Intercropping Switchgrass with Loblolly Pine Does Not Influence the Functional Role of the White-footed Mouse (*Peromyscus leucopus*)

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Abstract:

Intercropping biofuel feedstocks in managed forests of the southeastern United States is a potentially sustainable source of renewable energy. Ecological effects of energy crops in forests are poorly understood, and it is unknown whether the ecological role of native rodents is influenced by alternative food resources. Therefore, we used a stable isotope analysis to compare diet and trophic responses of white-footed mice (*Peromyscus leucopus*) in 1) plots where switchgrass (*Panicum virgatum*), a C_4 plant, was intercropped with loblolly pine (*Pinus taeda*), a C_3 plant, 2) plots of loblolly pine, and 3) plots of monocropped switchgrass. We collected fur from live-trapped rodents and potential dietary sources in 2010. We predicted $\delta^{13}C$ and $\delta^{15}N$ values of mice in switchgrass plots would reflect a C_4-based, granivorous, diet if there was an effect of intercropping on the functional role of mice. Del^{13}C values of mouse fur in monocropped switchgrass, but not intercropped switchgrass plots, shifted more toward a C_4 signal. However, $\delta^{15}N$ values indicated that mice remained functionally omnivorous across treatments. Our results were supported by isotope values from invertebrates across guilds. Diet and trophic position of white-footed mice was not influenced by intercropping switchgrass in pine plantations indicating they maintained their functional role in this biofuels management regime. Future research should focus on individual and population responses of rodents to altered vegetation structure where biofuels feedstocks are grown and indirect effects on inter- and intra-species interactions.

Keywords: Biofuels | Trophic position | Intercropping | Stable-isotopes | Nitrogen | Carbon

Article:

1. Introduction

Production of biofuels (liquid fuels derived from plant matter) is an important component of renewable fuels standards [1], [2] and [3]. At a commercial scale, biofuels may compete for land with food production, encroach on natural lands, and/or impact biodiversity [2], [4] and [5]. Within intensively managed forests, opportunities exist to source biomass via collection of residual woody debris, harvest of non-crop trees and vegetation, and establishment of purposely-grown energy grasses. However, these options have the potential to negatively affect biodiversity within these systems. Although interest in agro-forestry systems that produce both timber products and biofuel feedstocks is increasing, our understanding of effects on biodiversity and sustainability is limited [5]. Therefore, quantifying responses of animals to biofuels production is critical for evaluating ecological sustainability of expanding management regimes [5].

Currently, several research efforts are examining feasibility of producing cellulosic biofuel feedstocks from switchgrass (*Panicum virgatum*) grown within intensively managed pine (*Pinus* spp.) forest (hereafter, pine plantations) in the southeastern USA [6] and [7]. Switchgrass is a perennial C_4 grass native to eastern North America, is highly productive across a wide geographic range, and has relatively low demand for water and nutrients [1], [8] and [9]. Switchgrass has potential to be intercropped between rows of planted pine trees within tens of thousands of hectares of pine plantations across the southeastern United States. Still, little is known about ecological effects of establishing switchgrass in a managed forest landscape compared to typical intensive forest management [5] and [10]. Pine plantations often include mechanical and chemical site preparation, selective use of chemical and fertilizer treatments, planting of specific genotypes, and/or mid-rotation thinning. Growing switchgrass in alleys between rows of planted pines (i.e., intercropping) may require additional site preparation or other treatments that may change habitat conditions for a variety of wildlife species supported within pine plantations [11]. Likewise, the addition of switchgrass to plantations may provide alternative food and/or cover that could alter ecological relationships among wildlife species.

From the perspective of ecological sustainability, rodents are appropriate study species because they disperse seeds and fungi, contribute to soil aeration, regulate invertebrate populations, and are an important prey source for higher order consumers [12], [13], [14], [15] and [16]. Rodents respond rapidly to changes in resource availability or other environmental factors, making them ideal for examining ecological perturbations [17]. Generalist omnivore rodents such as deer mice (*Peromyscus* species) can quickly increase population densities in response to pulsed resources such as oak (*Quercus* species) mast[18] and [19]. Further, diet shifts in *Peromyscus* species from pulsed resource events can lead to trophic changes, whereby mice alter their functional role depending on available food resources [20]. Intercropping switchgrass in pine plantations could

also lead to diet and trophic shifts among rodents after seed set in the fall, when switchgrass seeds are available to a number of consumers including mice and insects [21], [22],[23] and [24]. Therefore, intercropping switchgrass in pine plantations could alter inter-specific interactions and energy flow in the forest food web, thus impacting ecological sustainability.

As a C_4 grass, switchgrass has $\delta^{13}C$ signatures distinguishable from isotope signatures of more common C_3plants [25], [26], [27] and [28]. Both carbon and nitrogen stable isotopes (SI) exhibit unique patterns of enrichment relative to consumer diets [29] and [30], and the SI ratios of food sources are incorporated into tissues of animal consumers [31] and [32]. Carbon isotope ($\delta^{13}C$) signatures of consumers are enriched by about 1‰ (parts per mil) relative to their diet so that the carbon signal (i.e., relative amounts of C_3 and C_4carbon sources) of ingested nutrients can be tracked.

Similarly, nitrogen isotope ($\delta^{15}N$) signatures of consumers generally are enriched 3–5‰ with each trophic level [29] and [30], so that a consumer can be compared to the $\delta^{15}N$ base of the food web to evaluate trophic position.

Due to importance of rodents, especially generalist species that consume a variety of food sources, to ecological function [12], [13], [14], [15] and [18] and the increasing potential for establishment of biofuel feedstocks within pine plantations in the southeastern USA, our goal was to determine whether intercropping switchgrass in pine plantations changes the functional role of rodents by examining dietary carbon source and trophic position of white-footed mice. The white-footed mouse is a common rodent native to the southeastern USA and a dietary generalist that consumes fruits, nuts, seeds, green foliage, fungi, and insects [33], [34], [35] and [36]. Our previous work indicated that planting switchgrass did not affect structure or composition of the rodent community [37]. However, we detected a negative effect of planting switchgrass, especially in a monoculture, on survival and abundance of white-footed mice, whereby both survival and abundance was less in monoculture switchgrass plots compared to control pine plots and pine plots intercropped with switchgrass [37]. Here, using SIs, we determined whether the functional role of white-footed mice as a consumer in pine plantations was influenced by presence of switchgrass grown in monoculture or intercropped within rows of pine. We predicted that diet of white-footed mice would shift towards a C_4 carbon source in presence of switchgrass, either due to direct consumption of switchgrass seeds or assimilation of switchgrass-derived carbon into white-footed mouse prey items. Further, we predicted white-footed mice would consume more switchgrass seeds in plots with switchgrass and thus have a lower trophic position (i.e., be more granivorous).

2. Materials and methods

2.1. Study area

The Lenoir 1 Intercropping Sustainability Study was a collaborative experimental research study with industry, university and government partners and was established and maintained by

Weyerhaeuser Company and Catchlight Energy LLC, (CLE) a joint venture between Chevron and Weyerhaeuser Company. The following description is from Leggett and Sucre [38]. Our was located in eastern North Carolina in Lenoir County, USA in a region dominated by commercial forestland and agriculture. The stand used in our study was previously comprised of 109 ha of loblolly pine planted in 1974 and clearcut harvested in 2008. As is typical for the region, a series of linear drainage ditches, which improve hydrologic conditions for pine growth and survival in plantations, occurred parallel to one another through the study area (Fig. 1). Pine trees were established using standard Weyerhaeuser methods including clearcut harvest of the existing stand followed by mechanical and chemical site preparation and planting, vegetation management, and fertilization. The overall objective of this long-term study is to examine effects of intercropping switchgrass and/or biomass management on sustainability and site productivity in a loblolly pine plantation. In this system, the loblolly pine plantation served as the control treatment because if intercropping switchgrass did not occur, normal intensive management would have occurred. Moreover, intensively managed pine is the background condition of the forest matrix where the experiment was established. White-footed mice were a major component of biodiversity in loblolly pine plantations in eastern North Carolina and the study area [37]. The long-term Lenoir 1 Intercropping Sustainability Study site was a complete randomized block design with five treatments replicated four times (n = 20 plots) on ≈0.8 ha treatment plots (Fig. 1).

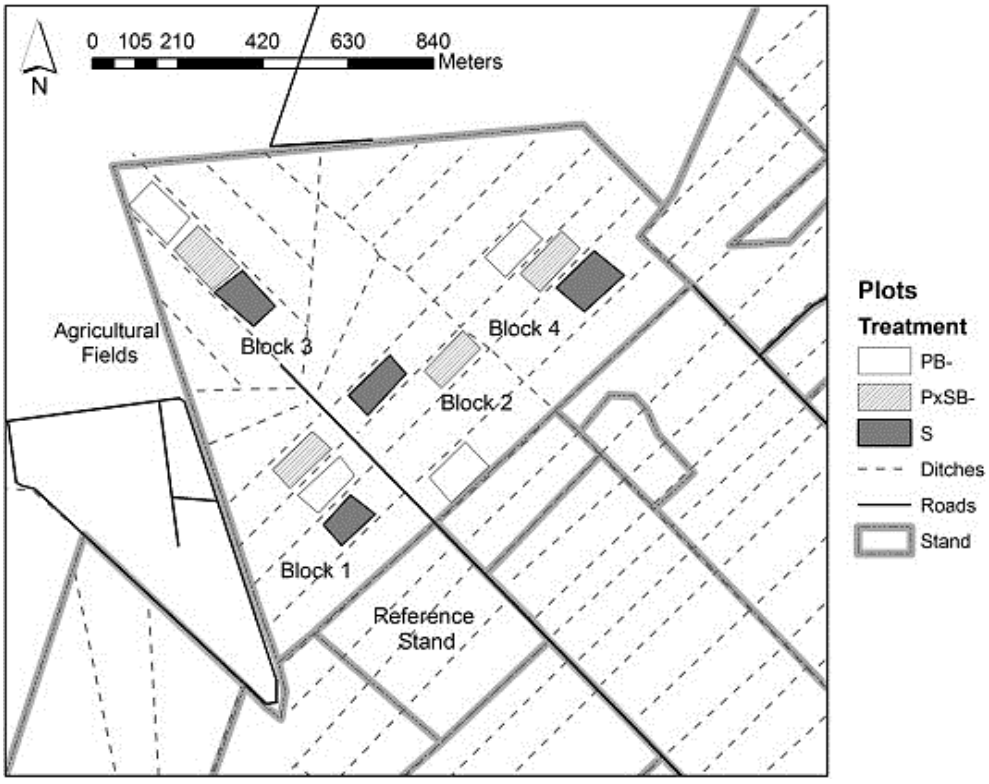

Fig. 1. The Lenoir 1 Sustainability Site. Effects of biofuels treatments on diet and trophic level of the white-footed mouse was examined at the Lenoir 1 Sustainability Study Site, Lenoir County, NC.

Treatments selected for this study included: pine with residual woody debris removed (PB−), pine and switchgrass intercropped with residual woody debris removed (P × SB−), and switchgrass only (S).

Of the five treatments available at the long-term study site, we sampled from the following three because they were relevant to our study objectives:

1.Traditional pine establishment with biomass (residual downed, woody material) removed (PB-). This serves as the control for this study as explained above.

2.Intercrop pine-switchgrass establishment with biomass removed (P × SB−).

3.Switchgrass only (S). Managed forests are unlikely to convert to monocultures of switchgrass and this treatment was included for comparative purposes only.

Treatments were installed with loblolly pine seedlings planted December 2008 at approximately 1100 trees/ha and switchgrass planted summer June 2009 at 9 kg of pure live seed per ha using a modified corn (*Zea mays*) planter. Treatments containing switchgrass incurred additional site preparation for the 3 m strips between crop tree rows (intercropped) or the entire plot to plant switchgrass [38]. After the first growing season but before the second growing season, switchgrass was mowed with a tractor in April 2010 but not harvested (debris left on ground). This is consistent with the general recommendation to not bale switchgrass after the first growing season due to low yields. However, switchgrass was mowed, raked, and baled in December 2010 after the second growing season.

In November 2008, in preparation for planting pine seedlings, standard liquid suspension fertilizer with 3% nitrogen (N), 6.2% phosphorus (P), 2.5% potassium (K), 4.5% magnesium (Mg), and 2% calcium (Ca) was incorporated into the soil where pine trees were planted to promote seedling root development and establishment (PB− and P × SB−). In June 2010, switchgrass (P × SB− and S) was fertilized (by broadcasting) at a rate of 65 kg N, 6.6 kg P, and 0.24 kg B per hectare during the second growing season (2010).

For additional description of treatments, site preparation, and vegetation management see Refs. [6],[38] and [39]. Treatments had their intended effects with respect to switchgrass establishment [6]. Native, non-planted grasses and sedges accounted for 64.80 ± 4.10% of cover in PB− plots. Native grasses, mainly consisting of planted switchgrass accounted for 75.15 ± 4.73% of cover in P × SB− plots. Planted switchgrass accounted for 95.60 ± 1.60% of cover in S plots [37]. Planted switchgrass yield was 82% and 25% greater in S plots when compared to P × SB− plots, in 2009 and 2010 respectively [38] and [39].

2.2. Mouse tissue collection

To determine if diet and trophic position of white-footed mice were influenced by intercropped switchgrass, we live-trapped mice as part of a capture-mark-release program in summer (July-

September) and fall (October–November) of 2010. We established 30 m × 60 m trapping grids (10-m spacing, with four rows of seven traps) in each plot. Each row had one randomly placed Longworth (Rogers Manufacturing Co., Peachland, British Columbia, Canada) and six Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, Florida). Longworth traps are more efficient at capturing small newly emerged/dispersing juveniles. We baited traps with oats (*Avena sativa*) in the summer and oats and sunflower (*Helianthus annuus*) seeds in the fall, set them at sunset (1700–2030 pm) and checked them the following morning (0600–0830) for three consecutive nights (i.e., trapping period). Live trapping occurred during six, three night trapping periods from 19 July 2010–14 November 2010. Upon each capture, we marked each individual with a unique numbered ear-tag (Monel Numeric, size 1005-1, National Band and Tag Company, Newport, Kentucky), collected fur samples from uniquely marked white-footed mice, and released individuals at the site of capture. Individuals from whom samples were collected were captured from 1 to 11 times (2.6 ± 2.5) on a single plot. Even when individuals were only captured once on a plot, we assumed they were feeding on their plot of capture because adult/sub adult mice in this area were rarely captured on more than one plot (3.75% of mice were captured on more than one plot). We excluded any samples from mice captured in more than one plot.

We collected mouse tissue samples by trimming fur from the dorsum of adult and sub-adult white-footed mice with scissors. Within 3 h of collection we stored fur samples dry in micro-centrifuge tubes at −20 °C until processing. All animal handling and tissue collection were conducted according to Sikes et al. 2011 [40]and conducted under a North Carolina State Wildlife Collection License Permit #10-SC00162 and University of North Carolina at Greensboro IACUC Permit # 09-09 and 10-04.

We chose to sample fur because it is a good tissue for tracking stable isotopes in the diet. Few studies have measured tissue-diet discrimination using fur, but DeMots et al. [41] found mean tissue-diet discrimination values of 1.1‰ ($\delta^{13}C$) and 2.9‰ ($\delta^{15}N$) for white-footed mice, which is consistent with widely accepted tissue-diet discrimination factors in most avian and mammalian species [29] and [30]. During the molting period, stable isotopes in the diet are immediately incorporated in the fur and remain fixed until growth resumes [42] and [43]. In northern temperate climates adult *Peromyscus* typically undergo a single winter molt in the fall [44] and [45]. However, brush mice (*Peromyscus boylii*) in the lower midwestern USA undergo two seasonal molts in the spring (April–May) and fall (November–December) with some additional molting throughout the year [46]. Due to the moderate temperatures in the coastal plain of the southeastern USA, mice in our project region also likely underwent a continuous molt. This continuous molt is supported by our trapping data that does not show a clear seasonal pattern. Thus, white-footed mice in our region are likely incorporating isotopes from their diet continuously so that their tissues should reflect their diet from the plot on which they were captured. Having said this, sampling metabolically active blood or plasma would have been ideal. However, we were only able to sample fur for logistic and human health/safety reasons.

2.3. Invertebrate and vegetation sampling

To aid in interpretation of SI signatures of white-footed mice and to compare them with other invertebrate consumers and potential food resources on our study plots, we collected and analyzed samples of pine, switchgrass, and herbivorous, omnivorous and predacious invertebrates. We sampled pine and switchgrass from the vegetation present because we wished to determine if white-footed mice shifted from a C_3-based diet to a C_4-based diet of planted switchgrass, and because these were the dominant plant forms. We collected vegetation samples from treatment plots in summer (22 June–11 September) and fall (6 October–20 November) 2010. We collected pine needles from PB− and P × SB− plots, and switchgrass seeds from P × SB− and S plots. We randomly selected 4 trap stations from each plot (n = 48) and collected samples of switchgrass seeds and loblolly pine needles from these locations. We collected pine needles in lieu of pine seeds because the young planted trees did not yet produce cones. Although we did not anticipate white-footed mice would consume pine needles, we collected needles to obtain $\delta^{13}C$ isotopic signals from pine for comparison to basal sources. Published $\delta^{13}C$ isotopic signal of loblolly pine seeds were not available for comparison, but values from slash pine (*Pinus elliottii*) in Florida, USA (composite value of −28.5‰) were within 0.08–0.33 ‰ of our loblolly pine needle estimates depending on treatment (see Results). Values from slash pine parts (i.e., roots, cones, bark, needles) were within 2% of the slash pine composite value [47]. Therefore, loblolly pine needles are appropriate surrogates for seeds to obtain isotopic signals. Material collected from an individual plant was defined as one sample. All plant material was placed in clean freezer bags and stored at −20 °C until analysis.

For invertebrates, we used a combination of branch-beating [48] and hand-collecting on each treatment type twice per month from 22 June-20 November 2010. Invertebrate sampling occurred during 1600–1930 h. During each sampling session, we randomly selected four mouse live-trap stations and sampled four surrounding plants for invertebrates within a 3-m radius, by branch-beating for 1 min each (16 min/plot). We also collected ground-dwelling invertebrates by hand-picking for an additional minute at each trap station (4 min/plot). We placed invertebrates in vials with 95% ethanol and later identified most invertebrates to family level and general feeding guild (e.g., herbivore, omnivore, and predator) using Marshall [49] and Arnett[50]. We considered unidentified spiders (Araneae) and butterfly/moth larvae (Lepidoptera) as predators and herbivores, respectively. Millipedes (Diplopoda) were identified to class.

2.4. Tissue processing for isotope analysis

To prepare for SI analysis, we rinsed mouse fur samples in 2:1 chloroform: methanol solution and air-dried samples for 48 h under a fume hood. Invertebrate and plant samples were rinsed with deionized water and dried at 60 °C for 48 h. Once dry, we ground invertebrate and plant samples with a mortar and pestle. All samples were weighed (fur and invertebrates: 0.20–1.0 mg

and plants: 1.0–6.0 mg) in tin foil capsules on a microbalance. Weighed samples were placed into a small ball and placed in a 96-well plate.

Rather than analyzing all samples for SI analysis, we selected samples (plant, invertebrate, mouse) to represent all combinations of age (for mice only), treatment, and season. We only analyzed samples from adult and sub-adult mice to avoid potential mother-offspring enrichment effects [51]. We tried to balance samples earlier (summer) or later (fall) in the field season in case there was a seasonal signature in our SI values. We randomly chose plant and invertebrate samples to distribute our sample size (where possible) among treatments and between seasons.

All SI analyses were performed with a Carlo Erba elemental analyzer (Milan, Italy) interfaced to a Thermo Finnigan Delta Plus XP isotope ratio mass spectrometer (Bremen, Germany) at the University of California Santa Cruz Stable Isotope Laboratory. Both $\delta^{13}C$ and $\delta^{15}N$ were analyzed simultaneously. Differences in abundances of heavy and light isotopes were expressed in delta notation (δ) as parts per mil (‰) change from a standard, as follows: $\delta^{H}X = [(R_{sample}/R_{standard})-1]*1000$, where X was the element, H was the heavy isotope, and R was the ratio of the heavy and light isotope. Pee dee belemnite limestone and atmospheric nitrogen were the standards of comparison for $\delta^{13}C$ and $\delta^{15}N$, respectively [29].

To describe contribution of C_4 (switchgrass) and C_3 (pine) sources in the assimilated diet of mice and invertebrates among treatments, we calculated diet fractions from switchgrass ($f_{switchgrass}$) and pine (f_{pine}) sources using a 2 end-point mixing model using equation 2 from Phillips [32] as follows:$f_{switchgrass} = (\delta^{13}C_{consumer} - \delta^{13}C_{pine})/(\delta^{13}C_{switchgrass} - \delta^{13}C_{pine})$ and $f_{pine} = 1 - f_{switchgrass}$. For our models, we applied a diet-tissue discrimination correction of 1.1‰ based on DeMots et al. [41] to our plant $\delta^{13}C$ values. We calculated plant values used in mixing models as follows: $\delta^{13}C_{pine}$ from PB− and P × SB− treatments were mean values from all pine samples collected from PB− and P × SB− treatments, respectively and $\delta^{13}C_{switchgrass}$ from P × SB− and S treatments were mean values from all switchgrass samples collected from P × SB− and S treatments, respectively. In the PB− treatment mixing model, the $\delta^{13}C_{switchgrass}$ value was the mean $\delta^{13}C$ value of all switchgrass samples collected from both P × SB− and S treatments and in the S treatment mixing model, the $\delta^{13}C_{pine}$ value was the mean $\delta^{13}C$ value of all pine samples collected from both PB− and P × SB− treatments.

2.5. Statistical analyses

Raw data, uncorrected for diet-tissue discrimination, were presented as mean ± 1 standard deviation (SD) in a two dimensional $\delta^{13}C$ and $\delta^{15}N$ plot for ease of interpretation and comparison with other studies. To examine $\delta^{13}C$ and $\delta^{15}N$ isotope signals before and after fall molt of white-footed mice and before and after switchgrass seeds set and became available in fall, we examined $\delta^{13}C$ and $\delta^{15}N$ values of plants by season (summer = July–September;

fall = October–November). To determine if trophic position and basal carbon source of white-footed mice was influenced by intercropping, we separately compared $\delta^{15}N$ values and $\delta^{13}C$ values of mice across treatments. We also examined effects of intercropping on invertebrate tissues that we separated by functional group (herbivorous, omnivorous and predatory invertebrates) by comparing $\delta^{15}N$ and $\delta^{13}C$ values for each functional group across treatments. To compare $\delta^{15}N$ and $\delta^{13}C$ of consumers, we used both treatment and season, and a treatment × season interaction, in our ANOVA models. We did not statistically compare our values for contribution of C_4 (switchgrass) and C_3 (pine) sources in the assimilated diet of mice and invertebrates among treatments because these analyses were redundant with our $\delta^{13}C$ isotope signal statistical analyses. Rather, we used our mixing model results to describe relative contribution of C_4 and C_3 sources in the assimilated diet of mice and invertebrates where we found a treatment effect.

Our $\delta^{13}C$ and $\delta^{15}N$ isotope data did not meet assumptions of normality and homogeneity of variances using Shapiro–Wilk and Levene's tests, respectively. Rather than use non-parametric approaches to our analyses, we conducted our analyses using one or two-factor ANOVA approaches combined with Manly's unrestricted permutation tests (number of resampling repeats = 5000) [52]. We used this approach for all post hoc pairwise comparisons. Our rejection criterion was $P \leq 0.05$. We conducted all statistical analyses using *R*[53]. All data are presented as mean ± 1 standard deviation (SD).

3. Results

We captured 160 individual white-footed mice across 6048 trap nights. We analyzed SIs of fur samples from 75 individuals (PB− = 38, P × SB− = 27, S = 10). We collected 784 individual invertebrates from PB−, 912 individual invertebrates from P × SB−, and 808 individual invertebrates from S plots, representing eight orders, 40 families and four functional groups (herbivores, omnivores, predators, and decomposers;Appendix A). From all the individual herbivorous, omnivorous, and predatory invertebrates sampled, we selected 146 individuals for stable isotope analyses. Finally, we analyzed 44 loblolly pine (n = 22 from PB− plots and n = 22 from P × SB− plots) and 34 switchgrass (n = 12 from S plots and n = 22 from P × SB− plots) samples for SIs.

Mean $\delta^{13}C$ and $\delta^{15}N$ values were as expected for C_3 loblolly pine (−29.7 ± 0.5‰ and 3.0 ± 1.8‰, respectively) and C_4 switchgrass (−13.5 ± 0.26‰ and 2.2 ± 1.35‰, respectively) [47], [54] and [55]. There was no effect of season on $\delta^{13}C$ ($F_{1,42} = 0.11$, $P = 0.75$, Manly's $P = 0.77$) or $\delta^{15}N$ values ($F_{1,42} = 1.187$,$P = 0.28$, Manly's $P = 0.29$) for pine. There was no effect of season on $\delta^{13}C$ ($F_{1,32} = 0.06$, $P = 0.80$, Manly's$P = 0.81$) or $\delta^{15}N$ values ($F_{1,32} = 4.02$, $P = 0.05$, Manly's $P = 0.05$) for switchgrass.

In general, mean $\delta^{13}C$ values of white-footed mice, predatory invertebrates, omnivorous invertebrates, and herbivorous invertebrates were intermediate to $\delta^{13}C$ values from the C_3 loblolly pine and C_4 switchgrass (Fig. 2, Table 1). In examinations of the treatment effect on $\delta^{13}C$ values of white-footed mice, predatory invertebrates, omnivorous invertebrates, and herbivorous invertebrates, we did not detect a season $\times$ treatment interaction (Table 1). There was an effect of treatment, but not season, on $\delta^{13}C$ of white-footed mice with mice from S treatment plots being more enriched than mice from PB− and P $\times$ SB− treatment plots (Table 1). The assimilated diet of white-footed mice in the S treatment consisted of 39.32 $\pm$ 5.85% C_4 (switchgrass derived) sources and 60.68 $\pm$ 5.85% C_3 (pine derived) sources compared to 34.75 $\pm$ 2.61% C_4 sources and 65.25 $\pm$ 2.61% C_3 sources and 33.91 $\pm$ 2.93% C_4 sources and 66.09 $\pm$ 2.93% C_3 sources in PB− and P $\times$ SB− treatments, respectively. There was an effect of treatment, but not season, on $\delta^{13}C$ of predatory invertebrates with samples from S treatment plots being more enriched than samples from P $\times$ SB− treatment plots which in turn were more enriched than samples from PB− treatment plots (Table 1). The assimilated diet of predatory invertebrates in the S treatment consisted of 69.93 $\pm$ 30.46% C_4sources and 30.07 $\pm$ 30.46% C_3 sources. The assimilated diet of predatory invertebrates in the P $\times$ SB− treatment consisted of 47.87 $\pm$ 20.66% C_4 sources and 52.12 $\pm$ 20.66% C_3 sources. The assimilated diet of predatory invertebrates in the PB− treatment consisted of 32.61 $\pm$ 11.37% C_4 sources and 67.39 $\pm$ 11.37% C_3 sources. There was no effect of treatment or season on $\delta^{13}C$ values of omnivorous invertebrates (Table 1). However, there was an effect of both treatment and season on $\delta^{13}C$ values of herbivorous invertebrates (Table 1) with samples from S treatment plots being more enriched than herbivorous invertebrates from PB− and P $\times$ SB− treatment plots and samples from the summer being less enriched than samples from fall (Table 1). The assimilated diet of herbivorous invertebrates in the S treatment consisted of 68.47 $\pm$ 36.04% C_4 sources and 31.53 $\pm$ 36.04% C_3 sources compared to 26.27 $\pm$ 24.28% C_4 sources and 73.73 $\pm$ 24.28% C_3 sources and 31.19 $\pm$ 27.44% C_4 sources and 68.81 $\pm$ 27.43% C_3 sources in PB− and P $\times$ SB− treatments, respectively.

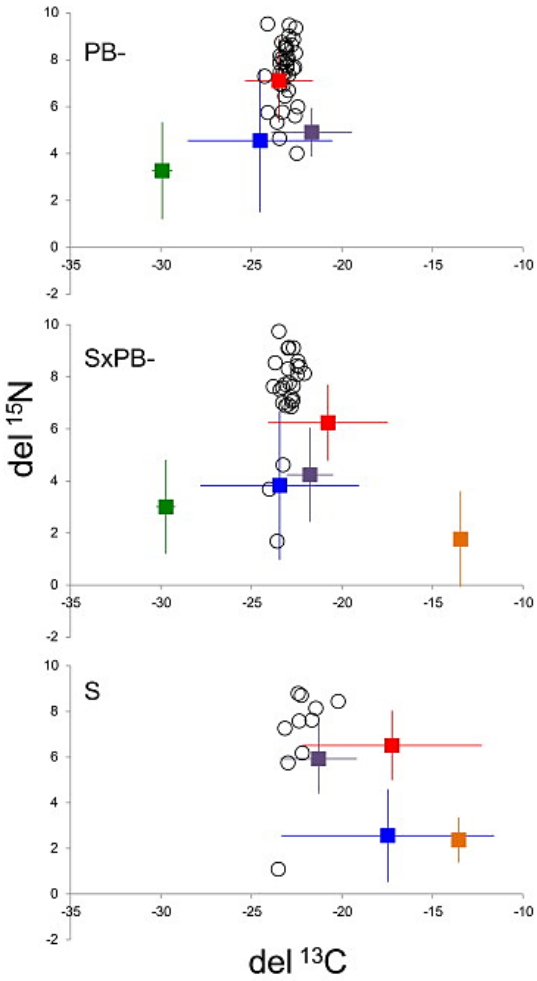

Fig. 2. Biplot of mean ± 1 SD δ ^{13}C and δ ^{15}N values of plants and consumers across treatments. Mean ± 1 SD δ ^{13}C and δ ^{15}N values [uncorrected for diet-tissue discrimination], for white-footed mice and invertebrate functional groups from each treatment from the Lenoir 1 Sustainability Study Site, Lenoir County, NC. Predatory insects (red squares). Omnivorous insects (purple squares). Herbivorous insects (blue squares). White-footed mouse (open circles) raw data are shown. Mean ± 1 SD values for loblolly pine needles (green squares) and switchgrass seed (orange squares) collected in 2010 reflect mean values within treatments where they were collected (i.e., pine value in P × SB− is a mean from samples of pine collected from this treatment only).

Table 1. Mean ± 1 SD δ ^{13}C and δ ^{15}N values [uncorrected for diet-tissue discrimination] for White-footed mice and invertebrate functional groups from each treatment [pine with residual woody debris removed (PB−), pine intercropped with switchgrass and residual woody debris removed (P × SB−), and switchgrass only (S) treatments] from the Lenoir 1 Sustainability Study Site, Lenoir County, NC. Results from standard and permutation ANOVA (*Pperm*) tests shown for season and treatment. Where there were differences among treatments, post-hoc comparison results are denoted with letters. Treatment groups with different letters are significantly different from one another.

$DEL^{13}C$							
	PB−	S × PB−	S	df	*F*	*P*	*Pperm*
Peromyscus leucopus	−23.1 ± 0.4a	−23.0 ± 0.5a	−22.2 ± 1.0b	2,69	13.19	<0.0001	0.0002
Predatory invertebrates	−23.5 ± 1.9a	−20.8 ± 3.3b	−17.2 ± 5.0c	2,40	13.24	<0.0001	0.0002
Omnivorous invertebrates	−21.7 ± 2.2	−21.8 ± 1.3	−21.3 ± 2.1	2,17	0.14	0.87	0.8600
Herbivorous invertebrates	−24.5 ± 4.0a	−23.4 ± 4.4a	−17.5 ± 5.9b	2,69	12.52	<0.0001	0.0002
	Fall	Summer					
Peromyscus leucopus	−22.9 ± 0.4	−23.0 ± 0.8		1,69	0.47	0.49	0.51
Predatory invertebrates	−20.9 ± 3.9	−21.0 ± 4.2		1,40	0.01	0.94	0.94
Omnivorous invertebrates	−21.5 ± 1.7	−22.1 ± 1.5		1,17	0.29	0.60	0.59
Herbivorous invertebrates	−20.7 ± 5.6	−23.7 ± 4.8		1,69	7.55	0.008	0.01
Peromyscus leucopus			Interaction	2,69	2.92	0.06	0.06
Predatory invertebrates			Interaction	2,40	0.01	0.94	0.94
Omnivorous invertebrates			Interaction	2,17	1.79	0.19	0.19
Herbivorous invertebrates			Interaction	2,69	1.43	0.25	0.25
$DEL^{15}N$							
	PB−	S × PB−	S	df	*F*	*P*	*Pperm*
Peromyscus leucopus	7.5 ± 1.3	7.4 ± 1.7	7.0 ± 2.3	2,69	0.18	0.84	0.85
Predatory invertebrates	7.1 ± 1.8	6.2 ± 1.5	6.5 ± 1.5	2,40	0.98	0.38	0.38
Omnivorous invertebrates	4.9 ± 1.0	4.2 ± 1.8	5.9 ± 1.5	2,17	2.09	0.15	0.16
Herbivorous invertebrates	4.6 ± 3.0	3.8 ± 2.9	2.6 ± 2.0	2,69	2.30	0.11	0.11
	Fall	Summer					
Peromyscus leucopus	7.9 ± 1.0	6.9 ± 2.0		1,69	7.02	0.01	0.01
Predatory invertebrates	6.9 ± 1.7	6.3 ± 1.5		1,40	1.42	0.24	0.24
Omnivorous invertebrates	5.0 ± 1.4	3.8 ± 2.8		1,17	2.09	0.17	0.17
Herbivorous invertebrates	3.2 ± 2.3	4.2 ± 3.1		1,69	2.34	0.13	0.13
Peromyscus leucopus			Interaction	2,69	0.18	0.83	0.83

Predatory invertebrates			Interaction	2,40	1.50	0.24	0.24
Omnivorous invertebrates			Interaction	2,17	3.11	0.96	0.11
Herbivorous invertebrates			Interaction	2,69	2.14	0.13	0.12

In all treatments, $\delta^{15}N$ values of white-footed mice were relatively high, compared to other consumers (Fig. 2, Table 1). We did not detect a season × treatment interaction for $\delta^{15}N$ values of white-footed mice, predatory invertebrates, omnivorous invertebrates, and herbivorous invertebrates, (Table 1). There was an effect of season, but not treatment, on $\delta^{15}N$ of white-footed mice with samples from the fall being more enriched than samples from the summer (Table 1). There was no treatment or season effect on $\delta^{15}N$ values for predatory, omnivorous, or herbivorous invertebrates (Table 1).

4. Discussion

Changes in structure and composition of the plant community can affect habitat use, dietary carbon sources, and trophic positions of animals, and these changes can be evaluated with carbon and nitrogen stable isotope analysis [56], [57] and [58]. Ours is the first study to examine ecological effects of switchgrass production in pine plantations using $\delta^{13}C$ and $\delta^{15}N$ values of white-footed mice, a common and important native rodent. Mice in the intercropped treatment functioned similarly to mice in pine only treatment as $\delta^{13}C$ and $\delta^{15}N$ mice in PB− and P × SB − were similar. Thus, the potential new biofuels management regime of intercropping pine with switchgrass did not affect the functional role of white-footed mice and intercropping pine with switchgrass may be ecologically sustainable from the stand point of maintaining functional roles of generalist omnivores.

4.1. Carbon source

Carbon isotope values of mice were similar between intercropped pine and control pine management plots indicating that white-footed mice did not incorporate large amounts of planted C_4 switchgrass into its' diet in this biofuels production treatment. Only when switchgrass was planted as a monoculture (>90% switchgrass cover) was carbon isotope enrichment of mice significantly greater than both pine treatments (PB−, P × SB−). Mixing model results show an approximate 5% difference between assimilated carbon sources for mice in switchgrass monoculture (S plots) compared to mice in plots with pine (PB− and P × SB− plots). Importantly, assimilated carbon sources for mice were similar in PB− and P × SB− plots indicating that intercropping switchgrass with pine did not influence assimilated carbon source.

Patterns of carbon isotope values of mice across treatments were similar to those of herbivorous and omnivorous invertebrates, supporting the conclusion that intercropping switchgrass with

pine did not influence the assimilated carbon source for consumers. The $\delta^{13}C$ values of herbivorous and omnivorous invertebrates did not differ between intercropped and control treatments indicating that their assimilated carbon source was also unaffected by the intercropped production regime. The $\delta^{13}C$ values of predatory invertebrates did differ among all treatments with the intercropped treatment (P × SB−) being intermediate between pine (PB−) and switchgrass monoculture (S) suggesting that particular components of prey selection, capture, and ingestion by predatory invertebrates (which include spiders) may play a role in which carbon source is assimilated in P × SB−. For example, spiders may be more likely to capture insects that fed on switchgrass in S treatment plots than either white-footed mice or omnivorous insects.

Regardless of treatment differences, across all plots, the $\delta^{13}C$ values were greater than expected if mice only consumed C_3 plants and this intermediate signal may be explained in part by the vegetative community. Sampling of vegetation structure and cover indicated that grasses, including planted switchgrass, some native *Panicum*, and other grasses comprised significant amount of cover across all treatments in October 2010 (means PB− = 64.83 ± 4.14%, P × SB − = 75.17 ± 2.73%, S = 95.58 ± 1.57%; [37]. Therefore, all plots supported a combination of native C_3 and C_4 plants in addition to the planted switchgrass in S and P × SB treatment plots. This vegetation composition may have contributed to the intermediate $\delta^{13}C$ signal in mice. Given that SI values in mice across all treatments were more enriched than expected (i.e., more enriched than basal source of C_3 pine), mice likely subsidized their diets with a variety of C_4 and C_3 resources, including invertebrates that fed on both C_4 and C_3 plants.

4.2. Trophic responses

Our comparison of mean $\delta^{15}N$ values of white-footed mice to invertebrate consumers suggests that omnivorous mice were predators that consumed a variety of resources, which was expected [33], [34],[35] and [36]. Within each treatment, white-footed mice and predatory invertebrates had similar $\delta^{15}N$ values. Although these results might indicate P × SB− mice were more predatory than generalist-omnivorous, we concluded that these mice are also maintaining omnivory, as their $\delta^{15}N$ also overlapped with omnivorous invertebrates in each treatment. Thus, it is likely that both plants and lower-level invertebrate consumers influenced isotopic signatures of white-footed mice. These results agree with those of Shaner et al. [35], who reported that white-footed mice preferred habitat patches with a mixture of foods (seeds and mealworms) in contrast to patches with fewer options (seeds only or mealworms only).

We predicted that $\delta^{15}N$ values of mice and invertebrates would reflect a trophic shift downward in presence of switchgrass. Instead, we found that $\delta^{15}N$ values of mice did not differ across treatments, indicating that trophic position of mice was unaffected by biofuels production regimes. In addition, $\delta^{15}N$ values of functional groups of invertebrates did not differ among

treatments, indicating that their trophic positions were also unaffected by either intercropping or a monoculture of switchgrass.

4.3. Important considerations and caveats

There are several possible explanations why mice in intercropped plots (P × SB−) did not have a C_4 signal or trophic shift when compared to pine only plots or why a stronger C_4 signal or trophic shift was not detected in white-footed mouse tissue from monocropped switchgrass (S). First, white-footed mice may have consumed fewer switchgrass seeds than expected because seeds were too small for efficient feeding. Theoretically, consumers maximize energy gained/unit of handling time for a prey item [59] and [60] and *Peromyscus* spp. prefer large seeds [61] and [62] and energy rich foods [63] and [64]. Thus, given the relatively small mass (~0.57 mg) [65] or potentially low energy content of switchgrass seeds [66] and [67], it may have been more profitable for white-footed mice to consume other available resources. Second, because our treatment plots were not enclosed, it is possible that mice, even though we only included those captured on a single plot, traveled to different treatments and were subsidized by food resources in other treatments, thereby making SI values intermediate.

There are two caveats to our study. First, the weak response to switchgrass by white-footed mice may be related to timing of the experiment. Our study took place during the first two years following treatment implementation (i.e., site preparation, switchgrass planting, etc.). Although switchgrass was well-established in fall 2009, it was a novel resource and white-footed mice may not have learned of its availability. In mammals, food finding may occur by trial and error, but more often it is the result of social learning from parents [68]. Novelty of switchgrass probably cannot explain the white-footed mouse's weak response to switchgrass because 1) we found no seasonal differences in $\delta^{13}C$ values for white-footed mice which we would expect if they only learned to eat switchgrass seeds in fall 2010, and 2) we found the opposite seasonal response in trophic position than would be expected if this were the case. Our only seasonal difference in $\delta^{15}N$ was for white-footed mice and suggested that summer mice fed at a lower trophic level than fall mice and, if switchgrass seeds were only discovered in fall 2010, the $\delta^{15}N$ value should have been less in 2010. However, revisiting this research question several years later could provide more insight on influence of novelty in the white-footed mouse's response presented herein. Second, the scale of this study was small. Trapping grids measured approximately 1800 m^2, which is smaller than documented home ranges of some male white-footed mice [34] and [69], but was greater than the mean home range size in this study (837.9 ± 245.2 m^2) (K. Lucia, unpublished data). Despite our efforts, it is possible that even though we only used mice captured on a single plot, the mice may have foraged on other plots. Therefore, replicating this study on a larger spatial scale would ensure that mice captured on one treatment plot only consume resources in that treatment plot.

5. Conclusion

This field experiment was one of the first to address potential ecological effects of intercropping biofuels in a pine plantation. Our results show that intercropping switchgrass in pine plantations did not impact food web interactions associated with white-footed mice. However, future work assessing other key forest consumers and food web interactions in the context of biofuels intercropping is critical to understanding ecological effects of producing biofuels in intensively managed pine forests.

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