The food web of a severely contaminated site following reclamation with warm season grasses

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We used the stable isotope $^{13}$C to distinguish between food web components that depended on warm season grasses with the C$_4$ photosynthetic pathway and those that depended on plants with the C$_3$ pathway. The study site was contaminated by heavy metals from a zinc smelter that operated near Palmerton, Pennsylvania, U.S.A. C$_3$ plants only contributed 1.16% of aboveground primary productivity, whereas recently seeded (5–7 year old) warm season C$_4$ grasses contributed the remaining 98.84%. Analyses of tissue samples revealed that the carbon content of invertebrates and vertebrates did not reflect the composition of the vegetation. Of 135 samples, 48 (36%) had greater than 75% of their carbon from C$_4$-derived sources, while 32 (24%) of the samples had less than 25%. However, carbon from C$_4$ grasses passed through to higher trophic levels, as shown by the abundance of predators with a high proportion of C$_4$-derived carbon. We document three channels of carbon flux through the food web, one based on warm season grasses, now supporting a functioning ecosystem at all key trophic levels, one based on C$_3$ plants, and a third based on detritus. Theoretical and empirical studies have shown that relative configurations of such channels are important to ecosystem stability. Our results suggest that functional groupings of plants based on photosynthetic pathway or other plant traits likely form the basis for food web compartments. By using diverse functional groups of plants for reclamation or restoration, practitioners may be able to aid the development of channels and thereby promote desired ecosystem states.

Key words: C$_4$ grasses, grassland restoration, stable isotopes, Superfund site, trophic position, zinc pollution

Implications for Practice

- Stable isotopes of carbon and nitrogen can be used to discern success of restoration or reclamation projects that use warm season grasses.
- Restoration or reclamation with several types of plants (grasses, forbs, and woody plants) may promote a more stable food web than food from a single plant type.

Introduction

Interest in ecological restoration has grown rapidly (Young et al. 2005) with increased instances of human impact on natural ecosystems. Following the publication of Jordan et al. (1987), investigators discussed the criteria for successful restoration for several years (Hobbs & Norton 1996; Allen et al. 1997; Hobbs & Harris 2001), culminating in a definition of ecological restoration and a set of structural and functional attributes characteristic of successfully restored ecosystems (Society for Ecological Restoration International Science Policy Working Group 2004). Here, we present a novel study of the food web of an ecosystem undergoing restoration. We used stable isotopes to gain insights into important attributes including species composition, functional groups, and linkage to the surrounding landscape.

Although the concept of a food web has a long history in ecology, our understanding and appreciation of the role of linkages between organisms has increased markedly in recent decades (Bardgett & Wardle 2003; Moore & de Ruiter 2012). May (1972) applied a general result for networks presented by Gardner and Ashby (1970) to show that the likelihood of stability of model food webs declined as the number of species and the connections between them increased. This effect could be offset if the web was organized into compartments of species interactions within a food web wherein the interactions within a compartment are more numerous, frequent, or stronger than outside the compartment.

In most published food webs, basal resources form the foundation for compartments, typically defined by broad categories such as detritus, plants, or algae (Moore & Hunt 1988; Cohen et al. 1990), by plant tissue type (Reagan & Waide 1996), or by plant species (Dawah et al. 1995). Here, we present evidence for...
food web compartments based on functional groups associated with the C\textsubscript{3} and C\textsubscript{4} photosynthetic pathways.

In 1898, a large zinc-smelting plant was constructed near Palmerton, Pennsylvania, U.S.A., and operated for more than 80 years. A second plant was added later. During this period, the forests of Kittatinny Ridge downwind from the smelter were destroyed by emissions of sulfur dioxide, zinc, cadmium, and lead (Beyer et al. 1984; Beyer 1988). In 1983, the area was designated a Superfund site by the U.S. Environmental Protection Agency under the Comprehensive Environmental Response, Compensation and Liability Act of 1980. Nearly all vegetation and lichens were eliminated on the mountainside south of the Lehigh River (Nash 1975; Latham et al. 2007), leading to the erosion of an estimated 30–60 cm of topsoil from the sides of the mountain. Following the failure of earlier efforts, a program of revegetation with warm season grasses as suggested by Dickerson et al. (1997) was begun in 2003.

Because warm season grasses possess the C\textsubscript{4} pathway, they have a higher proportion of the heavy isotope \textsuperscript{13}C than the surrounding vegetation and the few forbs on the site, which have the C\textsubscript{3} pathway (Farquhar et al. 1989). The difference in the discrimination of \textsuperscript{13}C between the pathways allowed us to differentiate those members of the food web that used the recently planted grasses and those that depended on the surrounding vegetation as well as the detritus from vegetation that previously existed on the site. This study addresses three questions: (1) Are the recently planted (5–7 year) warm season grasses a significant basal resource for carbon flux through the reclaimed ecosystem? (2) If so, is there an exchange of carbon between organisms that use C\textsubscript{3}-derived carbon and organisms that depend more on the planted grasses? (3) At what trophic levels does mixing of carbon sources occur? Answers to these questions will provide an indication of whether the introduced warm season grasses are integrated into the surrounding landscape or, alternatively, if they constitute a separate, isolated ecosystem.

**Methods**

**Study Site**

In 2002 a nonprofit group, the Lehigh Gap Wildlife Center, purchased 304 ha on Kittatinny Ridge, Pennsylvania, U.S.A. and decided to establish warm season grasses to avoid the problems encountered by earlier revegetation efforts. For vegetating the Lehigh Gap Wildlife Refuge (LGWR), warm season grasses possessed a number of advantages: (1) many are native to Pennsylvania, (2) they grow in poor soil conditions and are tolerant of heavy metals, (3) they have deep root systems, and (4) they contribute significantly to soil organic matter through the growth and death of the root systems and the accumulation of litter on the surface (Dickerson et al. 1997).

Test plots were established at LGWR on the lower mountain while steep slopes were hand-seeded (Frank & West Environmental Engineers, Inc. 2003; Hoopes 2007). The 1,200 m\textsuperscript{2} plot used for our study was planted in 2003 with a mixture of warm season grasses (Table 1). It was fertilized with 29.4 kg/ha N, 23.9 kg/ha P, 53.2 kg/ha K, and 9.2 kg/ha Fe. Limestone and mushroom compost were added at rates of 1,468 kg/ha and 3,671 kg/ha, respectively.

**Plant Species Composition**

In September 2010, we measured net primary productivity by harvesting aboveground plant biomass from 30 0.09 m\textsuperscript{2} quadrats in one of the test plots planted in 2003. Ten quadrats

| Species | Photosynthetic Pathway | Seeding Rate (kg/ha) | Proportion in Original Seed Mix (%) | Frequency (%) | AGPP (g/m\textsuperscript{2}) | Proportion of Total AGPP (%) |
|---------|-------------------------|----------------------|-------------------------------------|--------------|-----------------|----------------------------|
| *Sorghastrum nutans* (L.) Nash | C\textsubscript{4} | 0.7 | 11.8 | 44.8 | 88.5 | 53.4 |
| *Eragrostis trichodes* (Nutt.) Alph.Wood | C\textsubscript{4} | 0.7 | 11.8 | 58.6 | 33.6 | 20.3 |
| *Schizachyrium scoparium* (Michx.) Nash | C\textsubscript{4} | 0.7 | 11.8 | 20.7 | 12.2 | 7.34 |
| *Panicum amarum* Elliott var. amarulum (Hitchc. & Chase) P.G. Palmer | C\textsubscript{4} | 0.7 | 11.8 | 24.1 | 8.72 | 5.26 |
| *Panicum virgatum* L. | C\textsubscript{3} | 1.1 | 17.6 | 6.9 | 8.55 | 5.16 |
| *Tripsacum dactyloides* (L.) L. | C\textsubscript{3} | 0.7 | 11.8 | 20.7 | 6.76 | 4.08 |
| *Andropogon gerardii* Vitman | C\textsubscript{4} | 1.1 | 17.6 | 3.4 | 5.38 | 3.25 |
| *Andropogon hallii* Hack. | C\textsubscript{4} | 0.4 | 5.9 | 0 | 0 | 0 |
| *Minuartia patula* (Michx.) Mattf. | C\textsubscript{3} | 6.9 | 0.972 | 0.587 |
| *Buddleja davidii* Franch. | C\textsubscript{3} | 13.8 | 0.760 | 0.459 |
| *Cerastium nutans* Raf. | C\textsubscript{3} | 3.4 | 0.185 | 0.112 |
| Unknown forb | C\textsubscript{3} | 3.4 | 0.007 | 0.004 |
| *Betula populifolia* Marshall | C\textsubscript{3} | 3.4 | 0.003 | 0.002 |
| Total | | | | | 165.6 | 100 |
Table 2. Sampling dates and methods used to collect specimens for isotope analyses.

| Group        | Dates Collected          | Methods                        |
|--------------|--------------------------|--------------------------------|
| Plants       | 18 July 2008             | Harvest                        |
|              | 21 July 2008 – 24 August  | Sweep net, pitfall trap        |
|              | 10 June 2009 – 10 September 2009 | Capture, malaise tent         |
|              | 10 August 2010 – 10 September 2010 | Wasp trap, bee trap, bait, fly trap |
| Birds        | 18 July 2008, 8 July 2009, 10 August 2010 | Mist net                      |
| Mammals      | 24 July 2008, 12 June 2009, 27 June 2010 | Live trap, fecal collection   |
| Reptiles     | 8 September 2008         | Shed skin                      |

were located randomly along each of three 30 m transects in a 1,200 m² plot located close to the center of the recently re-vegetated area (40°47’35”N, 75°37’19”W). Except for isolated trees, the plot was 170 m from the nearest woods, an isolated patch of about 0.5 ha, and almost 0.5 km from the nearest continuous forest. Because the vegetation was almost entirely herbaceous and visible evidence of herbivory was very slight, the harvested biomass samples were considered to approximate net primary productivity closely. Samples were sorted to species, dried at 65°C, and weighed. We also estimated leaf area index (LAI) of vegetation along each transect using a LAI-2000 plant canopy analyzer (LiCor, Inc., Lincoln, NE, U.S.A.).

Sample Collection and Processing

From July 2008 through October 2010, we sampled from within the 1,200 m² plot targeting plants, invertebrates, and vertebrates at two- to six-week intervals during the growing season. Sweep samples of 100 sweeps each were collected along 40 m transects across the plot. Invertebrates were also collected with five pitfall traps and other methods (Table 2). Spiders and ants were preserved in 70% alcohol; other insects were stored dry. Voucher specimens were sent to the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., and to the Department of Entomology, University of Delaware, Newark, Delaware, U.S.A., for identification. Small mammals were live-trapped with Sherman traps, and birds were captured during the breeding season with mist nets (Table 2). The live-trapping protocols of vertebrates were approved by the PA Game Commission, Harrisburg, Pennsylvania, U.S.A., and the U.S. Bird Banding Laboratory, Laurel, Maryland, U.S.A. In addition to live vertebrates, coyote (Canis latrans) scat and the fresh skin of an eastern rat snake (Pantherophis alleghaniensis) were found near the site and used as samples. A live eastern rat snake of similar size had been observed on the site 2 weeks previously. Taxonomic and collection data were managed with Biota 2, a taxonomic database (Colwell 2004).

From 668 specimens, we selected 146 for stable isotope analysis, consisting of 11 plant samples, 123 invertebrate samples, and 12 vertebrate samples. Specimens were selected to cover a broad range of taxa and trophic levels (Table 3). Frequently encountered taxa were sampled multiple times. Tissue samples were sent to the Stable Isotope Facility (SIF) at the University of California, Davis, California, U.S.A. Sample preparation followed SIF-recommended protocols (http://stableisotopfacility.ucdavis.edu/13cand15nsamplepreparation.html). Plant tissue was ground in a ball mill. For large arthropods, small pieces of legs (approximately 1 mg) were crushed in tin capsules, while for small arthropods the whole organism was used. Specimens preserved in alcohol were dried beforehand. For birds we collected contour feathers from the back and breast whereas for small mammals we shaved a small patch of hair from the abdomen. All vertebrates (birds and mammals) were tagged and then immediately released at the site of the capture. The SIF analyzed the sample for 13C and 15N using a PDZ Europa ANCA–GSL elemental analyzer connected to a PDZ Europa 20–20 continuous flow isotope ratio mass spectrometer. Stable isotope ratios (δ13C and δ15N) are reported relative to Vienna PeeDee Belemnite and air, respectively.

Data Analysis

Mean δ13C values for C3 and C4 plants (see results) were used to estimate the percent of carbon that came from C4 plants using a two-source mixing model defined as Percent C4 Carbon = 100 × (δ13Csample − δ13C warm season grasses)/(δ13C C3 plants − δ13C warm season grasses) (Fry 2006). Means for δ13C C3 plants and δ13C warm season grasses were calculated from plants collected on the site. Samples with δ13C values less than δ13C C3 plants or greater than δ13C warm season grasses were assigned values of 0 and 100, respectively. For 143 of the samples, trophic level was determined by natural history and family characteristics. Organisms were classified on the basis of their mouthparts and our knowledge of their natural history into herbivores, detritivores, predators, omnivores, parasites, or parasitoids. For three specimens whose trophic position was uncertain, trophic level was calculated as 1 + (δ15N sample − δ15N base)/ΔN sensu Post (2002). Because there was no significant difference between δ15N of the C1 and the C4 species, δ15N base was estimated as the mean of the values for the two groups. For ΔN, we used a trophic enrichment factor of 3.4% (Post 2002). Regression analysis was used to analyze the relationship between trophic level and mean δ15N for each taxon. Plants were assigned a trophic level of 1; herbivores and detritivores, level 2; omnivores, level 2.5; and predators, parasites, and parasitoids, level 3.

Results

Plant Species and Isotopic Composition

LAI ranged from 0 to 3.78 with a median value of 0.80 (N = 62). Mean aboveground primary productivity (AGPP) was 165.6 g m⁻² yr⁻¹ ± 23.5 (SE). The distribution was skewed with a median of 123.2 g m⁻² yr⁻¹. Species with the C3 photosynthetic pathway were much less abundant than those with the C4
pathway, appearing in only 31% of sampled quadrats, whereas
C₃ species appeared in all of the quadrats. Plants with the C₃
pathway only contributed 1.16% of the total AGPP on the site,
whereas warm season grasses with the C₄ pathway contributed
the remainder (Table 1). Seven of the originally planted eight
species were still on the site, but not in the same proportions as
in the planting mix. *Andropogon hallii* had disappeared, while
*Andropogon gerardii* and *Panicum virgatum*, which were 35.2%
of the original seed mixture, comprised less than 9% of AGPP.
Mean values for δ¹³C were significantly less for C₃
plants (−26.85 ± 0.39 [SE%]) than those for the C₄ grasses
(−13.37 ± 0.09%, p < 0.001). On the other hand, values for
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Figure 1. Values of $\delta^{15}$N versus trophic level for 76 taxa collected on the warm season grassland at Lehigh Gap Wildlife Refuge. Plants = 1; herbivores (solid circles) and detritivores (open circles) = 2; omnivores = 2.5; predators, parasites, and parasitoids = 3.

$\delta^{15}$N = $-1.07 + 2.64 \times$ Trophic Level ($R^2 = 0.32$, $p < 0.0001$).

$\delta^{15}$N for C$_3$ plants (1.06 ± 0.42%) were not different from those for C$_4$ grasses (1.09 ± 0.36%).

Trophic Enrichment Factors

$\delta^{15}$N increased with trophic level with a mean trophic enrichment factor (slope) of 2.64% per trophic level (Fig. 1). However, there was considerable variation around the regression line ($R^2 = 0.32$), reflecting variation in food sources and trophic enrichment factors. Predators, parasitoids, and parasites showed the most variation, which may reflect a greater variety of trophic levels as their food sources. This value is considerably lower than the 3.4% proposed by Post (2002), though it is quite consistent with values from other studies. Vanderklift and Ponsard (2003) and Caut et al. (2009) reported trophic enrichment factors of 2.62 and 2.46, respectively, for insects, which formed the bulk of samples in our study. In contrast with $\delta^{15}$N, $\delta^{13}$C showed no significant change with increasing trophic level even when plants were eliminated from the analysis (data not shown).

Trophic Position and Diet Composition

The proportion of tissue samples from consumers that acquired most of their carbon from C$_4$ sources did not reflect the composition of the vegetation. Forty-eight of the 135 animal samples (36%) had more than 75% of their carbon from C$_4$-derived sources whereas 24% of the samples had less than 25% (Fig. 2). The remaining 40% appeared to derive their carbon from a mixture of C$_3$ and C$_4$ sources. When the pool of species was restricted to organisms that likely resided solely or predominantly within the site, that is, eliminating highly vagile animals such as birds and wasps, the proportion of samples with greater than 75% C$_4$-derived carbon increased to 39% ($N = 118$) and the proportion of samples with less than 25% C$_4$-derived carbon decreased to 19%. Nevertheless, a substantial fraction of the carbon in the food web appears to come from sources that are poorly represented on the site.

The distribution of the percent of carbon derived from C$_4$ sources differed dramatically between trophic positions (Fig. 3). Herbivores showed a largely bimodal distribution with one peak consisting of organisms that used mostly C$_4$ carbon and another peak consisting of those that used mostly C$_3$ carbon (Fig. 3B). Only 36% of the 41 sampled herbivores contained between 20 and 80% C$_4$-derived carbon, with the remainder having less than 20% or greater than 80%. In contrast detritivores derived their carbon from both sources, with 82% falling in the range between 20 and 80% C$_4$-derived carbon (Fig. 3C). The omnivore group, which consisted largely of ants, derived its carbon largely from C$_3$ sources (Fig. 3D). Predators, parasites, and parasitoids showed a fairly uniform distribution of carbon sources (Fig. 3E). Carbon from the recently planted grasses was apparently passed through to the higher trophic levels, as shown by the abundance of predators (mainly spiders) with a high proportion of C$_4$-derived carbon (Figs. 3E and 4).

Within most orders that were represented by more than one sample, there was a great deal of variation in carbon source (Fig. 4). The exceptions were Araneae (spiders) and Rodentia, which appeared to get most of their carbon from the warm season grasses. Rodentia were represented by Peromyscus leucopus (seed eaters) and Microtus pennsylvanicus (grazers). On the other hand, Soricomorpha (shrews) appeared to get most of their carbon from C$_3$ sources. Shrews generally range over a larger area (>2 ha) than mice and voles and may be foraging away from the plot more frequently because of their substantially higher energy demands and carnivorous diet. The families Cicadellidae and Cixiidae (leafhoppers) in the Hemiptera also showed a high proportion of C$_4$-derived carbon in their tissue (Table 3). Lepidoptera was unique in that the seven samples from that order either contained no C$_4$-derived carbon or consisted entirely of C$_4$-derived carbon. $\delta^{15}$N varied little for Passiformes, Rodentia, Soricomorpha, Cicadellidae, and Cixiidae.
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Figure 3. Histograms of percent of C4-derived carbon for plants (A), herbivores (B), detritivores (C), omnivores (D), and predators (E) collected on warm season grassland at Lehigh Gap Wildlife Refuge. Parasites and parasitoids are included with predators. Sample size is in parentheses except for plants where aboveground primary productivity (AGPP) is shown.

compared with Coleoptera, Diptera, and Hymenoptera, which included species with greatly varying diets. For the vertebrate orders, the lack of variation in $\delta^{15}N$ may be a result from small sample size, whereas for the Cicadellidae ($n = 7$) and Cixiidae ($n = 3$) it more likely reflects dietary specialization. We constructed a food web (Fig. 5) using the natural history of the organisms found in the reclaimed grassland at Lehigh Gap and the information in Figure 2.

Discussion

Food Web Structure

The food web for the planted grasslands at LGWR appears to be divided into three compartments or energy channels (Moore & Hunt 1988; Rooney et al. 2006; Moore et al. 2004), one based on the warm season grasses that possess the C4 photosynthetic pathway, another based on plant species that use the C3 photosynthetic pathway, and a third based on detritus that originated from past and present plant species that possessed either C3 or C4 pathways. The stable isotope analysis of consumers indicates fidelity in the feeding relationships between the consumers and resources beyond what could be explained by chance encounters alone given the high proportion of C4 grasses relative to C3 plant species.

Terrestrial food webs contain grazer and detrital pathways (e.g., Marples 1966; Odum 1969; Moore et al. 2012, 1988; Polis & Strong 1996). Our results indicate that the grazer pathway at LGWR can be subdivided into two compartments, one based on warm season grasses and the other based on plants with C3 photosynthesis. We argue that the warm season grasses constitute a functional group given their similar traits, and as such, influence the structure of the food web. From the standpoint of an herbivore, there are several reasons to believe the C4 grasses might constitute such a functional group. First, they contain less protein in the form of Rubisco than C3 plants (Ehleringer & Monson 1993). Second, much of the protein is sequestered in bundle sheath cells, which are more mechanically resistant than mesophyll cells. Finally, grasses are less likely to rely on secondary compounds as defenses against herbivory than woody plant species (Tscharntke & Greiler 1995).

If the basal resources of grassland ecosystems are divided into functional groups on the basis of photosynthetic pathway or other traits, it may have important implications for analyses of the dynamic stability of these systems. Rooney et al. (2006) described several ecosystems with two channels that had one fast channel with high turnover and a slow channel in which organisms replace each other more slowly. An example would be the food chains based on bacteria (fast) versus those based on fungi (slow) in a rhizosphere ecosystem. Rooney et al. (2006) concluded that such systems were more likely to be stable.
when exposed to large perturbations when energy flows were asymmetric, that is, more energy flowed through one channel than the other. Although we currently have no information about the flux rate of carbon through the warm season grass channel at LGWR, it might be a candidate for a slow channel because of the large amounts of biomass consisting of structural materials that are mechanically resistant to herbivory.

The grassland food web at LGWR also resembles those studied by Rooney et al. (2006) in that vertebrate predators such as the rat snake (Elaphe obsoleta) and coyote (Canis latrans) as well as invertebrate predators contained a mixture of carbon from both channels. Vertebrate omnivores such as northern mockingbirds (Mimus polygloptus) and a field sparrow (Spizella pusilla) had similar values for δ15N as the predators and may have played a similar role in combining carbon from different channels. As top predators switch from one channel to the other in response to varying supplies of food, they act to stabilize the dynamics of prey populations (Post et al. 2000; Moore et al. 1988; Rooney et al. 2006).

The C4 grasses appear to be utilized by a broad array of organisms at higher trophic levels. Consumers that were collected by sweep net such as Trichordestra legitima (Lepidoptera: Noc-tuidae) as well as leafhoppers obtained all or most of their carbon from plants with the C4 pathway. Two vertebrate consumers that showed a high proportion of C4-derived carbon were the meadow vole (Microtus pennsylvanicus) and the chipping sparrow (Spizella passerina). Four beetle specimens in the genus Harpalus consisted almost wholly of C4-derived carbon, although their values of δ15N ranged widely with values of 3.24, 3.72, 5.22, and 11.7, suggesting considerable variation in diet between individuals. Members of the genus Harpalus are commonly considered to be predators (Rothe & Gleixner 2004), but also feed on seeds (J. Rawlins 2012, personal communication).

The group with the highest percentage of C4-derived carbon also contained predators such as the jumping spiders (Salticidae) and spiders from the genus Tibellus (Philodromidae). An omnivorous group with high proportions of C4-derived carbon consisted of ants from several genera (Aphaenogaster, Camponotus, Formica, Solenopsis) that occupied relatively high trophic levels with values of δ15N from 4.56 to 8.30. Bluthgen et al. (2003) found that ants that were primarily predators had high values of δ15N whereas ants that attended species of homopterans or visited nectaries had lower values. Thus, the group of organisms that colonized the planted grasses during the 5–7 growing seasons after planting contained primary consumers, omnivores, and predators.

This result has some similarity to the findings of Heatwole and Levins (1972) who analyzed the species composition data of Simberloff and Wilson (1969) and found that trophic structure had recovered within a year following defaunation of mangrove islands under study even though the species richness had not completely recovered. Although there are important differences with Simberloff and Wilson (1969) in that the trophic structure in our study is based on a newly established plant community...
instead of a pre-existing one, the communities that developed at the LGWR also developed within the trophic structure shaped by the available plant species. Over time, the LGWR food web can be expected to become more complex, owing to the development of greater separation between consumers and predators (Rothe & Gleixner 2004) and the addition of more functional groups and connections (Neutel et al. 2007).

Approximately one fourth of the samples contained over 75% of C3-derived carbon. The mean trophic level for this group was lower than for the samples with greater than 25% C3-derived carbon because there were very few omnivores that contained mostly C3-derived carbon. Given the low representation of plants with the C3 pathway on the study site, it is not clear where the C3-derived carbon in consumers originated. This is especially puzzling because two of the C3 species, Minuartia patula and Buddleja davidii, do not experience significant herbivory. M. patula accumulates zinc and heavy metals, whereas B. davidii is an invasive species. In addition to predators and omnivores at higher trophic levels, the group of organisms with intermediate values (25–75%) of percent C3-derived carbon consisted mostly of detritivores such as crickets (Orthoptera: Grylliidae) and millipedes (Oxidus gracilis). Presumably, these organisms were feeding on leftover detritus as well as that from the warm season grasses. It is not clear where they were receiving their C3-derived carbon, unless it is from the detritus.

In our survey of the food web of a contaminated site undergoing reclamation, we found that many organisms, including herbivores, omnivores, and predators from several trophic levels, acquired much of their carbon from the recently planted warm season grasses. The introduction of warm season grasses not only increased the amount and diversity of vegetation on the site but also provided the basis for reclamation of a functioning ecosystem that includes viable components at all trophic levels. Over time, the LGWR food web instead of a pre-existing one, the communities that developed at the LGWR also developed within the trophic structure shaped by the available plant species. Over time, the LGWR food web can be expected to become more complex, owing to the development of greater separation between consumers and predators (Rothe & Gleixner 2004) and the addition of more functional groups and connections (Neutel et al. 2007).

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