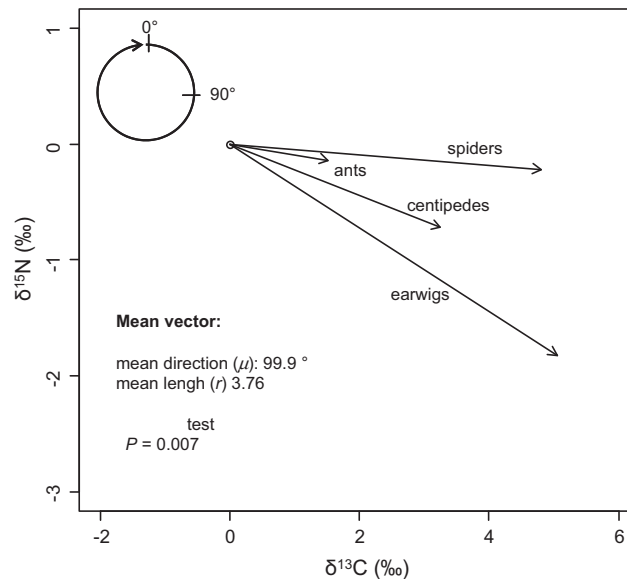


Fig. 2. Arrow diagrams for angle of change in trophic position caused by the addition of a cover crop in a banana agroecosystem. Each arrow represents the direction of change in trophic niche space for each taxon (ants, spiders, centipedes, and earwigs). The length of the arrow represents the magnitude of change.

the trophic position of the banana pest *C. sordidus*. Because C3 plants (like banana) and C4 plants have very different $\delta^{13}\text{C}$ values, and because $\delta^{13}\text{C}$ values are not greatly changed with trophic transfer, the $\delta^{13}\text{C}$ of a herbivore (and of consumers of that herbivore) indicates which plant(s) it consumed. In the current study, the $\delta^{13}\text{C}$ value was -25.1‰ for banana and -12.4‰ for the C4 cover crop. Similar values have been reported in previous studies. For example, Yakir and Israeli (1995) reported a $\delta^{13}\text{C}$ value of -26.5‰ for banana, and Staddon (2004) reported $\delta^{13}\text{C}$ values ranging from -17‰ to -9‰ for other C4 plants.

In the current study, the $\delta^{13}\text{C}$ value for *C. sordidus* was about -24.6‰ whether plots had bare soil or the C4 cover crop. This indicates that *C. sordidus* fed only on banana and that its diet was not influenced by the addition of the cover crop.

The mean $\delta^{15}\text{N}$ value was 2.8‰ higher in *C. sordidus* than in banana. This is in line with the expected enrichment of ^{15}N between an animal and its resource, which is usually considered to be about 3.3‰ (Minagawa & Wada 1984). Different species however, can have different $\delta^{15}\text{N}$ values even if they eat the same food (Ponsard & Arditì 2001).

Effect of cover crop on the trophic position of generalist predators

In plots with bare soil, the $\delta^{13}\text{C}$ signature of all predators ranged between -24.7‰ and -11.7‰ . Given that the $\delta^{13}\text{C}$ signature of banana was around -25‰ and that of earwigs was -22‰ , we infer that earwigs were consuming prey that had banana as the basal resource. The other predators, how-

ever, had substantially higher $\delta^{13}\text{C}$ values, indicating that they were consuming prey that had plants other than or in addition to banana as the basal resource; this was especially true of the ground beetles. We suggest two possible basal resources in addition to banana in the bare plots: weeds and litter. A few weeds were present on the bare soil (see “Materials and methods” section for species), and it is possible that some of the generalist predators consumed weed herbivores. Another potential basal resource that was not measured in this study was soil microorganisms (Wardle et al. 2004). Such bacteria and fungi are consumed by many soil organisms (for example, by bacterivorous and fungivorous mites and collembolans) that may then be consumed by other predators and eventually by the generalist predators measured in this study.

Spiders, ants, centipedes, and earwigs had $\delta^{15}\text{N}$ values between 6.6‰ and 10.0‰ whether or not a cover crop was present. All these species may be predators of phytophagous species consuming banana and *B. decumbens*, including *C. sordidus*. Spiders and ants had the highest $\delta^{15}\text{N}$ values (on bare soil, values were 5.0‰ higher for ants and 5.5‰ higher for spiders than for *C. sordidus*). High values of $\delta^{15}\text{N}$ fractionation have been documented for various predator species (e.g., Scheu & Falca 2000). These high $\delta^{15}\text{N}$ values may be due to high intraguild predation rates. This is consistent with the fact that spiders and ants feed partly on other predators and are mutual predators (Sanders & Platner 2007). Overall, there was no effect of the addition of the cover plant on the $\delta^{15}\text{N}$ values in the studied community except for earwigs. Decrease in $\delta^{15}\text{N}$ for earwigs may be the result of a decrease in intraguild predation by this taxon. Intraguild predation may be reduced because of an increase in alternative prey (Chen & Wise 1999; Rickers et al. 2006). The low $\delta^{15}\text{N}$

values for ground beetles suggest that they were consuming resources close to and even including the primary producers, as discussed later.

Addition of the cover crop caused a shift in the $\delta^{13}\text{C}$ signature of generalist predators, and the increase in $\delta^{13}\text{C}$ values indicates that a substantial part of the resource of these predators came from the *B. decumbens* pathway. In our study, the cover crop, *B. decumbens*, was probably a new resource that supported a more diverse community of insect herbivores, which constituted an alternative resource for the generalist predators. We identified three species of herbivores that were particularly abundant in the cover crop treatment: *Grillus assimilis* (Hexapoda, Orthoptera, Grillidae), *Ligyris ebenus* (Hexapoda, Coleoptera, Scarabaeidae), and *Coreidae* sp. (Hexapoda, Hemiptera, Heteroptera).

Shift in trophic position of generalist predators

As noted earlier, addition of the cover crop *B. decumbens* changed the $\delta^{13}\text{C}$ signature of the generalist predators, indicating that a substantial part of the resource of these predators came from the *B. decumbens* pathway. Three hypotheses could explain the shift in isotopic signature in ^{13}C for generalist predators with the addition of the cover crop: (i) a change in species composition within the generalist predator community, (ii) a change in the relative abundance of different species within the community, and (iii) a change in prey consumed by the generalist predators (without changes in species composition and relative abundances). Because the same species of generalist predators were present in both treatments, we can reject the first hypotheses. Although the second hypothesis cannot be rejected, we suspect that the first two hypotheses may be better supported in more complex systems that contain many more species than are present in banana plantations. Because generalist predators often change their food as different prey become available, the third hypothesis is probably correct. While arthropods have been collected at one particular period, we expect that the observed effect on generalist predator trophic niche would be observed at least at the same moment in the mowing cycle.

Conclusion

The addition of a cover crop could increase the number of prey (herbivores of the cover crop) and therefore increase the number of predators and the top-down control of the pest. Furthermore, the presence of more diverse resources associated with a cover crop could increase the fitness of the predators. Beneficial effects of dietary mixing on the growth and survival of generalist predators have been reported for various species (Scheu & Folger 2004; Rickers et al. 2006). Although a cover crop could reduce pest control by increasing intraguild predation, the addition of the cover crop did

not increase the $\delta^{15}\text{N}$ signature, a finding that is inconsistent with an increase in intraguild predation.

Further field and laboratory research will be needed to determine whether the addition of a cover crop does increase predator numbers and control of *C. sordidus*. Trophic links must also be verified, and abundances of the different species of predators and herbivores quantified. By crossing data of abundances and proportion of different resources consumed by species, it will be possible to estimate the part of the crop consumed directly by the pest and indirectly by the predators of the pest.

Acknowledgments

We thank Dr. Charlie Scrimgeour, Dr. Meier-Augenstein, and Mr. Lee Hunter (SCRI, Dundee, Scotland) for isotope analyses of samples; Eddy Dumbardon (FREDON), Patrick Marechal (MNHN, Paris), and Jacques Delabie (Santa Cruz University, Brazil) for their help in arthropod identification; Gracien Theodoze (CIRAD-PRAM, Martinique, France) for the maintaining of banana crop in the field; and Sergine Ponsard (Univ. Paul Sabatier, Toulouse, France) for comments on an earlier version of this manuscript. We also thank Bruce Jaffee for English revision and four anonymous referees for their useful comments on the manuscript.

References

- Abera-Kalibata, A. M., Gold, C. S., & Van Driesche, R. (2008). Experimental evaluation of the impacts of two ant species on banana weevil in Uganda. *Biological Control*, *46*, 147–157.
- Abera-Kalibata, A. M., Gold, C. S., Van Driesche, R. G., & Ragama, P. E. (2007). Composition, distribution, and relative abundance of ants in banana farming systems in Uganda. *Biological Control*, *40*, 168–178.
- Abera-Kalibata, A. M., Hasyim, A., Gold, C. S., & Van Driesche, R. (2006). Field surveys in Indonesia for natural enemies of the banana weevil, *Cosmopolites sordidus* (Germar). *Biological Control*, *37*, 16–24.
- Arim, M., & Marquet, P. A. (2004). Intraguild predation: A widespread interaction related to species biology. *Ecology Letters*, *7*, 557–564.
- Bell, J. R., King, R. A., Bohan, D. A., & Symondson, W. O. C. (2010). Spatial co-occurrence networks predict the feeding histories of polyphagous arthropod predators at field scales. *Ecography*, *33*, 64–72.
- Box, G. E. P., & Cox, D. R. (1964). An analysis of transformations. *Journal of the Royal Statistical Society Series B (Methodological)*, *26*, 211–252.
- Cardinale, B. J., Harvey, C. T., Gross, K., & Ives, A. R. (2003). Biodiversity and biocontrol: Emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, *6*, 857–865.
- Chen, B. R., & Wise, D. H. (1999). Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology*, *80*, 761–772.

- Costello, M. J., & Daane, K. M. (2003). Spider and leafhopper (*Erythroneura* spp.) response to vineyard ground cover. *Environmental Entomology*, *32*, 1085–1098.
- Dornelas, M., Moonen, A. C., Magurran, A. E., & Barberi, P. (2009). Species abundance distributions reveal environmental heterogeneity in modified landscapes. *Journal of Applied Ecology*, *46*, 666–672.
- Ehmer, B., & Hölldobler, B. (1995). Foraging behavior of *Odonotomachus bauri* on Barro Colorado Island, Panama. *Psyche*, *102*, 215–224.
- Gearing, J. N., Gearing, P. J., Rudnick, D. T., Requejo, A. G., & Hutchins, M. J. (1984). Isotopic variability of organic-carbon in a phytoplankton-based, temperate estuary. *Geochimica Et Cosmochimica Acta*, *48*, 1089–1098.
- Gold, C. S., Pena, J. E., & Karamura, E. B. (2001). Biology and integrated pest management for the banana weevil *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae). *Integrated Pest Management Reviews*, *6*, 79–155.
- Hooks, C. R. R., & Johnson, M. W. (2004). Using undersown clovers as living mulches: Effects on yields, lepidopterous pest infestations, and spider densities in a Hawaiian broccoli agroecosystem. *International Journal of Pest Management*, *50*, 115–120.
- Koppenhofer, A. M. (1993a). Egg predators of the banana weevil, *Cosmopolites sordidus* (Germar) (Col. Curculionidae) in western Kenya. *Journal of Applied Entomology*, *116*, 352–357.
- Koppenhofer, A. M. (1993b). Observations on egg-laying behavior of the banana weevil, *Cosmopolites sordidus* (Germar). *Entomologia Experimentalis Et Applicata*, *68*, 187–192.
- Koppenhofer, A. M., Reddy, K. V. S., Madel, G., & Lubega, M. C. (1992). Predators of the banana weevil, *Cosmopolites sordidus* (Germar) (Col. Curculionidae) in western Kenya. *Journal of Applied Entomology*, *114*, 530–533.
- Kupfer, A., Langel, R., Scheu, S., Himstedt, W., & Maraun, M. (2006). Trophic ecology of a tropical aquatic and terrestrial food web: Insights from stable isotopes (^{15}N). *Journal of Tropical Ecology*, *22*, 469–476.
- Landis, D. A., Gardiner, M. M., van der Werf, W., & Swinton, S. M. (2008). Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 20552–20557.
- Lövei, G. L., & Sunderland, K. D. (1996). Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, *41*, 231–256.
- Macfadyen, S., Gibson, R., Polaszek, A., Morris, R. J., Craze, P. G., Planque, R., et al. (2009). Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecology Letters*, *12*, 229–238.
- Mariotti, (1984). Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. *Nature*, *311*, 251–252.
- Minagawa, M., & Wada, E. (1984). Stepwise enrichment of $\delta^{15}\text{N}$ along food-chains – further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica Et Cosmochimica Acta*, *48*, 1135–1140.
- Moonen, A.-C., & Barberi, P. (2008). Functional biodiversity: An agroecosystem approach. *Agriculture, Ecosystems & Environment*, *127*, 7–21.
- O'Rourke, M. E., Liebman, M., & Rice, M. E. (2008). Ground beetle (Coleoptera: Carabidae) assemblages in conventional and diversified crop rotation systems. *Environmental Entomology*, *37*, 121–130.
- Oelbermann, K., & Scheu, S. (2002). Stable isotope enrichment ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): Effects of prey quality. *Oecologia*, *130*, 337–344.
- Patek, S. N., Baio, J. E., Fisher, B. L., & Suarez, A. V. (2006). Multifunctionality and mechanical origins: Ballistic jaw propulsion in trap-jaw ants. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 12787–12792.
- Perfecto, I., & Casteñeras, A. (1998). Deployment of the predaceous ants and their conservation in agroecosystems. In P. Barbosa (Ed.), *Conservation Biological Control* (pp. 269–290). San Diego, CA: Academic Press.
- Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, *18*, 293–320.
- Pinheiro, J. C., & Bates, D. M. (2004). *Mixed-effects models in S and S-PLUS*. New York: Springer.
- Ponsard, S., & Ardit, R. (2000). What can stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) tell about the food web of soil macro-invertebrates? *Ecology*, *81*, 852–864.
- Ponsard, S., & Ardit, R. (2001). Detecting omnivory with $\delta^{15}\text{N}$ – Comment from Ponsard & Ardit. *Trends in Ecology & Evolution*, *16*, 20–21.
- Post, D. M., & Takimoto, G. (2007). Proximate structural mechanisms for variation in food-chain length. *Oikos*, *116*, 775–782.
- Raimundo, R. L. G., Freitas, A. V. L., & Oliveira, P. S. (2009). Seasonal patterns in activity rhythm and foraging ecology in the neotropical forest-dwelling ant, *Odontomachus chelifer* (Formicidae: Ponerinae). *Annals of the Entomological Society of America*, *102*, 1151–1157.
- R Development Core Team. (2004). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rickers, S., Langel, R., & Scheu, S. (2006). Stable isotope analyses document intraguild predation in wolf spiders (Araneae: Lycosidae) and underline beneficial effects of alternative prey and microhabitat structure on intraguild prey survival. *Oikos*, *114*, 471–478.
- Rosenheim, J. A. (2007). Intraguild predation: New theoretical and empirical perspectives. *Ecology*, *88*, 2679–2680.
- Sanders, D., & Platner, C. (2007). Intraguild interactions between spiders and ants and top-down control in a grassland food web. *Oecologia*, *150*, 611–624.
- Scheu, S., & Falca, M. (2000). The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: Stable isotope analysis of a macro- and a mesofauna-dominated community. *Oecologia*, *123*, 285–296.
- Scheu, S., & Folger, M. (2004). Single and mixed diets in *Collembola*: Effects on reproduction and stable isotope fractionation. *Functional Ecology*, *18*, 94–102.
- Schmidt, M. H., Roschewitz, I., Thies, C., & Tschamtk, T. (2005). Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology*, *42*, 281–287.
- Schmidt, S. N., Olden, J. D., Solomon, C. T., & Vander Zanden, M. J. (2007). Quantitative approaches to the analysis of stable isotope food web data. *Ecology*, *88*, 2793–2802.
- Snyder, W. E., & Wise, D. H. (1999). Predator interference and the establishment of generalist predator populations for biocontrol. *Biological Control*, *15*, 283–292.
- Staddon, P. L. (2004). Carbon isotopes in functional soil ecology. *Trends in Ecology & Evolution*, *19*, 148–154.

- Tixier, P., Malezieux, E., & Dorel, M. (2004). SIMBA-POP: A cohort population model for long-term simulation of banana crop harvest. *Ecological Modelling*, *180*, 407–417.
- Vander Zanden, M. J., & Rasmussen, J. B. (1999). Primary consumer delta $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology*, *80*, 1395–1404.
- Vinatier, F., Chailleux, A., Duyck, P. F., Salmon, F., Lescourret, F., & Tixier, P. (2010). Radio telemetry unravels movements of a walking insect species in heterogeneous environments. *Animal Behaviour*, *80*, 221–229.
- Vinatier, F., Tixier, P., Le Page, C., Duyck, P.-F., & Lescourret, F. (2009). COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields. *Ecological Modelling*, *220*, 2244–2254.
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, *304*, 1629–1633.
- Wise, D. H., Moldenhauer, D. M., & Halaj, J. (2006). Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications*, *16*, 865–876.
- Yakir, D., & Israeli, Y. (1995). Reduced solar irradiance effects on net primary productivity (NPP) and the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in plantations of *Musa* sp., Musaceae. *Geochimica Et Cosmochimica Acta*, *59*, 2149–2151.

Available online at www.sciencedirect.com

