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Cultivar diversity as a means of ecologically intensifying dry matter production in a perennial forage stand

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Abstract. The relationship between genotypic diversity and productivity has not been adequately explored in perennial forage production systems despite strong theoretical and empirical evidence supporting diversity's role in ecosystem functioning in other managed and unmanaged systems. We conducted a two-year field experiment with six cultivars of an agriculturally important forage grass, *Lolium perenne* L. (perennial ryegrass). Dry matter production of *L. perenne* and the weed community that emerged from the soil seed bank were measured each year in treatments that ranged from cultivar monocultures to three- and six-way cultivar mixtures, all sown at a constant seeding rate. Mean *L. perenne* dry matter production increased with increasing cultivar diversity and was highest in mixtures that contained cultivars representing the greatest additive trait range (calculated on rankings of three traits: winter hardiness, heading date, and tolerance to grazing). Mixtures had greater yields than those predicted by the mean of their component monoculture yields, but there was evidence that highly productive cultivars may have dampened over-yielding in mixtures. Weed abundance was correlated with *L. perenne* dry matter, but not *L. perenne* cultivar diversity. These results suggest that multi-cultivar mixtures may have utility as an approach to ecologically intensifying perennial forage production. Additional research will be necessary to determine the mechanisms responsible for the over-yielding observed in this study and the generality of these findings.

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INTRODUCTION

Over the coming decades, agriculture will be tasked with meeting the challenges of supporting a growing global population and adapting to a changing and increasingly variable climate (Kurukulasuriya and Rosenthal 2003, Anwar et al. 2013). Previous analyses indicate that by 2050 crop demand will increase by 100–110% over 2005 demand levels (Tilman et al. 2011), and that global demand for meat and milk products is projected to increase by 81 and 170 million metric tons, respectively, by 2020 (Delgado 2005). With sustainability as a benchmark, agriculture will be required to meet this demand without contributing substantially to additional environmental degradation (Tilman et al. 2011). While no single strategy will be adequate to address all of these challenges, a suite of strategies, known collectively as ecological intensification (Cassman 1999, Dore et al. 2011, Bommarco et al. 2013) could play an important role in achieving our global food security objectives while reducing dependence on external inputs such as fertilizers

and pesticides (Bommarco et al. 2013).

Ecological intensification involves the management of biological interactions that contribute positively to agricultural production (Cassman 1999, Dore et al. 2011, Bommarco et al. 2013). Interactions that occur between genetically diverse plant species (i.e., interspecific diversity) are one example, and these have been shown to contribute to important ecosystem functions such as resource capture, productivity, resistance to weed invasion, and stability in both unmanaged (Tilman et al. 1996, Aarssen 1997, Hector et al. 1999, Tilman et al. 2001, Leps 2004, van Ruijven and Berendse 2005, Grace et al. 2007, Mueller et al. 2013) and managed ecosystems (Tracy et al. 2004, Tracy and Sanderson 2004*a*, *b*, Sanderson et al. 2005, Smith et al. 2008, Lin 2011).

Much less explored, but potentially equally important for ecosystem functionality, are interactions that occur between genetically diverse individuals *within* a species (i.e., intraspecific or genotypic diversity). Data to support the utility of increasing intraspecific diversity in agricultural systems come primarily from experiments conducted with annual grain crops and some perennial tree crops. In these studies, monocultures and multi-cultivar mixtures of a single crop species are compared in terms of yield and other agronomic response variables. Demonstrated effects of multi-cultivar plantings include increased grain yield (Kovacs and Abranyi 1985, Jedel et al. 1998, Gallandt et al. 2001), increased disease resistance (Akanda and Mundt 1996, Hariri et al. 2001, Zhu et al. 2005), increased pest resistance (Beres et al. 2007, Tooker and Frank 2012), increased grain quality (Swanston et al. 2000, Swanston et al. 2005, Mille et al. 2006), and increased yield stability (Dubin and Wolfe 1994, Tadesse and Blank 2003). Proposed mechanisms responsible for improved performance of multi-cultivar mixtures include facilitation, trait complementarity, and differential resistance to disease (Newton et al. 2009).

While increasing intraspecific diversity has been shown to be a promising approach to ecologically intensifying annual grain and perennial fruit crop production, it has not been adequately explored in perennial forage systems. Given that ruminant livestock will account for 27% of the projected global increase in meat consumption by 2020 (Delgado 2005), and presumably the majority of the increase in milk consumption (Knights and Garcia 1997, Fuller et al. 2006), development of effective strategies for ecologically intensifying perennial forage systems is crucial. Without such strategies, future gains in productivity will likely depend wholly on the development and adoption of new biotechnologies, increased use of synthetic agrochemicals and/or conversion of other types of land uses to perennial forage systems (Bommarco et al. 2013).

To address the dearth of information concerning the effects of intraspecific diversity in perennial forage systems, we report data from an experiment in which we examined the effects of increasing intraspecific (i.e., cultivar) diversity on the stand-level productivity of an agriculturally important forage grass, *Lolium perenne* (perennial ryegrass) in the absence of external inputs of fertilizer, pesticides, and irrigation. Treatments ranged from single cultivar monocultures to mixtures of three and six cultivars, all at a constant total seeding rate. We examined three main questions: (1) Does increasing cultivar diversity increase stand-level productivity of *L. perenne*? (2) Are cultivar mixtures more resistant to weed invasion from the soil seed bank? (3) Are productivity responses in mixtures related to the trait diversity present in the component cultivars?

MATERIALS AND METHODS

Site description

The experiment was conducted at the University of New Hampshire Kingman Research Farm in Madbury, NH (43°11′ N, 70°56′ W). Dominant soil type at this site is a Charlton fine sandy loam (Charlton = coarse-loamy, mixed, mesic Entic Haplorthods) (USDA NRCS 2014). Mean monthly precipitation during the growing season (May–September) at the site was 86 mm and 136 mm for 2012 and 2013, respectively. Annual mean minimum and maximum temperatures were 5°C and 16°C for 2012 and 4°C and 15°C for 2013. The coldest temperatures were −19°C for 2012 and −20°C for 2013, and the hottest temperatures were 35°C for 2012 and 34°C for 2013. For several years prior to the experiment the site had been under a conventionally managed vegetable-winter rye cover crop rotation as

part of a squash and pumpkin (Cucurbitaceae) breeding program.

Experimental design and methodology

The experiment was established in August 2011 to examine the effects of manipulating the number of cultivars of *L. perenne* grown in mixture on aboveground dry matter production and weed suppression. The treatments included monocultures of each of six *L. perenne* cultivars ('Barsprinter', 'Mara', 'Remington', 'Bargala', 'Dunluce', and 'Bealey', henceforth referred to as cultivars A–F), 17 of the possible 20 three-way mixture combinations, and a mixture that included all six cultivars. Three of the possible three-way combinations were accidentally omitted due to a technical error. The monocultures and three-way mixtures were replicated once in each of four blocks ($n = 4$) and the six cultivar mixture was replicated twice in each block ($n = 8$). The cultivars were obtained from a commercial seed company (Barenbrug USA, Tangent, OR). Each of the six *L. perenne* cultivars differed with respect to their ranking for each of three physiological traits: winter hardiness, heading date, and grazing tolerance (D. Singh, *personal communication*). Total seeding rate was held constant at 22.5 kg/ha across all treatments, representing the high end of the recommended rate for *L. perenne* when seeded without a companion crop (Cool and Hannaway 2004). Mixtures comprised even proportions of each cultivar; therefore, within the three-way and six-way mixtures, individual cultivars were seeded at 1/3 and 1/6 the rate, respectively. Treatments were assigned randomly to plots within each block. The four replicate blocks were separated by 1 m buffer strips which were periodically mowed. Individual plots (experimental units) measured 2 m by 2 m with no buffer strips between plots. Prior to establishing the treatments, the field was moldboard plowed and the seedbed was prepared using a Perfecta II field cultivator (Unverferth Equipment, Kalida, OH). Seeds were broadcast by hand on 17 August 2011 and incorporated into the soil with a rake. No fertilizers, irrigation, or pesticides were used during the experiment.

Dry matter production of *L. perenne* and weeds that emerged from the soil seed bank were measured in each plot three times during the study period: once during the establishment year (June 2012) and twice in 2013 (June and September). Dry matter was sampled by clipping all aboveground biomass to a height of 7.5 cm from a 50 cm by 50 cm square sub-plot placed within the center of each plot. Immediately following plant sampling, all plots were mowed to a height of 7.5 cm to simulate uniform grazing or haying, and the clippings were removed from the plots. For each sampling period, shoots of *L. perenne* and the emergent weed community were separated and dried to constant weight within two weeks of sampling, and then weighed to the nearest 0.01 g.

Statistical analysis

All analyses were conducted in SYSTAT 13 (Systat Software 2013) or R 3.0.1 (R Development Core Team 2013). We employed a mixed model approach to quantify the response of *L. perenne* dry matter production (yield) to *L. perenne* cultivar diversity (CD). First, a model using both years of data was evaluated, with either *L. perenne* yield or total weed biomass as the dependent variable. The variables CD, year, and their interaction were considered fixed effects. The variables plot (to account for repeated measurements from the same plot), treatment (to account for differences in yield based on the cultivar or cultivars present), and block were included as random effects. If an interaction between year and CD was detected, years were analyzed separately. Because crop biomass and weed suppression are often positively associated, and because diversity has been linked to community invasibility in past studies, we also evaluated the relationship between weed abundance (biomass of weeds that emerged from the soil seed bank) and *L. perenne* yield and weed abundance and CD using the same approach. Weed biomass was natural log transformed to satisfy the assumptions of the analyses. To determine if weed species richness was associated with CD or *L. perenne* yield, generalized linear mixed effects (GLMER) models with poisson error distribution (to account for the fact that the response variable was a count of weed species) were used. GLMER models were evaluated with year by CD or *L. perenne* yield interactions as above with plot and block as random effects.

To evaluate the effect of CD on the spatial stability of *L. perenne* yield, the coefficient of variation (CV) was calculated for *L. perenne* yield

across treatment replicates. CV was used as a dependent variable in an ANOVA with CD, year, and their interaction as independent variables. We did not evaluate temporal stability of *L. perenne* yield because only two years of data were available.

To compare the yield of *L. perenne* mixtures to the predicted yield based on component monoculture yields, a yield index (*YI*) was calculated for each mixture treatment plot in each block in each year using the following method:

$$YI = \frac{Y_{obs}}{\left(\dfrac{\sum\limits_{i=1}^{n} Y_m}{n}\right)}$$

where Y_{obs} = the observed *L. perenne* yield for the mixture plot, Y_m = the monoculture yield of cultivar i in that block, and n is the number of cultivars in the mixture. With this index, values of 1 indicate that the observed yield was equal to the predicted yield, while values of less than or greater than 1 indicate under-yielding and over-yielding, respectively (Trenbath 1975). Over-yielding has been attributed to facilitation or niche complementarity (Hooper 1998, Jonsson and Malmqvist 2003), while under-yielding is indicative of competition (Hooper 1998). The departure of *YI* from the predicted value was assessed with a two tailed one sample t-test (95% confidence level). *YI* was natural log transformed to meet the assumption of normality, so the null hypothesis was that $YI = 0$ (or observed yields = predicted yields). This analysis was performed for both years separately, with all cultivar mixtures analyzed together, and with three cultivar and six cultivar mixtures analyzed separately. To determine whether mixtures transgressively over-yielded, i.e., the mixture yields exceeded the yield of the highest yielding cultivar in monoculture (Trenbath 1975), an identical analysis was performed where the yield index, YI_{high}, was simply the observed mixture yield divided by the yield of the highest yielding component cultivar.

The cultivars differed in winter hardiness, tolerance to grazing, and heading date, and were ranked according to these characteristics by the seed company (D. Singh, *personal communication*). To determine if these specific traits or the range of these traits present in a given mixture were associated with its performance, we calculated two trait values for each mixture: the average trait value for each trait and the additive trait range. Average trait value was calculated for each individual trait in each mixture as the sum of the trait values present in the mixture divided by the number of cultivars in the mixture. Additive trait range was calculated by first taking the maximum rating present in the mixture minus the minimum rating present in the mixture for each trait in each mixture treatment. For example, if a mixture included cultivars with winter hardiness ratings ranging from 4 to 7, the trait range for winter hardiness in that mixture would be 3. The additive trait range was calculated by adding the trait ranges for each of the three traits together for each mixture. This gave a rough approximation of the functional diversity present within each mixture based on these three traits. Lastly, the monoculture yield of the highest yielding cultivar in each mixture in each block (yield_high) was used as a simple approximation of the competitive environment within that mixture. Average trait value, additive trait range, and yield_high were then used as fixed effects to model the response of *YI* in separate mixed models with block and plot (for analysis of data from both years together) or block (for analysis of data separated by year) as random factors. The variable *YI* was natural log transformed to meet the assumptions of the analyses.

RESULTS

Effects of cultivar diversity on *L. perenne* yield

The highest yielding cultivar varied from block to block, and from year to year (Table 1). A summary of the mean yield values for the individual treatments is presented in Table 2. There was no significant interaction between year and *L. perenne* CD, indicating that data from both years could be pooled for analysis. However, there was a year effect on mean *L. perenne* yield ($p = 0.005$, $F_{1,99} = 8.16$) due to generally lower yields in 2013 (Table 2). When data from both years were analyzed together, *L. perenne* yield increased with CD ($p = 0.01$, $F_{2,99} = 4.855$; Fig. 1). A post hoc Tukey test indicated that relative to the mean monoculture cultivar yield, *L. perenne* yields were significantly greater in the three cultivar mixtures (mean increase = 67 g/m², $p = 0.03$, $t = -2.61$) and the six cultivar mixture (mean

Table 1. *Lolium perenne* monoculture dry matter yield (g/m^2) for each block in each year of the study and the mean of blocks. Values in boldface represent the highest yields for the indicated block and/or time period. Cultivar A = 'Barsprinter', B = 'Mara', C = 'Remington', D = 'Bargala', E = 'Dunluce', and F = 'Bealey'.

Cultivar	2012					2013				
	1	2	3	4	Mean	1	2	3	4	Mean
A	178	**471**	259	**391**	325	235	**507**	312	364	354
B	205	362	411	199	294	**257**	489	**475**	**372**	**398**
C	296	286	**667**	388	**409**	197	406	330	346	320
D	106	174	278	258	204	72	283	431	322	277
E	245	382	416	225	317	148	358	376	253	284
F	**351**	439	383	353	381	199	367	251	229	262

increase = 125 g/m^2, $p = 0.03$, $t = -2.59$). Cultivar diversity had no effect on the spatial stability (CV) of *L. perenne* yield across replicates ($p = 0.73$, $F_{2,49} = 0.321$), and there was no significant year effect or interaction.

Effects of cultivar diversity and yield on weed biomass and species richness

There was no evidence that CD affected weed biomass in either growing season ($p = 0.93$ and 0.47 for 2012 and 2013, respectively). The rela-tionship between *L. perenne* yield and weed biomass was inconsistent between years (*L. perenne* yield by year interaction, $p = 0.05$, $F_{2,104} = 3.07$). When weed biomass data were analyzed separately by year, there was no association between weed biomass and *L. perenne* yield in 2012 ($p = 0.8$, $F_{1,103} = 0.05$), but there was a negative association in 2013 ($p < 0.001$, $F_{1,107} = 26.35$; Fig. 2). We observed no significant associ-ations between either CD or *L. perenne* yield and weed species richness (data not shown).

Table 2. Mean and standard deviation (SD) of *Lolium perenne* dry matter yield (g/m^2) for each year of the study. 'Average' is the average of 2012 and 2013 yields (g/m^2), 'ΔYield' is the proportion by which the average yield (g/m^2) changed from 2012 to 2013, negative numbers indicate a decrease in yield. Values in boldface and italics represent the highest yield of all treatments within a cultivar diversity category (1 or 3). Values followed by a dagger (†) represent the highest overall yield. Cultivar A = 'Barsprinter', B = 'Mara', C = 'Remington', D = 'Bargala', E = 'Dunluce', and F = 'Bealey'.

| Cultivar(s)	2012		2013		ΔYield	Average (g/m^2)
	Mean (g/m^2)	SD	Mean (g/m^2)	SD		
A	325	131	354	115	0.09	340
B	294	108	*398*	108	0.35	346
C	*409*	178	320	88	−0.22	*365*
D	204	80	277	151	0.36	240
E	317	96	284	106	−0.10	300
F	381	41	262	73	−0.31	321
A, B, F	405	189	371	135	−0.08	388
A, C, D	444	23	369	166	−0.17	406
A, C, E	455	73	356	78	−0.22	405
A, C, F	508	214	371	73	−0.27	439
A, D, E	423	255	337	88	−0.20	380
A, D, F	346	77	265	98	−0.23	306
A, E, F	397	168	381	58	−0.04	389
B, C, D	330	82	356	43	0.08	343
B, C, E	371	112	344	43	−0.07	357
B, C, F	312	148	292	111	−0.06	302
B, D, E	422	189	311	76	−0.26	366
B, D, F	353	120	340	90	−0.04	347
B, E, F	519	249	337	151	−0.35	428
C, D, E	397	93	*563*†	60	0.42	480
C, D, F	345	126	392	103	0.13	369
C, E, F	*610*†	186	419	114	−0.31	*515*†
D, E, F	349	159	327	156	−0.06	338
A, B, C, D, E, F	486	239	402	146	−0.17	444
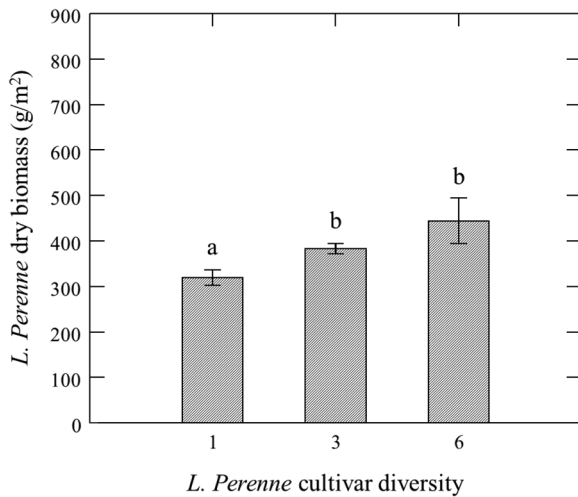
Fig. 1. Dry matter yield (g/m²) of *Lolium perenne* at different levels of cultivar diversity (no. cultivars) for 2012 and 2013 data combined.

L. perenne yield indices

Analysis of the yield index data indicated that yields of the mixture treatment plots were greater than what would be predicted based on the yields of the individual component cultivars grown in monoculture. In all cases, with the exception of the six cultivar mixture in 2013,
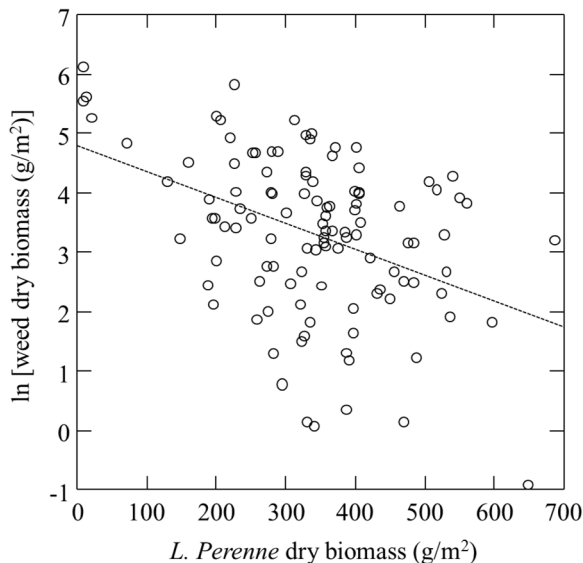

Fig. 2. The relationship between natural log transformed weed dry matter (g/m²) and *L. perenne* dry matter yield (g/m²) for 2013.

yields in the mixture treatments were significantly higher than the predicted yield, based on *YI* (Table 3). We found no evidence that the yield of the mixtures was significantly higher than that of the highest yielding component grown in monoculture, based on YI_{high} (Table 3). We examined associations between *YI* and *L. perenne* average cultivar trait values and found no significant relationships. In contrast, *YI* was positively associated with the additive trait range of the mixture when data from both years were combined ($p = 0.03$, $F_{1,76} = 4.896$; Fig. 3), and year did not affect this relationship. When evaluating the response of *YI* to $yield_{high}$, there was a significant interaction between $yield_{high}$ and year. Specifically, *YI* decreased as $yield_{high}$ increased in 2013 ($p < 0.001$, $F_{1,71} = 17.3$); however, this trend was only marginally significant in 2012 ($p = 0.09$, $F_{1,71} = 3.02$).

DISCUSSION

Our data support the hypothesis that *L. perenne* productivity at the stand level (dry matter g/m²) increases with increasing cultivar diversity. Since productivity differed among individual cultivars, one possible explanation would be that increasing the number of cultivars in a mixture increased the chances of including high yielding cultivars, thereby increasing the average productivity of treatments as cultivar diversity increased. These types of sampling effects have been discussed extensively (Aarssen 1997, Tilman et al. 1997, Wardle 1999). However, if our results were due solely to sampling effects, we would not expect the productivity of any of the mixtures to exceed the mean of the component cultivar yields. This was clearly not the case, as productivity of many of the mixtures exceeded the mean of the component monocultures (Tables 2 and 3). However, we did not find that the mixture yields were greater than the yield of the highest yielding component cultivar, i.e., there was over-yielding, but not *transgressive* over-yielding (sensu Schmid et al. 2008).

While over-yielding in this case can be used as evidence that other processes besides simple sampling effects were occurring, the interpretation of our results as over-yielding relies on the assumption that all of the component cultivars remained present and in relatively equal propor-

Table 3. Mean untransformed yield index (YI) and standard deviation (SD). The p values are from two tailed one sample t-test using natural log transformed yield index values (H_0 mean yield index = 0). No subscript = predicted mixture yield index calculation, the subscript "high" = highest yielding cultivar index calculation, no. cultivars = cultivar diversity treatments considered in the index calculation and t-test, n = number of treatment plots.

No. cultivars	YI	SD	p	YI_{high}	SD_{high}	p_{high}	n
2012							
3 and 6	1.31	0.46	<0.001	1.01	0.38	0.15	76
3	1.29	0.45	<0.001	1	0.37	0.15	68
6	1.45	0.52	0.04	1.04	0.69	0.82	8
2013							
3 and 6	1.3	0.67	0.004	1.04	0.47	0.29	76
3	1.29	0.68	0.009	1.04	0.48	0.23	68
6	1.36	0.55	0.19	1.05	0.4	0.87	8

tions in the mixtures throughout the duration of the study. The possibility exists that the higher yield indices observed for mixtures were due to the highest yielding component cultivar somehow dominating within the mixture treatment. Although all cultivars within mixture treatments were planted in equal proportions, it is possible that the highest yielding cultivar for each particular plot could have been present in greater proportions than expected, thereby contributing more than the expected amount to the observed

Fig. 3. The relationship between additive trait range of cultivar mixtures and *L. perenne* yield index (YI). Additive trait range is calculated as the sum of the ranges of each of three ratings (heading date, winter hardiness, and grazing tolerance) based on the *L. perenne* cultivars present in the mixture.

yields. This seems unlikely, however, as the observed mixture yields were virtually identical to the yield of the highest yielding cultivar (Table 3), and in light of this, that explanation would require the proportion of the highest yielding cultivar in any given mixture to have increased to 100%. The unlikeliness of this explanation has been elaborated on elsewhere (Schmid et al. 2008); however, we are unable to conclusively rule out this explanation with the current data. Additionally, we observed no obvious reduction in the density of individuals present in any of the monoculture treatments over the course of the study, such as might occur if particular cultivars were maladapted to or otherwise intolerant of the conditions specific to our study site. Taken together, the data from this experiment suggest that the observed increase in productivity was not solely due to a sampling effect, and that facilitation or complementarity among cultivars likely contributed to the productivity response we observed in the mixtures.

The additive trait range, which is an approximation of functional diversity, was positively associated with YI in our study. This supports the hypothesis that greater functional diversity can lead to facilitation or complementarity (Hooper 1998, Fridley 2001, Hooper and Dukes 2004). Although the ideas of complementarity and facilitation have traditionally been discussed in the context of mixtures of species (Fridley 2001), there is no reason to think that these same relationships might not also apply to mixtures of cultivars of the same species with physical, physiological, and phenological differences (Newton et al. 2009). Our data suggest that as
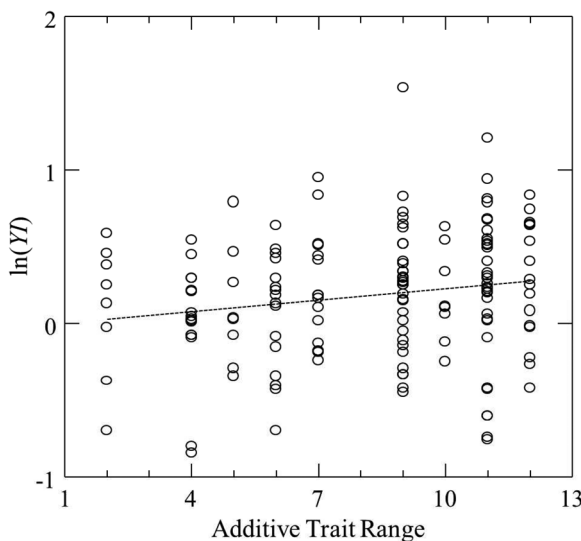
the range of functional diversity among cultivars in a mixture increases, at least in terms of winter hardiness, heading date, and grazing tolerance, their potential to over-yield also increases. However, we did find evidence that competitive interactions may also have determined the amount of over-yielding observed.

Although we could not evaluate the effects of competition between cultivars within the mixture treatments directly, leaf area and dry matter yield have been linked to competitive ability (Goldberg 1996, Lemerle et al. 1996, Rosch et al. 1997). Thus, we used the observed monoculture yield of the highest yielding cultivar present in a mixture (yield$_{high}$) as an approximation of the intraspecific competitive environment within that mixture. This relies on the assumption that higher values of yield$_{high}$ would equate with more intense competition, i.e., that more productive cultivars are more competitive. Since yield$_{high}$ values were specific for each block, this served to further differentiate potential competitive effects from the effects of environmental heterogeneity. As one would expect, within a given block, if a mixture had a larger value for yield$_{high}$, it also had a larger predicted yield (Pearson correlation = 0.96). In the absence of competition between cultivars, we would expect that having a higher yielding cultivar in a mixture would also increase the observed yield of that mixture. However, there was no significant relationship between yield$_{high}$ and observed mixture yields. Furthermore, in the second year of the study we observed significantly lower yield index (*YI*) values in mixtures with higher yield$_{high}$ values (data not shown), indicating less over-yielding in the mixtures with the more competitive higher yielding cultivars. This suggests that facilitative effects between cultivars were dampened by the inclusion of more competitive cultivars; however, additional research will be necessary to test this hypothesis.

We expected to observe a negative relationship between *L. perenne* biomass and weed abundance, and indeed this was the case. Since *L. perenne* biomass was positively associated with CD, one could hypothesize that weed biomass would also be related to CD. However, our data did not support this hypothesis. This indicates that while the number of cultivars present in a mixture is an important determinant of overall *L.*

perenne dry matter production, dry matter production is more instrumental in determining weed biomass than is the number of cultivars. In other words, particularly productive *L. perenne* cultivars appear to be just as effective in reducing weed abundance as equally productive cultivar mixtures. While several of the cultivar mixtures in our study produced more biomass than individual cultivars, some did not, and this variability obviously affected the relationship between CD and weed biomass. It is also likely that there are other factors influencing weed abundance within a given level of CD aside from *L. perenne* biomass, thereby increasing the level of variability of weed biomass within a given level of CD beyond the level of variability in *L. perenne* biomass. Some possible factors include spatial variability in weed seed bank composition and abundance across the study site (Cardina et al. 1997, Rew and Cousens 2001, Conn 2006, Pollnac et al. 2008) and competition within the weed community (Clements et al. 1994, Pollnac et al. 2009).

Previous research has demonstrated that intraspecific or genotypic diversity may be an important predictor of productivity and other ecosystem services in a variety of ecosystems (Hughes et al. 2008), and our data support this premise for a perennial forage grass system. This suggests that ecological intensification via incorporation of intraspecific diversity could be a viable tool to help meet the challenge of rising demand for forage and grazing-based meat and dairy products. From an applied perspective, this provides an alternative to strict reliance on interspecific diversity as a means to ecologically intensifying perennial forage production systems, which could be particularly useful in situations where a single species is the typical management target, or where multi-species mixtures may be viewed negatively for cultural, agronomic, or logistical reasons (Newton et al. 2009). While we found no evidence that *L. perenne* cultivar mixtures transgressively over-yielded, they did perform just as well as the highest yielding cultivars in terms of both dry matter yield and weed suppression.

Another potential benefit to cultivar diversity in agricultural systems is enhanced stability or resilience to climatic variability or other types of disturbances (Hajjar et al. 2008). Genotypic

diversity has been shown to aid in recovery of marine seagrass communities after climatic extremes (Reusch et al. 2005) and may also provide similar benefits in terrestrial forage systems (Hughes et al. 2008, Newton et al. 2009). If this is the case, the stability of perennial forage yields over time could be enhanced by strategically incorporating genotypes with specific functional traits, such as drought tolerance or winter hardiness, that would help to expand the range of stand-level tolerance to variability in precipitation or temperature in order to counteract climatic variability. Although we did not see any reduction in spatial variability of yield across replicates with increased CD, we did see some evidence of decreased temporal yield variability, which may be of greater importance from a farmer's standpoint. Even in our relatively short term study, a qualitative assessment of the two year average yields reveals that the highest two year average was in a 3 cultivar mixture, and that over 60% of the mixtures outperformed their highest yielding component cultivars (Table 2). This likely occurred, in part, because there was a higher likelihood of at least one individual cultivar within a mixture having a positive response to a given weather condition that could compensate for any negative responses by the other cultivars as conditions changed from year to year. Additional research should examine the degree to which climatic tolerance (and hence stability) can be increased through strategic construction of cultivar mixtures of important perennial forages.

Our study examined a relatively limited number of cultivars (six) and mixture diversity levels for a single perennial forage species and at a single site. Thus, future research should address the generality of our results relative to *L. perenne*, the role of genotypically diverse mixtures of other perennial forage species, and the relationship between genotypic diversity and agroecosystem functioning across a greater range of diversity levels. One particularly intriguing question is how constructed mixtures that attempt to maximize both inter and intra-specific diversity might perform, given that each of these levels of diversity have been shown to affect ecosystem functioning (Hooper et al. 2005, Hughes et al. 2008), but have, to our knowledge, only been examined separately.

Although we observed no apparent signs of differential disease or insect damage among the cultivar diversity treatments, we did not expressly measure these variables and it is possible that these and other pest-related factors may have manifest themselves in ways that were not visually apparent while still impacting *L. perenne* performance and yield (e.g., Shoffner and Tooker 2013).

CONCLUSIONS

This study demonstrated that increasing intraspecific diversity led to greater productivity within a *L. perenne* stand, and that these benefits were not simply due to an increased probability of the inclusion of higher yielding cultivars. Furthermore, we observed that cultivar mixtures were no more susceptible to weed invasion than were cultivar monocultures, and thus would likely require no additional weed management relative to monocultures if implemented on a producer scale. Our data suggest that the additive trait range could potentially be a useful framework for constructing cultivar mixtures in lieu of more detailed information on the competitive and/or facilitative interactions which occur between specific cultivars. However, our results also emphasize the need for further research which can more fully test the effects of cultivar diversity in situations where the composition of mixtures can be tracked. We also highlight the need for more detailed research on the relative roles that facilitation, complementarity, and/or competition play in the interactions between cultivars in mixtures, similar to the body of research that has documented the interactions that occur between species in diverse communities. This will engender a better understanding of the relative roles that facilitation, complementarity, and/or competition play in determining agronomic outcomes in cultivar-diverse mixtures, and will help determine the potential for cultivar mixtures to increase productivity further via facilitative interactions and/or reduced competition. From a practical standpoint in the context of pursuing more sustainable systems of agriculture, our study provides evidence that producers might benefit from the addition of intraspecific or genotypic diversity in their perennial forage crop stands as a strategy for

ecologically intensifying productivity while dealing with increased climatic variability.

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