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Biomass Production and Nitrogen Accumulation by Hairy Vetch–Cereal Rye Mixtures: A Meta-Analysis

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ABSTRACT

Agroecosystem services from cover crop mixtures are linked to aboveground biomass and total N content (kg ha^{-1}). Reported values in the literature, however, vary for aboveground biomass and total N content of cover crop mixtures compared with monocultures. We conducted a meta-analysis using results from 55 site-years from 21 studies conducted in the United States to examine biomass and N content of hairy vetch (*Vicia villosa* Roth)–cereal rye (*Secale cereale* L.) mixtures compared with respective monocultures. Overall, hairy vetch–cereal rye mixtures produced 63 and 21% more biomass compared with hairy vetch and cereal rye monocultures, respectively. The N content of hairy vetch–cereal rye mixtures was 150% greater than that of cereal rye monocultures. When the proportion of hairy vetch seeds (by weight) exceeded 46% of the mixture, the mixtures accumulated equivalent or more N than the greatest yielding monocultures (usually hairy vetch). Compared with monocultures, a more consistent positive response of mixtures on biomass and N content was found on coarse-textured soils and following corn (*Zea mays* L.) rather than soybean [*Glycine max* (L.) Merr.] harvest. With increasing growing degree days (GDD), the biomass and N content of mixtures decreased relative to hairy vetch monocultures but increased relative to cereal rye monocultures, suggesting better performance of hairy vetch at higher GDD. We conclude that hairy vetch–cereal rye mixtures can produce equivalent or more biomass than both monocultures and accumulate as much N as hairy vetch, and that the relative productivity of mixtures depends on soil type, previous crop, seeding proportion, and GDD.

Core Ideas

- We reviewed aboveground biomass and total N content of hairy vetch–cereal rye mixtures vs. monocultures.
- Overall, mixtures produced equivalent or more biomass and N content as monoculture species.
- Environmental and cropping system factors affected relative productivity of mixtures.
- Mixtures performed better in coarse-textured soils and following corn harvest.
- With increasing GDD, mixtures productivity decreases relative to hairy vetch, but increases relative to cereal rye monocultures.

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Cover crop mixtures can provide more agroecosystem services than monocultures because of the combined benefits of the different species in the mixtures (Schipanski et al., 2014; Blanco-Canqui et al., 2015; Finney et al., 2016). In legume–grass mixtures such as hairy vetch (*Vicia villosa* Roth)–cereal rye (*Secale cereale* L.), hairy vetch fixes atmospheric N that can be utilized by companion cereal rye or the following cash crop through root exudates or decomposition of N-rich hairy vetch tissues (Fujita et al., 1992), while cereal rye provides rapid ground cover, produces large quantities of biomass, aggressively scavenges residual soil N, and suppresses weeds (Mirsky et al., 2011; Kaspar et. al., 2012; Hayden et al., 2012, 2014; Lawson et al., 2015). Research has shown that the intermediate C/N ratio (25–30:1) of the biomass from hairy vetch–cereal rye mixtures results in a more balanced mineralization–immobilization turnover of N (Ranells and Wagger, 1996; Rosecrance et al., 2000; Poffenbarger et al., 2015b). The reduced net N mineralization of hairy vetch–cereal rye mixtures compared with hairy vetch monocultures and reduced risk of N immobilization compared with cereal rye monocultures may not only reduces early season nitrate (NO_3^-) leaching and denitrification losses, but also sometimes improve synchrony between cover crop N release and N demand of the succeeding cash crops (Rosecrance et al., 2000; Poffenbarger et al., 2015a). Therefore, hairy vetch–cereal rye mixtures can increase N use efficiency from cover crop N and potentially increase cash crop yield during wet years with greater leaching potential. Moreover, hairy vetch–cereal rye mixtures have been reported to suppress weeds more effectively than hairy vetch monocultures, and at least as well as cereal rye monocultures depending on seeding proportions in the mixtures (Burgos and Talbert, 1996; Mirsky et al., 2011; Hayden et al., 2012, 2014; Lawson et al., 2015).

Aboveground biomass and N content are proxies that indicate the potential value of cover crop monocultures or mixtures in terms of agroecosystem services provisioned. Cover crop biomass is positively correlated with weed suppression and retention of N against leaching loss in some regions (Brennan and Smith, 2005; Brennan et al., 2009; Finney et al., 2016; Martinez-Feria et al., 2016; Blesh, 2017; R. Thapa et

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Abbreviations: CI, confidence interval; CV, coefficient of variation; GDD, growing degree days; LSD, least significant difference.

al., unpublished, 2018). Cover crop N content is a key predictor of N supply to the subsequent crop (Tonitto et al., 2006), particularly in combination with cover crop C/N ratio (White et al., 2017). According to diversity–productivity relationships (Tilman, 1999), cover crop mixtures may increase agroecosystem services not only through proportionally combining benefits of individual species, but also by resulting in greater biomass and/or N accumulation relative to monocultures. Indeed, research on cover crop mixtures has documented both overyielding (i.e., mixture produces more biomass than the average biomass of monocultures of each individual species; Wortman et al., 2012; Smith et al., 2014) and transgressive overyielding (i.e., mixture produces more biomass than the greatest yielding monoculture; Finn et al., 2013). There are few studies where cover crop mixtures have been found to underyield as compared with best monoculture species in the mixture (Mohler and Liebman, 1987; Brainard et al., 2011). When cover crop mixtures with complementary functional traits, such as legume–grass mixtures, overyields, they were likely to provide multiple ecosystem services (such as weed suppression, N retention, and N provisioning) than monoculture species (Finn et al., 2013; Blanco-Canqui et al., 2015; Storkey et al., 2015; Blesh, 2017).

Soil type, previous crop, seeding proportion, and accumulated GDD all potentially affect the performance of hairy vetch–cereal rye mixtures relative to monocultures. Since winter cover crops are generally grown without N fertilization, the productivity of cover crops, particularly non-legumes, can be strongly influenced by soil N availability. Moreover, legumes tend to be less competitive than grasses when soil N is high, but can out-compete grasses when soil N is low (Hauggaard-Nielsen and Jensen, 2001). Soil N availability during cover crop season is a function of residual soil N and N mineralized from previous crop residues. Seeding proportions (by weight) in the mixture also affects the biomass and N content of cover crop mixtures. To date, few studies (Clark et al., 1994; Hayden et al., 2014; Poffenbarger et al., 2015c) have evaluated gradients of cover crop mixtures with seeding proportions ranging from 100% hairy vetch to 100% cereal rye. These studies found that the seeding rates of hairy vetch and cereal rye in a mixture influence stand density, mixture composition, and hence, the biomass and N content of hairy vetch–cereal rye mixtures. Finally, cover crop productivity is affected by accumulated GDD over the cover crop growth period. Differences in seasonal growth pattern of hairy vetch and cereal rye when planted alone or in mixtures will influence the productivity of hairy vetch–cereal rye mixtures relative to monocultures across regions. In the northeastern and southeastern states of the United States, the biomass of hairy vetch monoculture increased by 4.1 to 5.3 kg ha^{-1} GDD^{-1} (Teasdale et al., 2004; Mirsky et al., 2017) and that of cereal rye monoculture increased by 4.1 kg ha^{-1} GDD^{-1} (Mirsky et al., 2011). In northwestern United States, Lawson et al. (2015) found that the biomass of hairy vetch and cereal rye monocultures increased by 1.8 and 11.0 kg ha^{-1} GDD^{-1}, respectively, whereas hairy vetch–cereal rye mixtures have been documented to gain 6.5 to 7.5 kg biomass ha^{-1} GDD^{-1}.

Numerous studies have examined hairy vetch–cereal rye mixtures in comparison with monocultures of hairy vetch and cereal rye. However, a meta-analysis is needed to synthesize how biomass and N content differ between mixtures and monocultures of these two species. Therefore, our objective was to synthesize this literature to determine: (i) the biomass and N content of hairy vetch–cereal rye mixtures relative to monocultures; and (ii) how soil type, management (previous crop, seeding proportions), and accumulated GDD drive the performance of mixtures relative to monocultures.

MATERIALS AND METHODS

Literature Review and Data Collection

An extensive review of publications that report biomass and N content of hairy vetch–cereal rye mixtures and respective monocultures was conducted using Web of Science (Thompson Reuters) and Google Scholar (Google Inc.) databases. The literature search was conducted in September 2016. The following search terms and their combinations were used: grass-legume, rye-vetch, vetch, rye, biculture, and biomass or N content. Additional articles were compiled from the citations found within the references of publications located in this search. To be considered for inclusion in this meta-analysis, studies had to report the following:

- Either biomass or N content for one or more hairy vetch–cereal rye mixtures and at least one monoculture (hairy vetch or cereal rye)
- Seeding rates of hairy vetch and cereal rye in monocultures and mixtures
- Means and sample sizes for each treatment comparison

We only selected studies that had in-field replication and randomization, clearly described experimental approaches and sampling protocols, and conducted in the United States.

We populated our database with a total of 21 (20 published and 1 unpublished) studies that met our inclusion criteria (Table 1). Data were extracted from both tables and figures. Data, if provided in graphs, were extracted using Webplotdigitizer Version 3.8 (Rohatgi, 2017). The response variables used in our meta-analysis were aboveground biomass and N content. The aboveground biomass and N content of hairy vetch–cereal rye mixtures represents the total aboveground biomass and total N content of both hairy vetch and cereal rye species in the mixtures for all pair-wise comparisons. Each pair-wise comparison between mixtures and monocultures was considered an observation or case in our meta-analysis. From each study, we collected information related to study site location, soil type (soil pH, soil texture), management factors (cover crop planting and termination date, seeding rate, establishment method, and previous crop), and environmental factors (such as GDD) as potential explanatory variables (Table 1). Residual soil N in the fall at the time of cover crop planting may also greatly influence cover crop growth and N content. However, residual soil N is not provided in most of these studies. Finally, we recorded means, sample size, and measures of variability (standard error, standard deviation, coefficient of variation, or least significant differences) for each response variable.

Categorical and Continuous Variables

Soil texture and previous crop were classified as explanatory categorical variables. Soil texture was categorized as fine (clay, silty clay, and sandy clay), medium (clay loam, loam, silty clay loam, silt, and silt loam), and coarse (sandy loam, sandy clay loam, and loamy sand). Most of the studies included in this meta-analysis were conducted in fields where the previous crop

Table 1. Summary of the studies included in the meta-analysis.

Reference	Location†	n‡	Soil texture	Soil pH	Previous crop§	Establishment method	Planting dates	Kill dates	GDD range¶	Seeding rate: Hairy vetch	Seeding rate: Cereal rye	Seeding rate: Mixture#	Aboveground biomass: Hairy vetch	Aboveground biomass: Cereal rye	Aboveground biomass: Mixture	N content: Hairy vetch	N content: Cereal rye	N content: Mixture
											kg ha^{-1}			Mg ha^{-1}			kg ha^{-1}	
Brainard et al., 2012	MI	2	Loamy sand	7.9	Sudangrass	No-till drilled	early Sept.	late May	1104–1211	45	125	22.5/62.5	3.8–4.4	na	5.7–7.0	113–147	na	72–113
Clark et al., 1994††	MD	2	Silt loam	na‡‡	Corn	Plowed/drilled	mid Sept.	early April–mid May	615–1204	28	94	(14–28)/(47–94)	0.7–5.2	2.9–7.1	2.6–9.3	38–161	58–90	74–219
Clark et al., 1997	MD	4	Silt loam	na	Corn	Plowed/drilled	mid Sept.–early Oct.	early–late Apr.	807–1010	28	94	28/47	2.1–3.7	1.6–3.9	3.1–5.8	69–139	22–51	99–166
Clark et al., 2007	MD	2	Silt loam	na	Corn	Plowed/disked	early Oct.	early May	843–1044	28	94	21/47	4.9–5.7	3.0–4.7	4.9–10.6	179–213	26–37	122–219
Cline and Silvernail, 2001	KY	4	Silt loam	6.4	Sweet corn	No-till drilled	early–late Sept.	late May	978–1472	45	120	22.5/60	3.3–4.2	1.8–9.7	3.7–10.7	110–139	21–69	92–135
Cline and Silvernail, 2002	KY	3	Silt loam	6.4	Corn, sweet corn	No-till drilled	mid–late Sept.	mid May	814–1236	45	120	22.5/60	na	na	na	115–164	28–64	104–152
Griffin et al., 2000	ME	3	Silt loam	6.3	Corn	Grain drilled	early–late Aug.	late May–early June	694–1009	–	112	56/56	na	2.4–3.2	2.1–4.5	na	37–49	46–170
Hayden et al., 2014††	MI	2	Loamy sand	6.6	Sudangrass	Broadcast/incorporated	early Sept.	early–mid May	965–1070	42	94	(7–35)/(16–78)	3.0–5.5	3.3–4.0	3.5–6.0	100–180	40	65–150
Kuo and Jellum, 2002	WA	4	Silt loam	na	na	Roto-tilled	late Sept.	late Apr.	798–998	28	101	20/71	1.1–2.3	1.0–2.5	1.7–2.4	42–71	13–33	40–57
Lawson et al., 2015	WA	1	Loam	6	Sudangrass	Grain drilled	mid Sept.–early Oct.	late Mar.–late Apr.	520–804	112	112	(56–84)/(28–56)	0.5–2.3	0.7–5.1	0.7–4.4	27–89	25–93	30–107
Mirsky (unpublished, 2014)††	MD	2	Loam	5.7–6.7	Soybean	Plowed/disked	late Sept.	mid May–early June	1118–1159	34	168	(7–27)/(34–134)	3.6–4.9	4.1–10.8	4.4–8.5	100–138	29–76	69–117
Mirsky et al., 2011	PA	2	Silt loam	6.5	Oat	Disked/drilled	late Aug.–mid Oct.	early–late May	643–2341	–	135	45/90	na	2.1–13.7	1.7–13.3	na	na	na
Parr et al., 2011	NC	2	Loamy sand, Loam	na	Sweet potato, soybean	Tye grain drill, no-till drilled	early–late Oct.	late Apr.–late May	1044–1578	28	118	28/56	2.6–6.3	1.8–12.6	2.7–9.7	64–204	12–69	49–217
Poffenbarger et al., 2015c††	MD	4	Loam	5.7–6.7	Soybean	Plowed/disked	mid Sept.–early Oct.	mid–late May	1189–1483	34	168	(7–27)/(34–134)	5.0–7.1	10.3–12.8	8.3–15.2	145–222	49–86	101–176
Ranells and Wagger, 1996	NC	2	Loamy sand	5.8	Corn	Plowed/disked	mid Oct.	mid Apr.	1372–1427	34	112	22/56	2.9–4.8	1.5–5.7	3.0–5.4	125–182	17–64	82–200
Ranells and Wagger, 1997	NC	2	Loamy sand	5.8	Corn	Plowed/disked	mid Oct.	late Dec.–mid Apr.	582–1427	28	50	18/25	0.1–5.0	0.4–7.9	0.4–5.4	3–224	6–123	11–200
Ruffo and Bollero, 2003	IL	4	Silt loam, Silty clay loam	6.2–6.4	Soybean	No-till drilled	early Oct.	.ate Apr.–early May	601–891	34	134	23/67	0.9–2.0	2.9–4.7	2.9–4.5	32–47	35–60	47–78
Sainju et al., 2005	GA	3	Silt loam	6.5	Corn, cotton, sorghum	Drilled	Oct.–Nov.	Apr.	1045–1545	28	40	19/40	2.4–5.2	2.3–6.1	5.7–8.2	76–167	25–68	84–310
Teasdale and Abdul-Baki, 1998	MD	2	Silt loam	na	na	No-till drilled	mid Sept.	late May	1157–1175	45	45	45/45	3.8–6.8	4.2–7.3	5.4–9.3	118–236	41–69	124–237
Teasdale et al., 2008	MD	3	Loamy sand	na	Sweet corn	No-till drilled	mid Sept.	early May–mid June	742–1232	45	–	45/45	4.7–5.8	na	9.0–11.2	197–228	na	249–259
Vaughan and Evanylo, 1998	VA	2	Silt loam, loam	na	na	Plowed/disked	mid Sept.–early Oct.	late Apr.–late May	579–809	28	101	19/67	0.3–2.3	5.1–10.4	4.2–10.0	14–86	55–124	67–125

† MI, Michigan; MD, Maryland; KY, Kentucky; ME, Maine; WA, Washington; PA, Pennsylvania; NC, North Carolina; IL, Illinois; GA, Georgia; VA, Virginia.

‡ Total number of site-years included from each study.

§ Corn (*Zea mays* L.), cotton (*Gossypium hirsutum* L.), oat (*Avena sativa* L.), sudangrass [*Sorghum sudanense* (Piper) Stapf], sorghum [*Sorghum bicolor* (L.) Moench], soybean [*Glycine max* (L.) Merr.], sweet potato [*Ipomoea batatas* (L.) Lam.].

¶ GDD, growing degree days accumulated during the entire cover crop growing period (base temperature of 4°C).

For mixtures seeding rate, the first and second value represents the hairy vetch and cereal rye seeding rate in the mixture.

†† Studies in which multiple mixture treatments were compared with a single monoculture.

‡‡ Data not available in the study.

was either corn (*Zea mays* L.) or soybean [*Glycine max* (L.) Merr.]; previous crop (corn or soybean) was therefore included as a potential categorical explanatory variable in our analysis.

Hairy vetch seeding proportions (by weight) in the mixture and GDD were classified as explanatory continuous variables. Hairy vetch seeding proportions (by weight) in the mixture were calculated by dividing the hairy vetch seeding rate in the mixture by the sum of both hairy vetch and cereal rye seeding rate in the mixture. Growing degree days during entire cover crop growth period were calculated using a base temperature of 4°C (Teasdale et al., 2004). Missing GDD were determined using computed cumulative GDD values, which were calculated as the sum of the monthly GDD values. Monthly GDD were calculated by multiplying the monthly mean temperature, minus 4°C, by the number of days in the month in which cover crops were growing. Monthly mean temperatures were either extracted from the study itself or were retrieved from local weather stations using study site coordinates.

Meta-Analysis Approach

We quantified the performance of hairy vetch–cereal rye mixtures compared with monocultures by calculating the natural log of the response ratio (ln*R*) as an effect size (Hedges et al., 1999):

$$\ln R = \ln\left(\frac{\bar{x}_{\text{mixture}}}{\bar{x}_{\text{mono}}}\right) = \ln(\bar{x}_{\text{mixture}}) - \ln(\bar{x}_{\text{mono}}) \qquad [1]$$

where $\bar{x}_{\text{mixture}}$ and $\bar{x}_{\text{mono}}$ are the mean values of the response variables (biomass or N content) for the mixtures and monocultures, respectively. The effect sizes were calculated for three monoculture controls: hairy vetch, cereal rye, and the greatest yielding monoculture. The greatest yielding monoculture refers to the monoculture with the higher mean among two monoculture treatments for a given response variable for each case. For example, if the aboveground biomass and N content of hairy vetch monoculture were 2 Mg ha^{-1} and 100 kg ha^{-1}, respectively, and that of cereal rye monoculture were 4 Mg ha^{-1} and 50 kg ha^{-1}, respectively, in a study, the greatest yielding monoculture will be cereal rye (4 Mg ha^{-1}) for aboveground biomass and hairy vetch (100 kg ha^{-1}) for N content for that study.

All of the studies included in this meta-analysis were conducted using randomized complete block design; the treatment (mixtures) and the control (monocultures) pairs within block may be correlated. Therefore, the variance (*v*) for each ln*R* was estimated using the following equation (Lajeunesse, 2011):

$$v = \frac{\text{SD}_{\text{mixture}}^{2}}{n_{\text{mixture}} \times \bar{x}_{\text{mixture}}^{2}} + \frac{\text{SD}_{\text{mono}}^{2}}{n_{\text{mono}} \times \bar{x}_{\text{mono}}^{2}} - \frac{2 \times r \times \text{SD}_{\text{mixture}} \times \text{SD}_{\text{mono}}}{n \times \bar{x}_{\text{mixture}} \times \bar{x}_{\text{mono}}} \qquad [2]$$

where $\bar{x}_{\text{mixture}}$, $\text{SD}_{\text{mixture}}$, and n_{mixture} represent the mean, standard deviation, and sample sizes for the hairy vetch–cereal rye mixtures, respectively. Similarly, $\bar{x}_{\text{mono}}$, SD_{mono}, and n_{mono} represent the mean, standard deviation, and sample sizes for the monocultures, respectively; and *r* represents the correlation coefficient to account for dependencies between the treatment and control pair in block-design. Since *r* was not reported in any of these studies, we assumed *r* to be 0.5. Sensitivity analysis was performed by the changing the value of *r* to 0.25 and 0.75. Changing the value of *r* did not change the conclusions of our study, indicating that the meta-analysis performed was highly robust.

Measures of variability for the response variables other than standard deviation were converted to standard deviations. For example, if the least significant differences (LSD) were reported, they were converted to standard errors using the following equation (Rosenberg et al., 2004):

$$\text{SE} = \frac{\text{LSD}}{t_{(0.975,n)}\sqrt{2bn}} \qquad [3]$$

where LSD is the least significant difference, *t* is the *t* test value, *n* is the sample size, and *b* is the number of blocks. Standard errors were then multiplied by the square root of the sample size to obtain standard deviations. For studies that did not report any measure of variability, the average coefficient of variation (CV) was first computed for a given response variable using other studies in the database, and then the missing standard deviations were estimated by multiplying the average CV by their respective means (Bai et al., 2013). Sensitivity analysis was also performed by excluding the studies that did not report any measures of variance. Removing the studies did not change the overall effect size estimates, providing more evidence for the robust nature of our analysis.

Weighted meta-analysis was performed using mixed-effects linear models in the nlme package in R (Pinheiro et al., 2014).a The effect sizes were weighted based on their sampling variances to calculate weighted mean effect sizes and their corresponding confidence intervals (CIs). Location, study, and site-year were included in the models as multiple, nested, random effects. In some studies, multiple mixture treatments were compared with the same monocultures (Clark et al., 1994; Hayden et al., 2014; Poffenbarger et al., 2015c). Thus, individual effect sizes were not independent. In such cases, a random effect was also included in the models to account for correlation among log response ratios calculated using the same monoculture estimates. The overall effect of hairy vetch–cereal rye mixtures relative to respective monoculture controls were tested using this model at $\alpha = 0.05$. We also performed sub-group analysis to test the effect of different monoculture controls within a given soil texture (medium or coarse) and previous crop (corn or soybean) class. For sub-group analysis, we first divided the data into subsets based on soil texture and previous crop and then used the mixed effects model as described above at $\alpha = 0.01$ to reduce the experiment-wise error rate. Random effects were subtracted from the log response ratios for presentation in Fig. 4 and 5.

For ease of interpretation, the results of the meta-analysis were exponentially back-transformed and presented as percentage change in response. The mean effect sizes for each response variables and monoculture controls were considered significantly different if their 95% CI did not include zero. The mean effect sizes for different sub-classes were considered significantly different from one another only if 99% CIs did not overlap.

RESULTS

Overview of the Dataset

We have summarized the results from 21 (20 published and 1 unpublished) studies that evaluated the overyielding effects

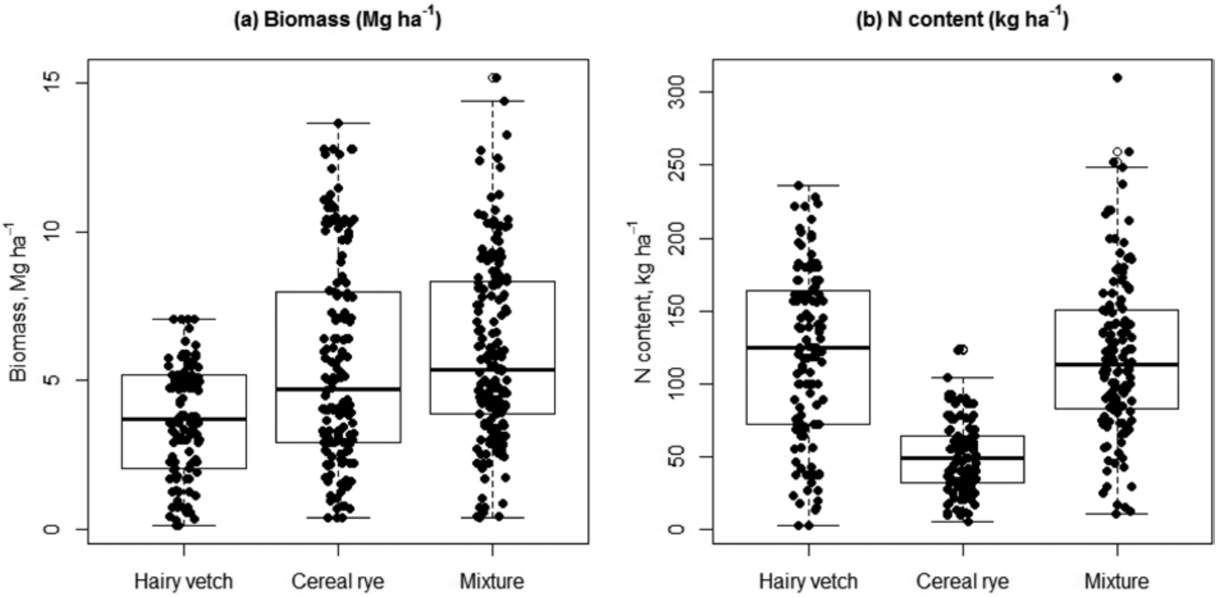

Fig. 1. Descriptive statistics for the response variables: (a) biomass and (b) N content of hairy vetch–cereal rye mixtures and respective monocultures using box and whisker plot. Solid circles are individual data points from all studies included in this meta-analysis. Note the differences in scale in the *y* axis.

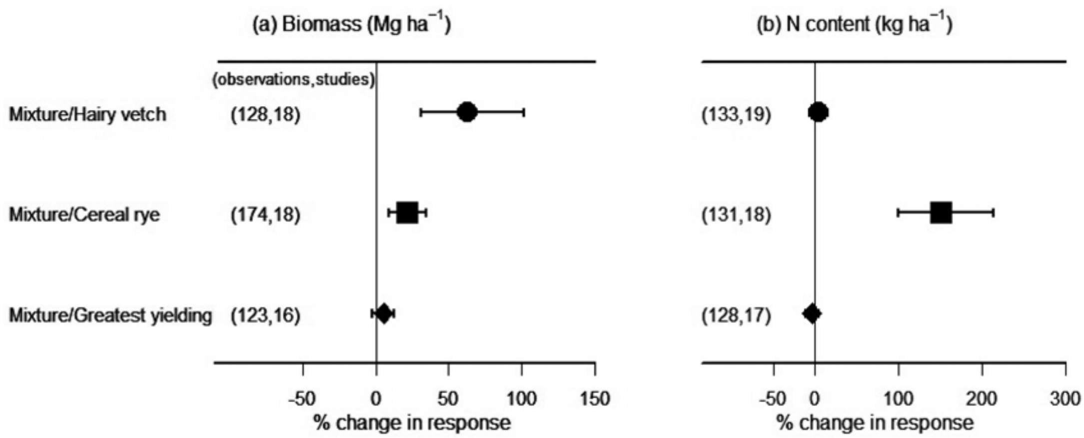

Fig. 2. (a) The biomass and (b) N content of hairy vetch–cereal rye mixtures relative to hairy vetch, cereal rye, and the greatest yielding monocultures (the monoculture with highest biomass or N content). Numbers in parenthesis represents number of independent observations or cases followed by the number of studies for each pair-wise comparison. Error bars are 95% confidence intervals (CIs). The mean effect sizes were considered significantly different only when the 95% CIs did not overlap with zero. The mean effect sizes for different subgroups are considered significantly different from one another only if their 95% CIs did not overlap one another. Note the difference in scale in the *x* axis. Asymmetrical CIs for the mean effect sizes was due to back-transformation.

of hairy vetch–cereal rye mixtures relative to monocultures (Table 1). All of the studies included in this meta-analysis were conducted in United States: Maryland (7), North Carolina (3), Michigan (2), Kentucky (2), Washington (2), and one study each in Maine, Pennsylvania, Illinois, Virginia, and Georgia. In total, we collected data from 55 site-years (1988–2015). The majority of these studies were conducted on medium to coarse-textured soils with slightly acidic pH (5.7–6.7). Seeding rates of hairy vetch and cereal rye in monocultures ranged from 28 to 112 kg ha^{-1} and 40 to 168 kg ha^{-1}, respectively. In mixtures, hairy vetch and cereal rye seeding rates ranged from 7 to 84 kg ha^{-1} and 16 to 134 kg ha^{-1}, respectively. Cover crops were planted in the fall (between late August and early November) and terminated the next spring (between late March and late May), with accumulated GDD ranging from 520 to 2341. Between hairy vetch and cereal rye monocultures, the greatest yielding monoculture was hairy vetch for biomass and N content in 26 and 85% of the cases, respectively.

Productivity of Hairy Vetch–Cereal Rye Mixtures

Aboveground Biomass

Aboveground biomass of hairy vetch and cereal rye monocultures averaged 3.6 (range: 0.1–7.1) and 5.6 (range: 0.4–13.7) Mg ha^{-1}, respectively (Fig. 1a; Table 1). The mean biomass of hairy vetch–cereal rye mixtures was 6.0 Mg ha^{-1} and ranged from 0.4 to 15.2 Mg ha^{-1}.

Mixtures vs. Hairy Vetch. Averaged across all studies, hairy vetch–cereal rye mixtures outperformed hairy vetch monocultures by 63% (CI: 31–102%) in terms of biomass yields (Fig. 2a). Meta-analysis further suggested that the hairy vetch–cereal rye mixtures consistently outyielded hairy vetch monocultures across a wide range of soil types, previous cash crops, and accumulated GDD (Fig. 3a, 4a). When compared with hairy vetch

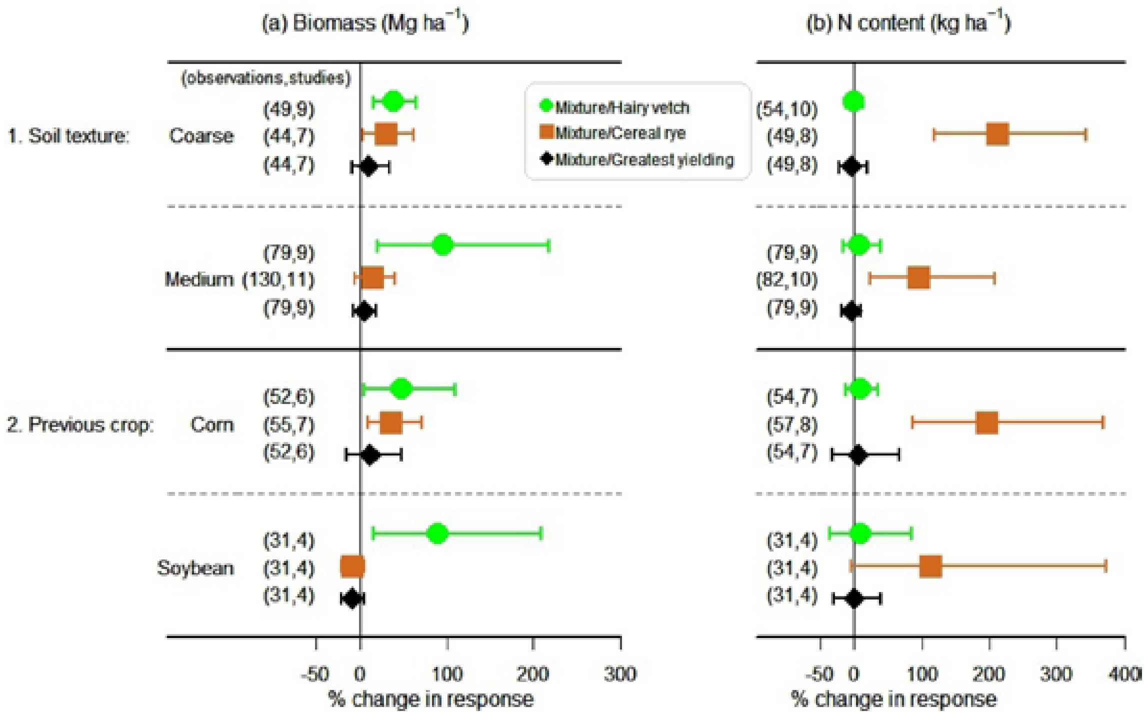

Fig. 3. (a) The biomass and (b) N content of hairy vetch–cereal rye mixtures relative to hairy vetch, cereal rye, and the greatest yielding monocultures (the monoculture with highest biomass or N content) for each sub-group within soil texture and previous crop class. Numbers in parenthesis represents number of independent observations or cases followed by the number of studies for each pair-wise comparison. Error bars are 99% confidence intervals (CIs). The mean effect sizes were considered significantly different only when the 99% CIs did not overlap with zero. The mean effect sizes for different subgroups are considered significantly different from one another only if their 99% CIs did not overlap one another. Note the differences in scale in the *x* axis. Asymmetrical CIs for the mean effect sizes was due to back-transformation.

monocultures, the biomass of hairy vetch–cereal rye mixtures was 39% (CI: 16–65%) higher in coarse-textured soils and 96% (CI: 21–218%) higher in medium-textured soils (Fig. 3a). Hairy vetch–cereal rye mixtures also outyielded hairy vetch monocultures following both corn (mean: 48%; CI: 5–110%) and soybean (mean: 90%; CI: 16–209%) harvest (Fig. 3a). It should be noted that the CI for the mixtures vs. hairy vetch monoculture effect sizes were much narrower in coarse-textured soils than in medium-textured soils and following corn than soybean harvest. This suggests greater uncertainty in the productivity of hairy vetch–cereal rye mixtures compared with hairy vetch monocultures in medium-textured soils and following soybean. In terms of biomass production, the log response ratio of hairy vetch–cereal rye mixtures relative to hairy vetch monocultures was always greater than zero across a wide range of GDD (Fig. 4a). Moreover, with increasing GDD, the biomass of hairy vetch–cereal rye mixtures decreased relative to the biomass of hairy vetch monocultures.

Mixtures vs. Cereal Rye. Averaged across all studies, the biomass of hairy vetch–cereal rye mixture was 21% (CI: 9–35%) higher when compared with cereal rye monocultures (Fig. 2a). In terms of biomass yields, the positive response of hairy vetch–cereal rye mixtures relative to cereal rye monocultures were only observed in coarse-textured soils (mean: 29%; CI: 4–61%) and following corn harvest (mean: 36%; CI: 9–71%; Fig. 3a). In medium-textured soils and following soybean harvest, the biomass of hairy vetch–cereal rye mixtures did not differ significantly from that of cereal rye monocultures. In terms of biomass produced, the individual effect sizes (ln$R$) of hairy vetch–cereal rye mixture relative to cereal rye monocultures exceeded zero across wide range of GDD (500–2340) (Fig. 4b). This suggests greater productivity of mixtures than cereal rye monocultures irrespective of climate and cover crop growth period.

Mixtures vs. the Greatest Yielding Monoculture. Our meta-analysis showed that hairy vetch–cereal rye mixtures produced equivalent biomass to that of the greatest yielding (cereal rye in 74% of the cases) monocultures (mean: 5%; CI: -2 to 13%; Fig. 2a). The biomass of hairy vetch–cereal rye mixtures relative to the greatest yielding monocultures was also unaffected by soil type, previous cash crop, and hairy vetch seeding proportion (by weight) in the mixture (Fig. 3a, 5a). Although not significant, mixtures tend to produce more biomass than the greatest yielding monocultures with increasing GDD (Fig. 4c).

Nitrogen Content

Nitrogen content in the aboveground biomass of winter cover crops varied widely among studies and species (Fig. 1b; Table 1). Aboveground N content in hairy vetch and cereal rye monocultures averaged 122 (range: 3–236) and 51(range: 6–124) kg ha^{-1}, respectively. The average N content of hairy vetch–cereal rye mixtures was 118 kg N ha^{-1} and ranged from 11 to 310 kg ha^{-1} (Fig. 1b; Table 1).

Mixtures vs. Hairy Vetch. Overall, our meta-analysis suggests that hairy vetch–cereal rye mixtures accumulated as much N as that by hairy vetch monocultures (Fig. 2b). Moreover, the N content of hairy vetch–cereal rye mixtures relative to hairy vetch monocultures did not differ by soil type and previous crop (Fig. 3b). However, at lower GDD (<1000), the individual effect sizes (ln$R$) were above zero, suggesting greater N accumulation in hairy vetch–cereal rye mixtures than hairy vetch

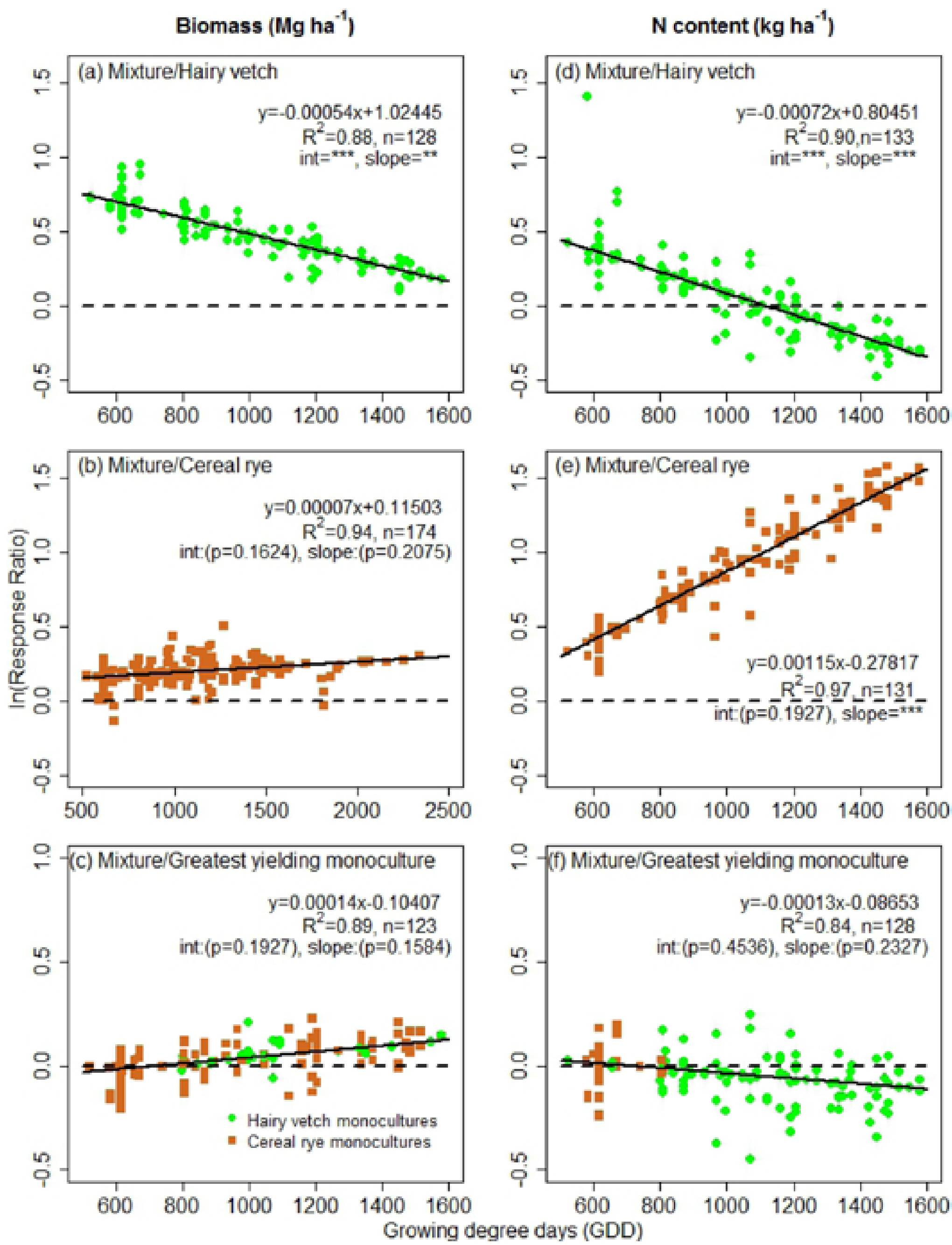

Fig. 4. The (a, b, c) biomass and (d, e, f) N content log response ratios of hairy vetch–cereal rye mixtures relative to hairy vetch, cereal rye, and the greatest yielding monocultures (the monoculture with highest biomass or N content) as a function of accumulated growing degree days (GDD). Green solid circles indicate that the greatest yielding monocultures were hairy vetch, and the brown solid rectangles indicate that the greatest yielding monocultures were cereal rye. Dashed horizontal lines at zero represent the log response ratio corresponding to equivalent performance of mixtures and monocultures. Symbols are used to indicate *P* values associated with intercept and slope estimates: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. For $P > 0.05$, the original *p* values were reported. Note the differences in scale in both the *x* and *y* axis.

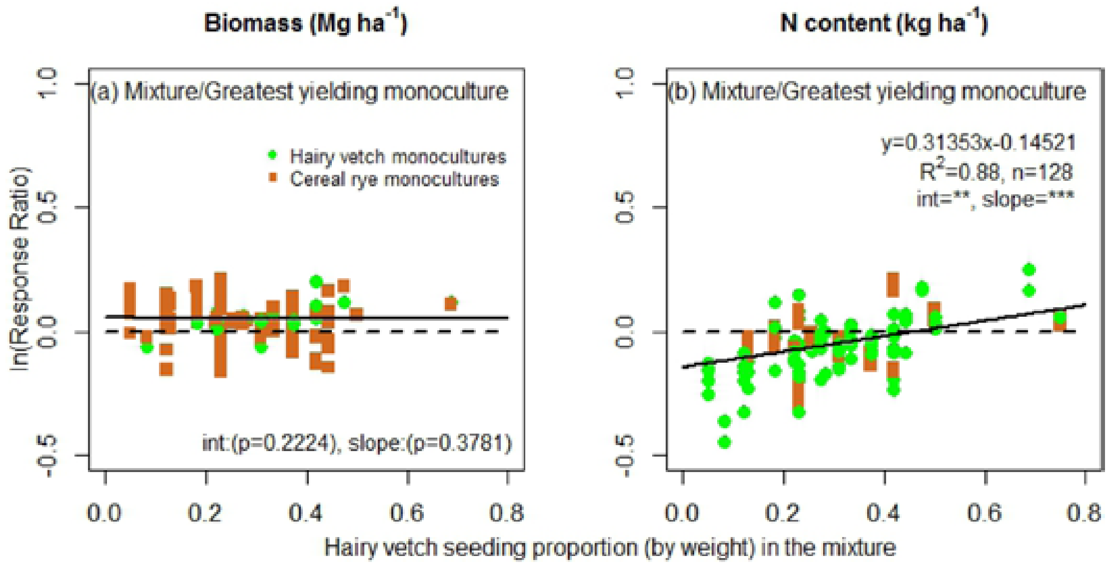

Fig. 5. The (a) biomass and (b) N content log response ratios of hairy vetch–cereal rye mixtures relative to the greatest yielding monocultures (the monoculture with highest biomass or N content) as a function of hairy vetch seeding proportion (by weight) in the mixture. Green solid circles indicate that the greatest yielding monocultures were hairy vetch, and the brown solid rectangles indicate that the greatest yielding monocultures were cereal rye. Dashed horizontal lines at zero represent the log response ratio corresponding to equivalent performance of mixtures and the greatest yielding monocultures. Symbols are used to indicate P values associated with intercept and slope estimates: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. For $P > 0.05$, the original p values were reported.

monocultures (Fig. 4d). The N content of hairy vetch–cereal rye mixtures decreased relative to hairy vetch monocultures with increasing GDD (Fig. 4d). At higher GDD (>1200), the individual effect sizes (ln$R$) were below zero, suggesting less N accumulation in hairy vetch–cereal rye mixtures than in hairy vetch monocultures.

Mixtures vs. Cereal Rye. Averaged across all studies, the N content of hairy vetch–cereal rye mixtures was 150% (CI: 99–214%) higher than that of cereal rye monocultures (Fig. 2b). Hairy vetch–cereal rye mixtures significantly outyielded cereal rye monocultures in terms of N accumulation in both coarse-textured (mean: 212%; CI: 120–344%) and medium-textured (mean: 95%; CI: 23–207%) soils and when following corn harvest (mean: 196%; CI: 87–368%; Fig. 3b). However, following soybean harvest, the overlap of CI with zero indicates similar N content in the mixtures and cereal rye monocultures. For cover crop N content, the log response ratio of hairy vetch–cereal rye mixtures relative to cereal rye monocultures was always greater than zero across a wide range of GDD (Fig. 4e). As the cumulative GDD increased, the N content of hairy vetch–cereal rye mixtures increased linearly relative to the N content of cereal rye monocultures (Fig. 4e).

Mixtures vs. the Greatest Yielding Monoculture. The N content of hairy vetch–cereal rye mixtures relative to the greatest yielding monocultures (hairy vetch in 85% of cases) remained unaffected by soil type and previous cash crop (Fig. 2b, 3b). Although not significant, hairy vetch–cereal rye mixtures tend to accumulate less N than the greatest yielding monocultures with increasing GDD (Fig. 4f). However, increasing hairy vetch seeding proportion (by weight) in the mixture increased N content of hairy vetch–cereal rye mixtures relative to the greatest yielding monocultures (Fig. 5b).

DISCUSSION

Productivity of Hairy Vetch–Cereal Rye Mixtures

Aboveground Biomass

Our meta-analysis shows that hairy vetch–cereal rye mixtures outyielded the respective monocultures in regard to biomass production (Fig. 2a). Averaged across all studies, mixtures produced 63 and 21% more biomass when compared with hairy vetch and cereal rye monocultures, respectively (Fig. 2a). These results suggest that mixtures help to ensure good performance in highly variable growing conditions as the best performing monoculture is always hard to predict. To maximize agroecosystem services associated with biomass production, some farmers prefer mixtures with transgressive overyielding or at least similar productivity to that of the greatest yielding monocultures (Lüscher et al., 2014). A 3-yr continental-scale field experiment by Finn et al. (2013) with 31 sites across 17 countries found that legume–grass mixtures exhibited transgressive overyielding in 60% of the sites, with a mean yield increase of 7% as compared with the greatest yielding monocultures. In this meta-analysis, however, we observed that hairy vetch–cereal rye mixtures produced equivalent, but not significantly higher, biomass to that of the greatest yielding monocultures (Fig. 2a).

The overyielding effect of mixtures has been attributed to either selection effects (the most productive species included in a mixture dominates mixture biomass production) or complementarity effects (efficient utilization of resources both in time and space due to species-niche partitioning or positive interspecific interactions) (Cardinale et al., 2006, 2007; Finney et al., 2016; Nyfeler et al., 2011; Tilman, 1999). The findings that mixtures produced equivalent or greater biomass than respective monocultures suggest that the hairy vetch–cereal rye mixtures were not merely dominated by the most productive species, but also benefitted from species resource complementarity and positive interspecific interactions. First, the roots of hairy vetch–cereal rye mixtures draw N from two different sources; hairy vetch fixes atmospheric N, whereas cereal rye accumulates N from the soil. Second, hairy vetch and cereal rye have complementary shoot characteristics and canopy architecture, allowing the mixtures to use light more efficiently compared with both monocultures (Keating and Carberry, 1993). The upright canopy architecture of cereal rye can be utilized as a climbing scaffold by hairy vetch, enhancing light interception and mixtures productivity. Third, hairy vetch grown in mixtures with cereal rye is less susceptible to over-winter mortality and produces higher biomass than hairy vetch grown alone (Brainard et al., 2012; Hayden et al., 2015). It has been observed that cereal rye grows quickly in the fall and insulates hairy vetch from extremely cool fall temperatures by reducing the extent of frost heaving and surface air movement and increasing snow retention (Brainard et al., 2012; Hayden et al., 2015; Smith, 1975). Other possible synergistic effects that could contribute to transgressive overyielding may include the ability of mixtures to reduce the incidence of pests and diseases, and efficient use of soil moisture due to differing root growth patterns of component species (Finn et al., 2013). Another possibility for the increased productivity of mixtures relative to the greatest yielding monocultures could be a positive effect of lower seeding rate of each species in a mixture, i.e., lower intraspecific competitions.

Total Nitrogen Content

Overall, our meta-analysis suggests that the N content of hairy vetch–cereal rye mixtures was greater than cereal rye monocultures, but equivalent to hairy vetch and the greatest yielding monocultures (Fig. 2b). The biomass overyielding effects of hairy vetch–cereal rye mixtures discussed above could be the potentially greatest contributor to greater or equivalent N content in hairy vetch–cereal rye mixtures. Moreover, the greater N content in hairy vetch–cereal rye mixtures could also be due to greater N concentration in hairy vetch–cereal rye tissues grown in mixtures. There are at least two possible reasons for greater or comparable N concentrations in hairy vetch–cereal rye mixtures to pure hairy vetch. First, cereal rye can stimulate the N-fixation capacity of legumes such as hairy vetch (Izaurralde et al., 1992; Karpenstein-Machan and Stuelpnagel, 2000; Nyfeler et al., 2011; Lüscher et al., 2014; Suter et al., 2015). The N-fixation capacity of legumes is largely regulated by the gap between plant N demand (sink) and soil N availability (source) in the cropping system (Hartwig, 1998; Soussana and Tallec, 2010). In hairy vetch–cereal rye mixtures, cereal rye grows quickly and its dense root system takes up most of the N available from residual soil N sources, creating an N-limited system. The N-limited environment created by the cereal rye induces hairy vetch to fix a higher proportion of N than it would in monocultures. Second, some of the N fixed in the legumes can be transferred to grasses, thereby increasing N concentration in the grasses intercropped with legumes (Fujita et al., 1992; Pirhofer-Walzl et al., 2012). The recently fixed N from legumes is available to grasses via root exudation or decomposition of dead roots and leaf litter of legumes (Fujita et al., 1992). Nyfeler et al. (2011) showed that N accumulation by grasses increases with increasing sown proportion of legume up to 20 to 30%; above this threshold, a decrease was observed. By contrast, N concentration of grasses was always increasing with legume proportion, but this could also be due to lower intraspecific competition. These mechanisms may underlie the disproportionately high N accumulation and concomitant transgressive overyielding of biomass that we observed in hairy vetch–cereal rye mixtures.

Factors Affecting the Productivity of Hairy Vetch–Cereal Rye Mixtures

The productivity of hairy vetch–cereal rye mixtures depends on soil type, previous cash crop, accumulated GDD, and mixture seeding proportions (by weight). In this meta-analysis, we found that the hairy vetch–cereal rye mixtures performed better than cereal rye monocultures in coarse-textured soils and following corn harvest. In medium-textured soils and following soybean harvest, the performance of hairy vetch–cereal rye mixtures relative to cereal rye monocultures was nonsignificant (Fig. 3a, 3b). This was presumably due to greater availability of soil N in medium-textured soils and following soybean, which likely enhanced the productivity and N content of cereal rye monocultures. Greater N availability to cover crops following soybean harvest, as compared with corn, may be likely due to lower residual N following corn due to uptake and potential immobilization of residual N by corn residues during its decomposition.

The productivity of hairy vetch–cereal rye mixtures compared with respective monocultures was also affected by accumulated GDD during the cover crop growth period (Fig. 4). Hairy vetch–cereal rye mixtures consistently produced more biomass than both hairy vetch and cereal rye monocultures across a wide range of GDD (Fig. 4a, 4b). Similarly, hairy vetch–cereal rye mixtures consistently accumulated more N than cereal rye monocultures across a wide range of GDD, but only at lower GDD (<1000) when compared with hairy vetch monocultures (Fig. 4d, 4e). The lower N content of mixtures relative to hairy vetch monocultures at higher GDD (>1200) was most probably due to lower hairy vetch biomass in the mixture. As accumulated GDD increased, the biomass and N content of hairy vetch–cereal rye mixtures decreased relative to the biomass and N content of hairy vetch monocultures (Fig. 4a, 4d). In sharp contrast, the N content of hairy vetch–cereal rye mixtures increased relative to the N content of cereal rye monocultures with increasing GDD (Fig. 4e). These trends suggest that hairy vetch grown in monocultures, but not in mixtures, performed relatively better and grow actively at higher GDD. Under hot and dry climates, Brainard et al. (2011) observed that grass species suppressed the growth of legume species in mixture resulting in low legume biomass and poor nodulation. Therefore, it can be concluded that the accumulated GDD during the cover crop growing season not only affects the productivity of cover crop species, but also the composition of cover crop mixtures. Farmers, especially from regions with lower GDD accumulation (either due to extremely long winters or a narrow window between planting and termination), could achieve greater biomass and N benefits by planting hairy vetch–cereal rye mixtures instead of hairy vetch monocultures. Conversely, growers in warmer climates or with longer opportunities for cover crop growth would achieve more N benefits with hairy vetch monocultures.

Increasing hairy vetch seeding proportion (by weight) in the mixture increased N content of hairy vetch–cereal rye mixtures compared with the greatest yielding monocultures (Fig. 5b).

This was primarily because the N content of hairy vetch–cereal rye mixtures depends on the relative biomass of hairy vetch in the mixture, which generally increases with increasing hairy vetch seeding proportion (by weight) in the mixture (Hayden et al., 2014; Poffenbarger et al., 2015c). Moreover, increasing hairy vetch seeding proportion (by weight) in the mixture has also been observed to increase N concentration in the cereal rye tissues (Hayden et al., 2014). Our meta-analysis further indicated that the proportion of hairy vetch seeds by weight in the mixture should exceed 46% to achieve comparable levels of total N content in the mixtures to that in the greatest yielding monocultures (usually hairy vetch). Farmers could reduce cover crop seed costs by replacing half of the hairy vetch seeds in monocultures with relatively cheaper cereal rye seeds without compromising aboveground biomass and N content. Moreover, the finding that mixtures typically generate greater biomass but accumulate a similar amount of N as hairy vetch monocultures suggests that the mixtures have higher C/N ratios compared with hairy vetch monocultures. The higher C/N ratios in the mixtures will result in slower N release and decomposition rates compared with hairy vetch monocultures, thereby reducing potential early season N losses and better synchronizing the N release with N demand of the succeeding cash crop.

Limitations of the Study

All studies included in this meta-analysis were conducted in the United States, a majority of which were performed in the northeastern and southeastern states of the United States. While there were studies that evaluated other legume–grass mixtures such as hairy vetch–oat (*Avena sativa* L.) or hairy vetch–barley (*Hordeum vulgare* L.) or multi-species legume–grass mixtures, these studies were not included in the meta-analysis. Therefore, caution should be taken while generalizing the results from this meta-analysis to other legume–grass mixtures that are commonly adopted by farmers.

Cover crop mixtures growth and productivity is highly influenced by residual soil N in the fall at the time of its planting. Residual soil N may come from fertilizer unused by previous cash crop or from decomposition of soil organic matter, manure or previous crop residues left in the soil. In a study conducted in Wisconsin, Bundy and Andraski (2005) observed that the biomass and N content of cover crops were highly correlated with the biomass and N content of previous crop residues left in the soil. Another factor that could potentially affect mixtures productivity is precipitation during the cover crop growing period. Ofori and Stern (1987) suggested that dry conditions during the growth period favored the productivity of grass species in legume–grass intercropping systems. Most of the studies included in this meta-analysis, however, did not provide any information on residual soil N or previous crop residues or precipitations during the cover crop growth period, limiting our analysis to understand the effect of these factors on the relative productivity of hairy vetch–cereal rye mixtures. Future studies evaluating cover crop mixtures over monocultures should also take into account of the multiple factors that influence mixtures productivity, including soil N availability and precipitation during cover crop growth period. Future studies should also prioritize research on belowground biomass and N accumulation with cover crop mixtures relative to monocultures. Although hairy vetch and cereal rye species in mixture takes up N from different sources and have complementary shoot characteristics, competition for resources such as light and water persists between species when grown in mixture. It is possible that such inter-specific competition induced within mixture may result in changes in root partitioning that might either outweigh or amplify the aboveground effects observed in this study.

CONCLUSIONS

Farmers must manage multiple cropping system objectives, and therefore need tools that can provide multiple services (e.g., erosion control, weed suppression N scavenging, N fixation). Cover crop biomass and N content are two indicators of the potential agroecosystem services cover crops can provide. Overall, our meta-analysis suggests legume–grass mixtures, in this case hairy vetch–cereal rye, may provide greater agroecosystem services (such as weed suppression, erosion control, N retention, and N supply) than either monoculture species by producing equivalent or more biomass than both monocultures and accumulating as much N as pure hairy vetch. Results further indicated that the benefits of adopting hairy vetch–cereal rye mixtures, relative to monocultures, is more pronounced in coarse-textured soils and following corn as compared with soybean. Accumulated GDD also impacted the performance of mixtures relative to monocultures, but the response differed depending on the monoculture species. While growers in cold climates and narrow growing periods (low GDD) benefit from hairy vetch–cereal rye mixtures, hairy vetch monocultures provide more N benefits in warmer climates and with longer opportunities for cover crop growth (high GDD). Based on our findings, hairy vetch–cereal rye mixtures are recommended over monocultures when the goal is to maximize both cover crop biomass and N content, and better synchronize N release with N demand of the succeeding cash crop. Future research should expand the evaluation of cover crop mixtures productivity and multi-functionality to a broader set of legume and grass species.

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