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Rye–Vetch Mixture Proportion Tradeoffs: Cover Crop Productivity, Nitrogen Accumulation, and Weed Suppression

Zachary D. Hayden,* Mathieu Ngouajio, and Daniel C. Brainard

ABSTRACT

Cereal–legume cover crop mixtures have the potential to combine the unique strengths of the component species while taking advantage of interspecific synergies. However, the relative proportion of each species in the mixture is likely to influence species interactions and entail important tradeoffs in cover crop performance. The objective of this study was to evaluate how the relative proportions of cereal rye (*Secale cereale* L.) and hairy vetch (*Vicia villosa* Roth) sown in mixtures influenced cover crop biomass production, winter annual weed suppression, vetch winter survival, and vetch N_2 fixation as measured by the ^{15}N natural abundance method. Following a replacement series design, treatments consisted of a gradient of seven rye–vetch mixture proportions ranging from 100% vetch to 100% rye. Density and biomass composition in the mixtures were highly correlated with rye and vetch seeding rates, with little evidence of substantial interspecific interference. Total shoot biomass in all mixtures was equal to or greater than that of either monoculture, but no differences were detected in vetch winter survival or the efficiency of N_2 fixation. Changing the proportions of rye and vetch in the mixtures resulted in tradeoffs related to N and weed management goals. Increasing vetch in mixtures led to greater fixed N accumulation but also increased seed costs and reduced winter annual weed suppression. A greater understanding of how rye–vetch mixture proportions influence cover crop performance can support more-informed decision-making regarding cover crop selection and mixture seeding rates.

The grass–legume association has long been of interest to researchers working in both natural and managed ecosystems. Mixtures of plants with complementary functional traits can benefit from more efficient capture of light, water, and nutrients compared with monocultures, and when interspecific interference is low, grass–legume mixtures can also benefit from potential facilitative interactions (Vandermeer, 1992). In particular, reductions in soil inorganic N by the grass can increase legume nodulation and N_2 fixation (Izaurralde et al., 1992; Streeter, 1988), while the presence of the legume can correspondingly increase N availability to the grass through biomass turnover or possible direct N transfer (Eaglesham et al., 1981; Ledgard and Steele, 1992; van Kessel et al., 1985). Light interception by vining legumes can also be enhanced by the opportunity to climb into the upright canopy of a companion grass or cereal (Keating and Carberry, 1993). By reducing frost heaving or buffering temperature extremes at the soil surface through reduced air movement or increased snow cover retention, the presence of a hardier grass species may also improve legume winter survival in northern climates (Jannink et al., 1997; Smith, 1975).

Cereal rye and the legume hairy vetch are widely studied as winter annual cover crop species, in part because their cold hardiness makes them suitable for production across a broad geographic range, including the northern United States (Clark, 2007). Rye is a rapid-growing, N-responsive grass that has demonstrated substantial capacity to provide erosion control, conservation of residual soil N, and weed suppression—both as a living cover crop and as a thick surface mulch in reduced tillage or no-till production systems (Clark, 2007; Ditsch et al., 1993; Peachey et al., 2004). These strengths, in addition to inexpensive and widely available seed, have made rye one of the most commonly grown cover crops in the United States. However, while rye residues can build soil organic matter, they are not a significant source of available N for subsequent cash crops, and depending on the stage at which rye is terminated, residue incorporation can result in net N immobilization (Sainju et al., 2000; Clark et al., 2007a). In contrast, hairy vetch is a legume known for its ability to accumulate considerable amounts of N (up to 190 kg ha^{-1}, even in northern temperate climates), much of which is rapidly available to cash crops in the first season after termination (Ranells and Wagger, 1996; Teasdale et al., 2004). However, vetch seed is relatively expensive, and its slower growth and readily decomposable residues generally make it less effective than rye at soil conservation and weed suppression both before

Dep. of Horticulture, Michigan State Univ., Plant and Soil Sciences Building, 1066 Bogue St., East Lansing, MI 48824. Received 29 Sept. 2013. *Corresponding author (haydenza@msu.edu).

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Abbreviations: CNF, cost of nitrogen fixed; GDD, growing degree days; LER, land equivalent ratio; %Ndfa, percentage of nitrogen derived from the atmosphere; PAR, photosynthetically active radiation; SNF, shoot nitrogen fixed.

and after termination (Mohler and Teasdale, 1993; McCracken et al., 1994; Mennan et al., 2009). Vetch can also become a problematic weed in winter annual and perennial cropping systems due to hard seed (Aarssen et al., 1986) and in reduced tillage systems as a result of incomplete kill and regrowth (Creamer and Dabney, 2002; Mischler et al., 2010).

Rye–vetch mixtures are often proposed as a way to combine the strengths of the two species while moderating their individual weaknesses, in addition to taking advantage of potential synergies that arise from the grass–legume association. In practice, the characteristics of cereal–legume cover crop mixtures tend to reflect the relative proportions of each species present, with the qualities of a given species becoming more prominent with a greater proportion in the mixture. Accordingly, many studies have found that qualities such as weed suppression, total dry matter production, and N availability in cereal–legume mixtures tend to be intermediate to the corresponding monocultures (e.g., Ranells and Wagger, 1997; Akemo et al., 2000b; Hauggaard-Nielsen et al., 2003; Clark et al., 2007b; Benincasa et al., 2010; Dordas and Lithourgidis, 2011). Studies have also demonstrated, however, that mixtures of vetch with a cereal can accumulate more total dry matter and N than either species in monoculture (Clark et al., 1994; Sainju et al., 2005), exhibit more efficient N accumulation by the components (Tosti et al., 2010), mineralize N at rates approaching that of a vetch monoculture (Ranells and Wagger, 1996), and provide weed suppression equivalent to that of a cereal monoculture (Teasdale and Abdul-Baki, 1998; Hayden et al., 2012). In addition, because legumes are generally sown at reduced rates in mixtures, the overall seed costs for cereal–legume mixtures tend to be lower than for monoculture legumes.

The performance of cereal–legume cover crop mixtures relative to monocultures depends heavily on both environmental conditions and management decisions that influence the competitive balance between species and final stand characteristics. Cereals, with their extensive root systems and higher relative growth rates, tend to be stronger competitors for belowground resources than legumes (Mariotti et al., 2009). Therefore, when resources other than N, including moisture, are limiting, cereals are likely to suppress legumes in mixtures (Ofori and Stern, 1987). However, N limitation often shifts the competitive balance to benefit legumes in mixtures, while high N fertility generally favors non-legumes (Jensen, 1996), including rye in rye–vetch mixtures (Shipley et al., 1992; Clark et al., 2007a). In addition, rye can germinate and grow at cooler temperatures than vetch (Nuttonson, 1958; Teasdale et al., 2004), which contributes to its ability to establish later in the fall and accumulate biomass faster in the spring (Shipley et al., 1992). As a result, colder weather, later planting dates, and earlier cover crop termination are all likely to shift the balance toward rye over vetch in mixtures.

Considering the importance of relative stand composition in influencing the properties of cereal–legume mixtures, seeding rates are a logical tool for managing mixture performance. The fundamental importance of component species density is recognized and often thoroughly investigated in studies of plant competition (Firbank and Watkinson, 1985) and agronomic intercropping (Willey, 1979b). However, few experiments have systematically evaluated the influence of sown species proportions on the characteristics of cover crop mixtures (Akemo et al., 2000b; Karpenstein-Machan and Stuelpnagel, 2000; Tosti et al., 2010), and most draw conclusions from only a single mixture, often where the species are sown at 50% of their recommended monoculture seeding rates. When multiple seeding rates of cereal–legume cover crops have been evaluated side by side, the differences in stand characteristics among the mixtures are often enough to significantly influence the provision of agroecosystem services by the cover crops, such as weed suppression, soil N fertility, and effects on subsequent crop yields (Clark et al., 1994; Akemo et al., 2000a, 2000b; Tosti et al., 2012).

Replacement series experiments, in which treatments consist of a monoculture of each species and a gradient of species mixtures, provide one approach for investigating species proportions in cover crop mixtures (Jolliffe, 2000). Replacement series are widely used in the study of plant competition and are commonly applied within agricultural contexts to evaluate crop–weed interactions and intercrop productivity. While total plant density is held constant in a traditional replacement series, a replacement series is *proportional* when the relevant monoculture seeding rates differ for the component species and total density therefore varies across the mixtures. The limitations to inference from such designs have been thoroughly reviewed (Snaydon, 1991; Jolliffe, 2000), but overinterpretation remains common in the literature. In particular, the densities of component species are confounded with each other and with total plant density in proportional designs. Therefore, without data on density-dependent yield responses for each species (Firbank and Watkinson, 1985), the design is not suited for drawing definitive conclusions regarding relative competitive abilities or the causal mechanisms contributing to species performance in mixtures. Despite these caveats, proportional replacement series are still effective in providing applied insights that can inform improvements in cover crop mixture management.

A greater understanding of how species proportions influence mixture stands is an important step toward maximizing the potential benefits from rye–vetch cover crop mixtures to better serve specific goals within cropping systems. Therefore, the objective of this study was to evaluate how the relative proportions of rye and vetch sown in a winter annual cover crop mixture influenced cover crop stand characteristics and performance with respect to establishment, biomass productivity, winter annual weed suppression, N accumulation, N_2 fixation, and costs relative to rye and vetch monocultures.

MATERIALS AND METHODS

Site Description

The study was conducted at the Michigan State University Horticulture Teaching and Research Center in Holt, MI (42°40′ N, 84°28′ W) during the course of two seasons, alternating between adjacent fields. Both fields were on level terrain and had a Spinks loamy sand soil (a sandy, mixed, mesic Lamellic Hapludalf). In each field, a summer cover crop of sorghum-sudangrass (*Sorghum bicolor* × *S. bicolor* var. *sudanense*) was flail mowed and incorporated using a rototiller at least 2 wk before sowing of winter cover crops in the fall. Initial

Table 1. Rye (R) and vetch (V) seeding rates and estimated seed costs across cover crop mixture proportions.

Cover crop treatment	Seeding rate		Cost of seed†		
	Vetch	Rye	Vetch	Rye	Total
	—— kg ha^{-1} ——		——— US\$ ha^{-1} ———		
100 V:0 R	42	0	176	0	176
83 V:17 R	35	16	146	6	152
67 V:33 R	28	31	118	12	130
50 V:50 R	21	47	88	18	106
33 V:67 R	14	63	58	25	83
17 V:83 R	7	78	30	30	60
0 V:100 R	0	94	0	37	37

† Seed costs were calculated using average prices paid for conventional vetch and rye seed at the time of this experiment (US\$4.19 and US\$0.39 kg^{-1}, respectively). Average prices paid for the organic seed sown in the experiment were US\$4.63 and US\$0.48 kg^{-1} for vetch and rye, respectively. Actual seed costs will vary with time, seed source, and whether conventional or organic seed is used.

Table 2. Dates of key field activities and data collection.

Activity	2009–2010	2010–2011
Cover crop seeding	1 Sept.	1 Sept.
Cover crop fall density sampling	19–21 Oct.	27–29 Sept.
PAR† light penetration readings	6 May	11 May
Spring cover crop and weed biomass and density sampling	10 May	14 May

† Photosynthetically active radiation.

soil chemical characteristics for the fields in 2009 and 2010 were similar and included on average pH of 6.6, cation exchange capacity of 7.1 cmol kg^{-1}, and P (Bray P1 extract), K, and Mg levels of 133, 145, and 47 mg kg^{-1}, respectively. The fields were managed according to National Organic Program guidelines (Agricultural Marketing Service, 2013) and had been in organic transition with a cropping history of warm-season vegetables under conventional tillage since 2008. No fertilizers or soil amendments were applied in either year of this study.

Treatment and Experimental Design

Following a proportional replacement series design (Snaydon, 1991; Jolliffe, 2000), winter cover crop treatments included rye and vetch sown in monocultures at rates of 94 and 42 kg ha^{-1}, respectively, and a gradient of species mixtures containing the following sown proportions of rye/vetch relative to their monoculture seeding rates: 83:17, 67:33, 50:50, 33:67, and 17:83. Rye and vetch seeding rates and seed cost estimates for the cover crop treatments are listed in Table 1. A no-cover-crop control was also included for comparison. Experimental plots were 6.7 by 8.5 m in 2009–2010 and 6.1 by 7.6 m in 2010–2011, arranged in a randomized complete block design with four replications.

Field Management and Data Collection

The dates of key field activities and data collection are summarized in Table 2. Rye and vetch cover crops were broadcast sown by hand, using a grid system that divided plots into quarters to help ensure uniformity, and then incorporated to a depth of about 5 cm using a field cultivator (Perfecta II, Unverferth Manufacturing Co.). Variety not stated (VNS) vetch seed grown in Oregon and VNS rye seed grown in Minnesota were used in both years (Albert Lea Seed House). Vetch seed was inoculated with N-DURE *Rhizobium leguminosarum* inoculant (INTX Microbials) at a rate of approximately 10 g inoculant kg^{-1} seed.

Rye and vetch plant densities were assessed in the fall from four 25- by 50-cm (0.125 m^{-2}) quadrats established in each plot. Spring cover crop densities, shoot biomass, and total weed biomass were sampled later from the same quadrats shortly before mowing and incorporation. At the time of spring sampling in both years, vetch was prebloom and rye was between ear emergence and anthesis. Potential differences in vetch winter survival across treatments were evaluated by calculating the percentage change in vetch population density between fall and spring sampling dates.

Shortly before sampling the cover crop biomass in the spring, photosynthetically active radiation (PAR) was measured both above the canopy and at the soil surface at four locations in each plot at least 1 m from a plot edge. Measurements were taken midday under clear skies with a 70-cm-long quantum flux sensor (MQ-301, Apogee Instruments) and used to calculate the percentage of PAR penetrating the cover crop canopies.

Rye, vetch, and total weed biomass samples were dried to a constant weight at 38°C before taking dry weights. Cover crop dry weights per plant were calculated using rye and vetch spring densities. Cover crop shoot biomass samples were then ground to pass through a 1-mm screen, and subsamples were submitted to Midwest Laboratories (Omaha, NE) for analysis of total C and N concentrations using a Leco TruSpec elemental analyzer (Leco Corp.). Subsamples were also submitted to the University of California–Davis Stable Isotope Facility for analysis of δ^{15}N using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 continuous flow isotope ratio mass spectrometer (Sercon Ltd.).

Corrections for Soil Contamination on Vetch Shoots

Near-saturated soil moisture conditions at the time of cover crop sampling in 2011 resulted in considerable amounts of soil adhering to vetch shoots that could not be completely removed from the samples before drying and analysis. Therefore, vetch dry weight and N concentration data were corrected for the presence of soil contamination following equations by Hunt et al. (1999). Briefly, the fraction by weight of vetch tissue (F_v) in a contaminated sample (vetch tissue plus contaminating soil) was estimated using

$$F_v = \frac{A_0 - A_s}{A_0 - A_v} \quad [1]$$

where A_s is the ash fraction of the contaminated sample, A_v is the ash fraction of uncontaminated vetch tissue, and A_0 is the ash fraction of the contaminating soil. The ash fraction of uncontaminated vetch tissue (A_v) was estimated as 0.2, based on vetch samples taken from 2010 and 2011 that were not visually contaminated with soil and did not exhibit outlier δ^{15}N values. The ash fraction of the contaminating soil (A_0) was estimated from soil sampled shortly before cover crop sampling in 2011 and sieved to remove large particles that were less likely to have adhered to vetch tissue. Ash fractions were determined for the soil and for all vetch tissue samples using a muffle furnace (2-h drying period at 105°C, followed by 4 h at 500°C).

The corrected vetch tissue dry weight (M_v) was then derived from the dry weight of the contaminated sample (M_s) using

$$M_v = M_s F_v \qquad [2]$$

Finally, the concentration of N in the vetch tissue (N_v) was estimated from the sample N concentration (N_s) and the concentration of N in the contaminating soil (N_0) as

$$N_v = \frac{N_s - N_0\left(1 - F_v\right)}{F_v} \qquad [3]$$

For consistency, the correction was applied to vetch samples from both years of the study; however, it did not significantly affect the 2010 data due to the lack of soil contamination in that year. No correction was necessary for rye data in either year because the upright nature of the shoots minimized the risk of soil contamination during sampling.

Land Equivalent Ratios

Partial and total land equivalent ratios (LERs) were calculated for each mixture on the basis of rye and vetch dry weights (de Wit and Van Den Bergh, 1965; Willey, 1979a). Partial LERs (relative yields) for rye (L_r) and vetch (L_v) were calculated as the ratio of the dry weight of each species in a mixture to its dry weight in monoculture. The total LER for mixtures was then calculated as the sum of the partial LERs. Relative yields greater than relative sown proportions indicate greater biomass productivity in mixtures per unit rye or vetch seed sown, while total LER > 1.0 demonstrates greater overall biomass productivity (dry weight per seed sown) for the mixture relative to the monocultures.

Vetch Nitrogen Fixation Estimates

Vetch N_2 fixation was estimated using the ^{15}N natural abundance method, which relies on the slight enrichment of ^{15}N generally present in soil N relative to atmospheric N_2 (Shearer and Kohl, 1986). Because biological N_2 fixation exhibits little isotopic fractionation, legumes tend to have a lower proportion of ^{15}N in their tissues than plants that derive their N entirely from the soil (Hogberg, 1997). Isotopic composition is expressed relative to atmospheric N_2 using δ^{15}N values in parts per thousand (‰), with higher δ^{15}N indicating greater ^{15}N enrichment.

The percentage of vetch N derived from the atmosphere (%Ndfa) was calculated as (Rochester and Peoples, 2005)

$$\%\text{Ndfa} = \frac{\delta^{15}\text{N}_{\text{ref}} - \delta^{15}\text{N}_{\text{leg}}}{\delta^{15}\text{N}_{\text{ref}} - B} \times 100 \qquad [4]$$

where $\delta^{15}\text{N}_{\text{ref}}$ is the shoot δ^{15}N value for rye in monoculture (used as the non-N_2–fixing reference plant), $\delta^{15}\text{N}_{\text{leg}}$ is the shoot δ^{15}N value for vetch, and B is the estimated δ^{15}N of vetch when grown entirely dependent on atmospheric sources of N. Following Møller Hansen et al. (2002) and Hansen and Vinther (2001), the lowest $\delta^{15}\text{N}_{\text{leg}}$ value in each study year was used to approximate B, resulting in conservative estimates of vetch %Ndfa. Rye monoculture $\delta^{15}\text{N}_{\text{ref}}$ values were 2.52 and 1.49‰ in 2010 and 2011, respectively.

Vetch shoots contaminated with soil (ash content >0.2) in 2011 exhibited unreasonably high δ^{15}N values (1.10–5.58‰) that could not be explained by contributions from soil ^{15}N alone. We speculate that microbial N transformations (such as denitrification) may have occurred preferentially on contaminated vetch shoots before sampling in the field or during sample processing before drying, potentially resulting in significant isotope fractionation (Mariotti et al., 1981; Shearer and Kohl, 1986). Therefore, contaminated vetch tissue was excluded from the analysis. As a result, the 2011 mean %Ndfa estimates are reported only for the three cover crop treatments where at least three field replicates of uncontaminated vetch tissue (ash content <0.2) were available.

The amount of vetch shoot N derived from N_2 fixation (SNF, in kg ha^{-1}) was estimated using the following formulas:

$$\text{Shoot N} = \left(\text{shoot dry weight}\right) N_v \qquad [5]$$

$$\text{SNF} = \left(\text{shoot N}\right)\%\text{Ndfa} \qquad [6]$$

where N_v is the contamination-corrected concentration of N in the vetch shoots. Estimates of SNF for 2011 were calculated assuming a consistent %Ndfa across the cover crop treatments equal to the average %Ndfa obtained from the uncontaminated samples in that year.

Cost of Nitrogen Fixed

To estimate the relative costs incurred by growers for the additional fixed N contributed to the system by vetch, the cost of N fixed (CNF) was estimated for each vetch-containing cover crop treatment following Brainard et al. (2012), using

$$\text{CNF} = \frac{P_v Q_v + P_r Q_r - 94 P_r}{\text{SNF}} \qquad [7]$$

where P_v and P_r are the prices (US\$ kg^{-1}) of conventional vetch and rye seed, respectively; Q_v and Q_r are the seeding rates (kg ha^{-1}) of vetch and rye, respectively; and SNF is the vetch shoot N fixed (kg ha^{-1}) estimated from Eq. [6]. The CNF is an estimate of the price paid for the N fixed by vetch as influenced by legume performance and cover crop seed costs. The calculation controls for costs associated with cover crop establishment by assuming that it applies to growers who already seed rye at 94 kg ha^{-1} and therefore just have to substitute legume seed in their planting equipment. Because rye is a common cover crop in many agronomic and vegetable cropping systems, CNF provides a reasonable estimate of both the additional costs a grower may incur to gain fixed N from vetch in their system and the relative effects of a rye–vetch mixture proportion on the estimated price of additional fixed N. Because some fixed N also accumulates in root tissue, calculations of CNF based on Eq. [7] probably overestimate the cost of total fixed N in the vetch biomass.

Statistical Analysis

The fixed effects of year, cover crop mixture proportion, and their interaction were analyzed using mixed model ANOVA with the MIXED procedure of SAS (Version 9.2, SAS Institute). Block (replication) was included as a random factor in all models. Assumptions of normality and equality of variances were evaluated, and unequal variance models were used when necessary. Unless otherwise noted, effects were judged significant when $P < 0.05$. Where the effect of cover crop mixture proportion was significant, the nature of the response in each year was investigated using linear or polynomial regression with the REG procedure of SAS. In the case of PAR, the effects of year and the interaction between year and cover crop were not significant, so the data were pooled across years and fitted with a single regression equation. The significance and nature of the relationship between rye shoot N concentration and cover crop mixture proportion were evaluated in the context of an analysis of covariance using the MIXED procedure of SAS because the response was linear and had a common slope in both years. Individual partial and total LER estimates for cover crop mixtures were compared with their respective critical values using *t*-tests. Finally, due to missing data in 2011, vetch %Ndfa data were analyzed separately by year.

RESULTS AND DISCUSSION

Weather Conditions

Table 3 presents the total growing degree days (GDD) base 4°C accumulation and rainfall at the experiment station during the periods of cover crop growth. Heat accumulation and total rainfall were similar in the fall of both study years, but the spring of 2011 saw 113 fewer GDD and 125 more millimeters of rainfall than spring 2010. Previous research has demonstrated a good correlation between GDD base 4°C accumulation and winter cover crop biomass in the spring (Teasdale et al., 2004). While wetter soil conditions in 2011 contributed to difficulties with vetch biomass sampling that season (see above), rainfall was sufficient in both years to make a water deficit during cover crop growth unlikely, suggesting that compared with heat accumulation, soil moisture was probably a minor contributor to variability in cover crop growth across study years.

Table 3. Monthly growing degree days (GDD) and rainfall totals in Holt, MI, during cover crop growth, 2009–2011.

Month	GDD† 2009–2010	GDD† 2010–2011	Rainfall 2009–2010	Rainfall 2010–2011
			mm	mm
September‡	393	364	24	92
October	173	228	92	34
November	99	81	24	50
March	81	28	16	66
April	233	125	74	135
May§	91	139	52	65
Sept–Nov.‡	665	673	141	176
Mar.–May§	405	292	141	266

† Calculated using base 4°C (Baskerville and Emin, 1969).

‡ Cumulative GDD beginning at cover crop seeding (see Table 2). Data for December–February not presented due to negligible GDD accumulation and unreliability of measurements of frozen precipitation.

§ Cumulative GDD ending at cover crop biomass sampling (Table 2).

Cover Crop Density and Vetch Winter Survival

Rye and vetch spring population densities across treatments were similar in the 2 yr of the study, with rye and vetch monocultures averaging 146 and 271 plants m^{-2}, respectively (Fig. 1). The densities of both species in a mixture were highly correlated with their relative sown proportions, and the relationships were predominantly linear. This suggests that interspecific interactions had little effect on the germination and establishment of rye and vetch under the conditions of our field study and that seeding rates can be good predictors of final population composition in rye–vetch mixtures.

The influence of mixture proportions on vetch winter survival, in particular, was investigated by observing the change in the vetch population density between counts taken in the fall and spring from the same quadrats. There were no significant differences in vetch population change among the treatments in either year (Table 4); however, contrary to expectation, in most cases our estimates of vetch density

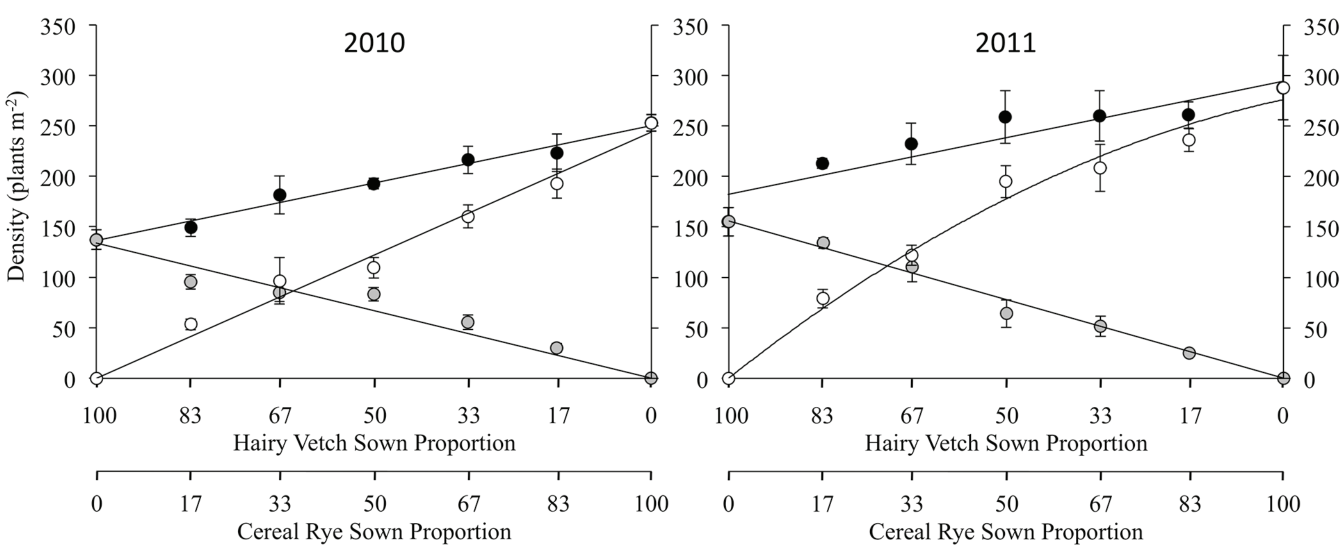

Fig. 1. Spring density of vetch (gray), rye (white), and vetch + rye (black) across cover crop mixture proportions in 2010 and 2011 (means ± SE). The 2010 responses of vetch: $y = 1.34x$, $r^2 = 0.81$, $P < 0.001$; rye: $y = 2.44x$, $r^2 = 0.87$, $P < 0.001$; and vetch + rye: $y = 1.14x + 136.23$, $r^2 = 0.73$, $P < 0.001$. The 2011 responses of vetch: $y = 1.56x$, $r^2 = 0.84$, $P < 0.001$; rye: $y = 0.006x^2 + 0.46x$, $r^2 = 0.80$, $P < 0.001$; and vetch + rye: $y = 1.12x + 182.26$, $r^2 = 0.47$, $P < 0.001$.

Table 4. Vetch apparent overwinter survival (population change) across rye (R)–vetch (V) cover crop mixture proportions.

Cover crop treatment	Overwinter survival† 2010	Overwinter survival† 2011
	%	%
100 V:0 R	137	94
83 V:17 R	119	98
67 V:33 R	127	106
50 V:50 R	157	105
33 V:67 R	123	91
17 V:83 R	126	95
F‡	ns§	ns

† In most cases, our estimates of vetch density actually increased between the fall and spring, resulting in apparent overwinter survival estimates greater than 100%.

‡ Significance of fixed effect of cover crop mixture proportion within years.

§ ns, not significant at the 0.05 probability level.

actually increased between the fall and spring, resulting in apparent overwinter survival estimates >100%.

This has been observed in previous studies (Brainard et al., 2012) and may in part be attributed to delayed germination from vetch hard seed (Aarssen et al., 1986). In addition, individual vetch plants are increasingly difficult to distinguish from each other in situ as the shoots sprawl and intertwine. Therefore, we speculate that the in situ counts taken in the fall may have underestimated the vetch density compared with the spring counts, in which quadrats were destructively sampled and individual plants could more easily be identified by their roots. Later fall sampling (and more advanced vetch growth) in 2009 (Table 3) may also have contributed to greater undercounting that year, suggesting that the larger population change estimates in 2009 relative to 2010 ($p = 0.006$) could be an artifact.

Assuming that delayed vetch germination and potential sampling biases were consistent across treatments, we found no evidence that vetch winter survival was improved by mixing with rye. In contrast, Jannink et al. (1997) found that the presence of rye reduced overwinter mortality of vetch at two locations in Maine, and Brainard et al. (2012) observed a similar response in 1 out of 2 yr in Michigan. While increased legume winter survival is an often-stated benefit of cereal–legume cover crop mixtures, its significance will probably vary depending on both winter weather conditions and the establishment (and hardiness) of the legume. The presence of rye may have a greater influence on vetch winter survival, for example, when the vetch is seeded late in the fall or when winter temperatures are particularly harsh.

Cover Crop Biomass Production and Land Equivalent Ratios

Vetch shoot biomass in monoculture was 551 and 305 g m^{-2} in 2010 and 2011, respectively, while rye monocultures produced 414 and 330 g m^{-2} in those 2 yr (Fig. 2). Cooler spring temperatures in 2011 (Table 3) probably contributed to the overall lower biomass production observed that year, particularly for vetch (rye, $P = 0.03$; vetch, $P = 0.004$). As with population density, relative seeding rates were strongly correlated with rye and vetch shoot dry weights in mixtures, demonstrating that seeding rates can be a good predictor of biomass composition as well. During the course of the study, the total shoot biomass produced in the mixtures was generally equal to or greater than that produced in either monoculture. This was reflected in the total LER values for the mixtures, which ranged from 1.13 to 1.42, and in all cases were either equal to or significantly greater than 1 (Table 5). Furthermore, relative yields of both rye (L_r) and vetch (L_v) met, and in some cases significantly exceeded, their relative sown proportions in all mixtures, indicating that both species contributed to the equivalent or greater efficiency of biomass production (dry weight per seed sown) observed in the mixtures relative to the monocultures. In other words, just as much or more biomass was produced per cost of rye and vetch seed in mixtures as in monocultures.

Inference regarding the nature of interactions between species is limited from proportional replacement series designs because

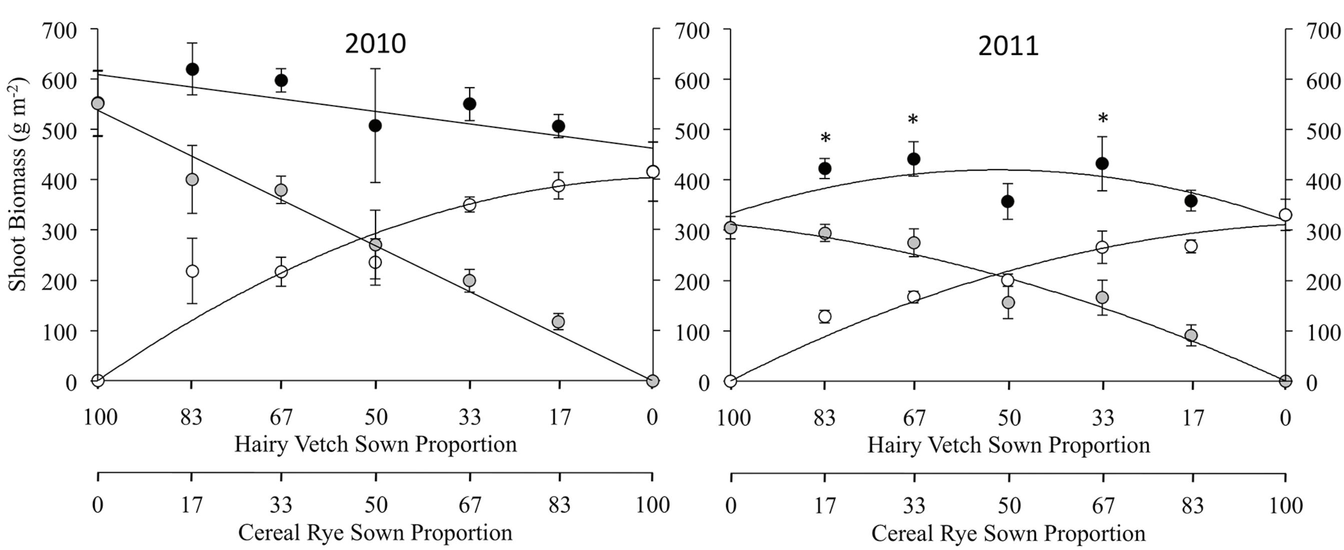

Fig. 2. Spring shoot biomass dry weights of vetch (gray), rye (white), and vetch + rye (black) across cover crop mixture proportions in 2010 and 2011 (means ± SE). The 2010 responses of vetch: $y = 5.38x$, $r^2 = 0.71$, $P < 0.001$; rye: $y = -0.036x^2 + 7.67x$, $r^2 = 0.50$, $P < 0.001$; and vetch + rye: $y = -1.46x + 607.32$, $r^2 = 0.16$, $P < 0.05$. The 2011 responses of vetch: $y = -0.020x^2 + 5.07x$, $r^2 = 0.69$, $P < 0.001$; rye: $y = -0.025x^2 + 5.62x$, $r^2 = 0.76$, $P < 0.001$; and vetch + rye: $y = -0.038x^2 + 3.62x + 332.52$, $r^2 = 0.23$, $P < 0.05$. Asterisks indicate where total biomass (vetch + rye) in a mixture was significantly greater than in either monoculture in that year at the 0.05 probability level.

Table 5. Partial land equivalent ratios for vetch (L_v) and rye (L_r) and total land equivalent ratios (LERs) in rye (R)–vetch (V) cover crop mixtures.

Cover crop treatment	2010			2011		
	L_v	L_r	LER	L_v	L_r	LER
83 V:17 R	0.76	0.51*	1.27	0.98	0.39*	1.38†
67 V:33 R	0.72	0.52	1.25	0.91*	0.51*	1.42*
50 V:50 R	0.54	0.66	1.20	0.53	0.62	1.15
33 V:67 R	0.37	0.90	1.27	0.55†	0.82†	1.37†
17 V:83 R	0.22	1.00	1.23	0.31	0.82	1.13

* Significant at the 0.05 probability level. Indications of significance refer to whether individual L_v and L_r means are significantly different from vetch and rye sown proportions in the mixture, respectively, and whether LER means are significantly different from 1.0 (based on *t*-tests).

† Significant at the 0.10 probability level.

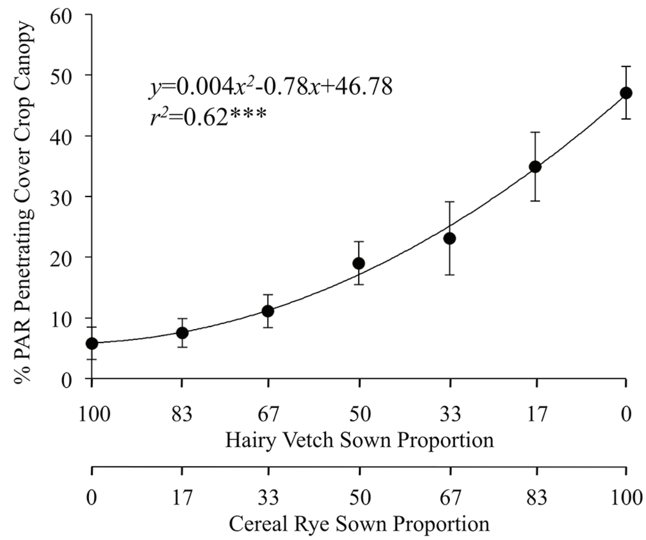

Fig. 3. Percentage of photosynthetically active radiation (PAR) penetrating the cover crop stand canopy across mixture proportions. Means are for 2010 and 2011 data combined (n = 8) ± SE. ***Regression model is significant at the 0.001 level.

total plant density is not constant across the treatments (Jolliffe, 2000). In the case of this study, total density increased with higher proportions of rye in the mixture (Fig. 1). Without data on the yield response of each species to changes in density, the balance between inter- and intraspecific interactions in mixtures cannot be determined with confidence (Firbank and Watkinson, 1985; Jolliffe, 2000). However, given that neither rye nor vetch productivity (dry weight per seed sown) was suppressed in any of the mixtures, interspecific interference between the two species appears to have been minimal under the conditions of this experiment. Furthermore, plants generally exhibit an inverse relationship between density and biomass production per individual (Avci and Akar, 2006; Boyd et al., 2009). Therefore, increased rye productivity in mixtures could simply be due primarily to the decrease in total plant density associated with decreasing proportions of rye in the mixtures. Conversely, vetch productivity was not reduced at the higher total plant densities associated with higher rye proportions (in opposition to the expected density-dependent response), suggesting that vetch may have benefitted from either weaker interspecific competition or possible facilitation from rye.

Decades of intercropping research have demonstrated that cereals are usually the dominant component in cereal–legume mixtures, suppressing the growth of the legume and contributing a greater proportion of biomass to the total mixture yield (Ofori and Stern, 1987). This competitive imbalance may be more severe for low-growing legumes than for those with climbing growth habits (Davis et al., 1984; Fukai and Trenbath, 1993), but the performance of vetch in mixture with cereals still varies across studies. Kurdali et al. (1996) and Tosti et al. (2010) both saw reduced vetch dry matter productivity in a mixture with barley (*Hordeum vulgare* L.), while Dhima et al. (2007) also observed suppression of vetch by barley and oat (*Avena sativa* L.) but not by wheat (*Triticum aestivum* L.) or triticale (×*Triticosecale* Wittmack). As with our results, Ranells and Wagger (1996) observed limited suppression of vetch in a mixture with rye; however, Brainard et al. (2012) observed one out of two seasons where the productivity of three vetch cultivars was reduced on average by rye, which yielded >400 g m^{-2} in the 50:50 mixtures. By comparison, rye yields were relatively low in our study. The sandy soils, prior growth and incorporation of sorghum-sudangrass, and absence of N fertilization probably contributed to low soil N conditions that favored vetch growth relative to rye, reducing the potential for competitive inhibition in the mixtures.

An important qualification to note is that measures of yield advantage or efficiency depend not only on the performance of the species in mixture but also on the characteristics of their respective monocultures. An implicit assumption in intercrop or mixture evaluation is that the monocultures chosen are the optimal ones for sole cropping of each species (Willey, 1979b). In this study, monoculture seeding rates were chosen with the goal of maximizing cover crop biomass production, especially for vetch. However, due to the high cost of seed, it is common to see vetch sown at 28 kg ha^{-1} in monoculture, particularly in agronomic cropping systems (e.g., Clark et al., 1994; Sainju et al., 2005; Parr et al., 2011). Furthermore, rye monocultures are often sown at rates of 125 kg ha^{-1} or more, which may better maximize biomass production, particularly under conditions where soil N is not limiting (Clark, 2007; Boyd et al., 2009). Outcomes in replacement-type mixtures and conclusions regarding mixture performance may vary when different monoculture seeding rates are used (Willey, 1979b).

Winter Annual Weed Biomass and Photosynthetically Active Radiation

The percentage of PAR penetrating the cover crop canopies in early May ranged from 6 to 47% for vetch and rye monocultures, respectively, averaged across the 2 yr of the study. In the mixtures, PAR penetration increased with a decreasing proportion of vetch and increasing proportion of rye (Fig. 3). All cover crop treatments significantly suppressed winter annual weed biomass relative to the control treatments in 2010 and 2011, and suppression increased with increasing rye in the cover crops (Fig. 4). Total weed biomass in the control treatments was 144 and 162 g m^{-2} in 2010 and 2011, respectively, and the dominant species included common chickweed [*Stellaria media* (L.) Vill.], annual bluegrass (*Poa annua* L.), and shepherd's purse [*Capsella bursa-pastoris* (L.) Medik.] in 2010 and corn chamomile (*Anthemis arvensis* L.), field pepperweed [*Lepidium campestre* (L.) R. Br.], and common chickweed in 2011. While suppression by high-rye

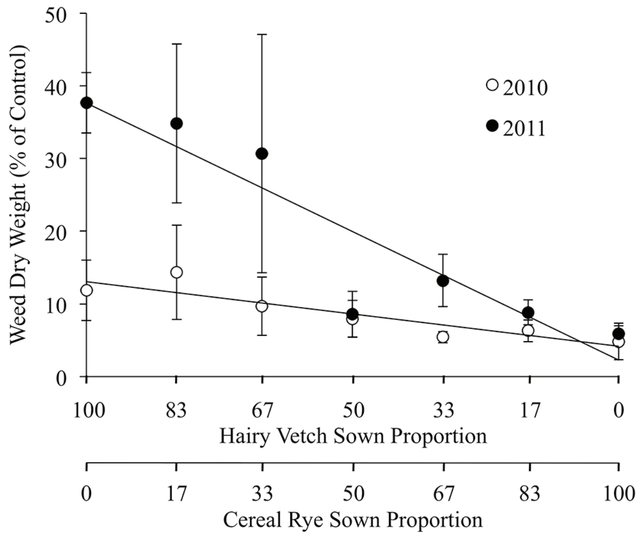

Fig. 4. Winter annual weed biomass (dry weight) across cover crop mixture proportions in 2010 and 2011, expressed as mean percentage of the no-cover-crop control treatment (± SE). The 2010 response: $y = 0.089x + 4.18$, $r^2 = 0.18$, $P < 0.05$. The 2011 response: $y = 0.35x + 2.27$, $r^2 = 0.40$, $P < 0.001$.

treatments was comparable between the 2 yr of the study, variability in weed suppression between 2010 and 2011 increased with a greater proportion of vetch sown. Although generally less of a management priority than summer annuals, winter annual weeds can interfere directly with crops in reduced tillage systems and serve as alternative hosts for important pests and diseases (Hayden et al., 2012).

Our results are consistent with previous studies demonstrating that weed suppression in cereal–legume mixtures is generally driven by the presence and relative proportion of the more competitive cereal component (Liebman and Dyck, 1993; Akemo et al., 2000b; Hayden et al., 2012). The increasingly lower weed suppression in 2011 relative to 2010 with greater vetch in the cover crops was probably a result of the cooler spring temperatures and lower biomass production that year, and also suggests that the ability to suppress weeds of vetch is less robust in the face of year-to-year environmental variability than rye. While both rye and vetch are known to exhibit allelopathic properties (Barnes and Putnam, 1986; White et al., 1989), shading is probably a more dominant mechanism of competition for vetch than it is for rye, which suppresses neighboring plants more predominately through competition for water and soil nutrients (Teasdale and Daughtry, 1993; Mariotti et al., 2009). This dominance of belowground interference in the ability to suppress weeds of rye is supported by the fact that weed biomass decreased with increasing rye in the cover crops, despite a corresponding increase in the amount of PAR reaching the soil surface in the spring. It is important to note, however, that canopy architecture changes substantially during rye growth, and PAR readings taken in the spring may not reflect the level of competition for light exerted by rye on weeds the previous fall.

Cover Crop Nitrogen Content

Total shoot N content across the cover crop stands in 2010 and 2011 was largely driven by rye and vetch biomass production. As expected, vetch biomass contributed the majority of N to rye–vetch mixtures, and total N content generally increased with increasing proportion of vetch sown (Fig. 5). In 2010, the total N content ranged from 3.8 g m^{-2} in the rye monoculture to 17.5 g m^{-2} in the vetch monoculture, while in 2011, the total N content ranged from 4.2 g m^{-2} in the rye monoculture to 11.6 g m^{-2} in the 83:17 vetch/rye mixture.

In both study years, a modest but significant increase in rye tissue N concentration was observed in mixtures with increasing proportions of vetch (Fig. 6). Combined with the equivalent or greater rye biomass productivity observed in mixtures relative to the rye monoculture (Table 5), this trend provides added support that the productivity of N accumulation by rye in mixtures was greater as well. Similarly, Tosti et al. (2010, 2012) saw increases in the tissue N concentration of barley with increasing vetch sown in

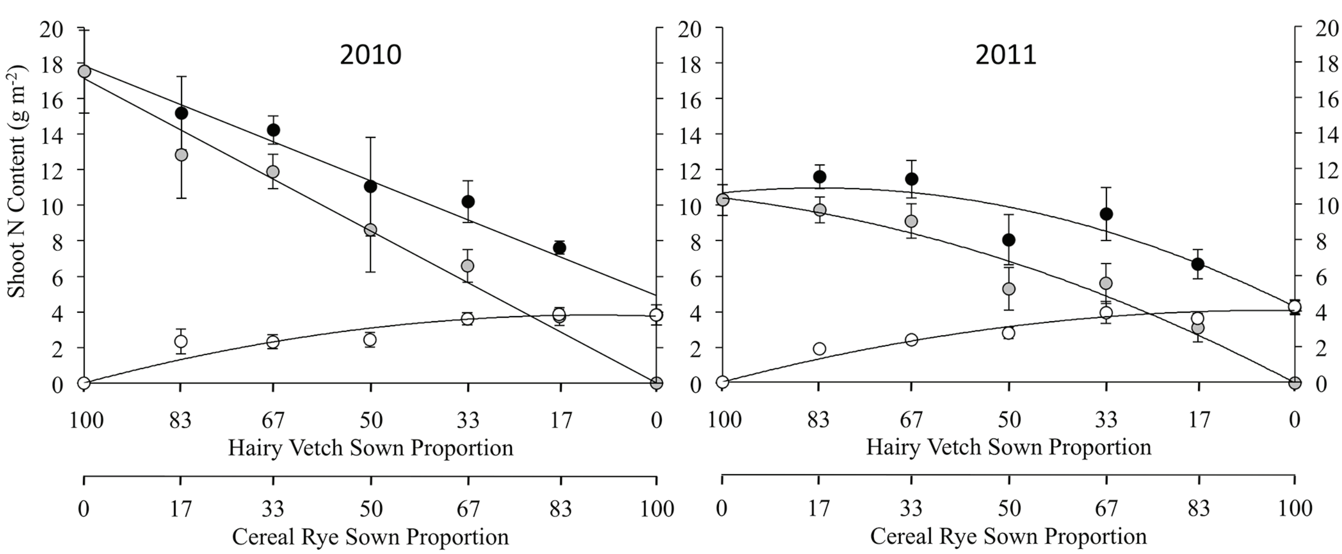

Fig. 5. Shoot N accumulated in vetch (gray), rye (white), and vetch + rye (black) across cover crop mixture proportions in 2010 and 2011 (means ± SE). The 2010 responses of vetch: $y = 0.92x$, $r^2 = 0.66$, $P < 0.001$; rye: $y = -0.00048x^2 + 0.086x$, $r^2 = 0.36$, $P < 0.001$; and vetch +r ye: $y = -0.13x + 17.83$, $r^2 = 0.67$, $P < 0.001$. The 2011 responses of vetch: $y = -0.00066x^2 + 0.17x$, $r^2 = 0.66$, $P < 0.001$; rye: $y = -0.00044x^2 + 0.084x$, $r^2 = 0.61$, $P < 0.001$; and vetch + rye: $y = -0.00097x^2 + 0.032x + 10.69$, $r^2 = 0.58$, $P < 0.001$.

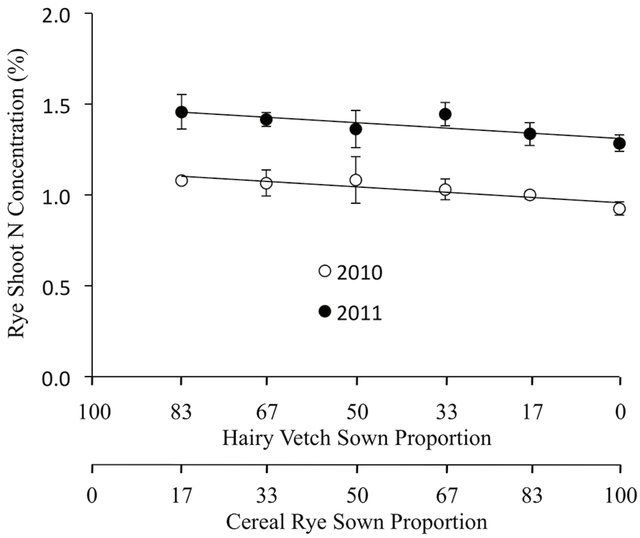

Fig. 6. Rye shoot N concentration across rye–vetch cover crop mixture proportions in 2010 and 2011 (means ± SE). The slope of the response to rye–vetch proportion was equal in both years and significant overall (analysis of covariance, $P < 0.001$). The 2010 equation: $y = 0.0018x + 0.96$, $r^2 = 0.15$. The 2011 equation: $y = 0.0018x + 1.31$, $r^2 = 0.13$.

replacement-style mixtures. In both cases, the mechanism behind the increase cannot be clearly established. Improved cereal N economy in cereal–legume mixtures is consistent with a facilitative increase in N availability due to the legume. In proportional replacement series designs, however, greater legume proportions in mixtures are also accompanied by a corresponding reduction in cereal density. Because rye is a stronger competitor for soil N resources than vetch, reduced rye intraspecific competition for soil N could also account for the increase in rye tissue N concentration across the gradient of rye–vetch mixtures. The overall higher rye N concentrations in 2011 compared with 2010 ($P < 0.001$) probably reflect a more immature rye growth stage at sampling due to the lower GDD accumulation during the 2010–2011 season.

Vetch Nitrogen Fixation

Estimates of vetch shoot %Ndfa were relatively high in both years, ranging from 81 to 88%. Although %Ndfa was marginally lower for vetch in monoculture than for vetch in mixtures with rye on average in 2010 (linear contrast, P = 0.065), estimates of N_2 fixation did not differ significantly across the rye–vetch mixtures. In 2011, soil contamination compromised N_2 fixation estimates from cover crop treatments containing >50% vetch; however, for the three mixtures where reliable data were available, vetch %Ndfa averaged 82% and did not differ among the mixture rates.

Previous studies have observed increases in vetch N_2 fixation efficiency in mixtures with cereals (Kurdali et al., 1996; Brainard et al., 2012). We expected that higher proportions of rye in a mixture might lead to greater interspecific competition for available soil N and promote greater N_2 fixation by vetch. However, the relatively sandy soils, low organic matter content, and absence of N fertilization at our study site may have reduced the potential for observing such an effect. The presence of rye and its relative proportion in a mixture may be more likely to influence vetch N_2 fixation efficiency under conditions where soil N availability is high. On the other hand, excessive soil N may also shift the competitive balance in favor of the cereal, resulting in inhibition of legume growth and potential N_2 fixation capacity. While Brainard et al. (2011) observed increased nodulation of soybean [*Glycine max* (L.) Merr.] when grown in combination with Japanese millet [*Echinochloa frumentacea* (Roxb.) Link], the effect was not observed when composted manure was added to the system.

The amount of SNF was driven predominately by vetch biomass productivity. Across the gradient of rye–vetch cover crops, SNF varied from zero in the rye monoculture to 142 and 85 kg N ha^{-1} in the 2010 and 2011 vetch monocultures, respectively (Table 6). However, the total cost for conventional cover crop seed increased from US$37 to US$176 ha^{-1} across that same range of treatments (Table 1). As a result, the estimated cost of the N fixed by vetch (CNF) ranged from US$0.79 to US$1.90 kg^{-1} N during the 2 yr of the study, and

Table 6. Vetch shoot N concentration, percentage of N derived from the atmosphere (Ndfa), estimated shoot N fixed (SNF), and cost of N fixed (CNF) across rye (R)–vetch (V) cover crop mixture proportions.

Cover crop treatment	N concentration		Ndfa†		SNF§		CNF¶	
	2010	2011	2010	2011‡	2010	2011	2010	2011
	%				kg ha^{-1}		$ kg^{-1}	
100 V : 0 R	3.17	3.37	80.9	–	142.4	84.6	1.05	1.68
83 V : 17 R	3.18	3.30	87.9	–	110.8	80.1	1.13	1.47
67 V : 33 R	3.13	3.31	86.5	–	102.3	74.9	0.92	1.29
50 V : 50 R	3.12	3.36	88.4	84.0#	74.9	43.6	1.15	1.90
33 V : 67 R	3.28	3.37	87.5	82.8#	56.9	46.0	0.84	1.16
17 V : 83 R	3.18	3.36	84.5	80.1	31.5	25.5	0.79	1.11
F††	ns‡‡	ns	ns	ns	***	**	ns	ns

** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Calculated from Eq. [4].
‡ Means are reported for treatments only where at least three replicates of uncontaminated vetch tissue were available in 2011.
§ Calculated from Eq. [6].
¶ Calculated from Eq. [7].
# Means calculated from three replicates (***n*** = 3).
†† Significance of fixed effect of cover crop mixture proportion within years.
‡‡ ns, not significant at the 0.05 probability level.

despite a numerical trend toward decreasing costs in mixtures with more rye, CNF was not affected significantly by the rye–vetch mixture rate (Table 6). A similar range of CNF estimates was established by Brainard et al. (2012) for three vetch cultivars in monoculture and in mixtures with rye. For conventional growers in particular, acknowledging the value of fixed N as a potential fertilizer replacement may help justify the substantially higher seed costs of cover crops that contain greater proportions of vetch. Comparisons of CNF with the cost of synthetic N fertilizers are confounded by the incomplete first-season availability of N from organic residues and by the potential value of additional services that are provided by cover crops beyond N fertility. But as a reference, the average cost of urea fertilizer during the past 5 yr was fairly comparable to the CNF from vetch in this study, ranging from US\$1.10 to US\$1.35 kg^{-1} N (Economic Research Service, 2013). Furthermore, estimates of CNF in this study did not include fixed N accumulated in root tissue. Because vetch roots can account for 10% or more of the total tissue N (Rogers and Sturkie, 1939), our figures probably overestimate CNF. Nevertheless, while seed costs vary with time, source, and whether conventional or organic seed is used, our results suggest that under the conditions of this study, the relative cost for the N fixed by vetch was not significantly influenced by mixing with rye at any proportion.

CONCLUSIONS

The objective of this research was to evaluate the effects of rye–vetch species proportions on cover crop mixture stand characteristics and performance relative to rye and vetch monocultures. Seeding rates were good predictors of rye and vetch stand density and biomass composition in mixtures, with little evidence of substantial interference between the two species under the conditions of the study. While outcomes may vary depending on environment and management, we also saw little evidence of synergistic benefits in the mixtures, such as improved vetch winter survival, increased N_2 fixation, or reduced costs per unit of N fixed. However, changing the proportions of rye and vetch sown resulted in tradeoffs among some of the agroecosystem services provided by the living cover crops—for example, greater fixed N accumulation but higher seed costs and reduced winter annual weed suppression with increasing vetch. A greater understanding of the tradeoffs among cover crop services, as well as costs, in rye–vetch mixtures will support more-informed decision-making regarding cover crop selection and mixture seeding rates.

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