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Do cover crop mixtures give higher and more stable yields than pure stands?

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ABSTRACT

Planting cover crops after harvest of the main crop has become a key practice in temperate agriculture to reduce N leaching and increase soil organic matter. However, the growth of cover crops can be affected by adverse weather. Growing mixtures is thought to increase yield and reduce variation in productivity, but quantitative information on this subject is limited. Moreover, uncertainty remains on the optimal choice of species and mixture composition for cover cropping to obtain high cover crop yields and resilient performance under different conditions. Here we tested a broad selection of pure stands and mixtures of cover crop species in two years (2017–2018) at four sites: three sites in the Netherlands (Wageningen, Neer and Scheemda) and one site in Germany (Grundhof). All pure stands and mixtures were grown for a period of 11–13 weeks between August and November in each year. Aboveground biomass and N yield were determined. Yields in different treatments (unique pure stands or mixture compositions) in each site-year were regressed on the mean yields in each site-year to assess differences in responsiveness between treatments. Mixed effects models were used to estimate and compare yield variability in pure stands and mixtures at three levels: 1) between site-years, 2) between treatments and 3) between plots. This analysis was performed for biomass and N yield. Across all pure stands and mixtures tested, average biomass was greater in mixtures than in pure stands, but average biomass was similar when this comparison was made between the five highest yielding pure stands and the five highest yielding mixtures across all site-years. Thus, the lower mean productivity in pure stands was mostly due to some low yielding species. The five best mixtures had 9% higher N yield than the five best pure stands. The response of treatment yields to mean site-year yield was similar for mixtures and pure stands. Variation in cover crop yield over site-years was large in both pure stands and mixtures. On the other hand, mixing species significantly reduced the variability in biomass between treatments and between plots. However, when pure stands with low productivity were excluded, this difference in yield variability disappeared. This implies that the risk of choosing a sub-optimal cover crop is lower when a species mixture is used instead of a pure stand, unless the highest yielding species are known in advance. The results indicate that the positive effects of diversity on productivity and yield variability in cover cropping are restricted to reducing variability within the field and do not provide insurance against adverse conditions related to variability in growing conditions amongst sites and years.

1. Introduction

In temperate regions, winter cover crops are sown after harvest of a cash crop to capture mineral nitrogen and reduce leaching or volatilisation of N in autumn (Abdalla et al., 2019; Norberg and Aronsson, 2019). In conventional systems in north-western Europe, cover crops are ploughed under before the next cash crop is sown. The incorporated residues help build soil organic matter (Steele et al., 2012) while cover crop residues on the soil surface or incorporated into the top soil can reduce weed establishment (Kruidhof et al., 2009). Cover crops improve soil water infiltrability (Dabney et al., 2001), and some species were shown to improve the yield of the subsequent cash crop due to mineralization of N from the decomposing biomass during summer (Chu et al., 2017).

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Species traits vary among plant families, resulting in differences in the expected level of service provisioning. For instance, legumes fix atmospheric nitrogen but, under north-west European conditions, they are not as productive as grasses or crucifers (Ramírez-García et al., 2015). Crucifers are productive, and some species can elicit hatching of nematodes without being a suitable host for nematode reproduction such that they can suppress nematode populations (Stirling and Stirling, 2003; Monfort et al., 2007). However, crucifers are sensitive to soil compaction and water logging (Elhakeem et al., 2019). Grasses are productive and efficient in converting resources into biomass but they produce residues with high C:N ratio and lignin that can immobilize soil N (Li et al., 2020), thereby affecting the growth of a subsequent cash crop (Alonso-Ayuso et al., 2018). Positive effects of cover crop residues on the subsequent cash crop yield were observed when a legume, characterized by low C:N ratio, and cereal cover crop species were grown as a mixture (Abdalla et al., 2019). In this case, the high biomass accumulated by the cover crop mixture was associated with good litter quality. Thus, mixtures may help to combine strengths of different cover crop species and mitigate individual species' drawbacks.

Implementation of EU regulation 641/2014 resulted in payments to farmers for growing winter cover crops as mixtures in several European countries (European Commission, 2019). The promotion of mixtures is based on the assumption that cover crop mixtures provide greater ecological services than single species cover crops, for instance due to greater biomass accumulation (Blanco-Canqui et al., 2015). Differences in species responses to weather or soil conditions may result in compensatory growth responses in species mixtures where one species makes up for underperformance of a companion species (Li et al., 2001). Mixing species with different responses to the variable weather and soil conditions in autumn could therefore result in a reduction of risk of the cover crop failing to accumulate enough biomass and provide ecosystem services (Gfeller et al., 2018; Wendling et al., 2019). Furthermore, it is expected that complementary traits, e.g. different architecture or growing patterns, will improve the capture of resources in mixtures as compared to pure stands (Vandermeer, 1992). Earlier studies have shown these postulated advantages of species mixtures of cover crops (Finney et al., 2016; Raseduzzaman and Jensen, 2017; Wendling et al., 2017; Blesh, 2018; Couedel et al., 2018a, b; Elhakeem et al., 2019; Florence et al., 2019), natural grasslands (Tilman et al., 1996; Knops et al., 1999; Tilman et al., 2006; Fornara and Tilman, 2008; Cong et al., 2014) and food crops (Cong et al., 2015; Yu et al., 2015; Xu et al., 2020).

The benefits of mixing species of cover crops have been assessed in several studies, but yield stability was evaluated in only four studies (Wortman et al., 2012; Smith et al., 2014; Florence et al., 2019; Wendling et al., 2019). The term yield stability usually refers to a low variability in crop yield over years and environmental conditions. There are several ways to estimate variability (Lin et al., 1986). Variance and coefficient of variation are two commonly used indicators for characterizing variability in ecology and agronomy (Francis and Kannenberg, 1978; Rao and Willey, 1980; Knapp and van der Heijden, 2018). In previous studies on yield variability in cover crops, authors used the coefficient of variation of yield across replicates (spatial stability) and/or across years (temporal stability) (Wortman et al., 2012; Smith et al., 2014; Florence et al., 2019; Wendling et al., 2019). The coefficient of variation is defined as the ratio between the standard deviation and the mean. The interpretation of the coefficient of variation can be challenging because it varies not only with the standard deviation, but also with the mean (Doring and Reckling, 2018). Therefore, in this study, we decided to focus on variance. We assess the mean and variability separately.

Some authors have addressed the issue of yield variability by plotting individual crop yield (Finlay and Wilkinson, 1963; Faris et al., 1983) or deviations from average crop yield (Wendling et al., 2019) against the average yield level at different sites. This method may be used to characterize differences in responsiveness between different species or mixtures to site conditions. We used this approach as a first exploration of the yield variability present in our data set. We then estimated variance of yield and N yield at three levels: 1) across site-years, 2) across treatments, referring to the variance between species in pure stands and between species combinations in the mixtures, within a site-year, and 3) across plots within a field. These three variance components are considered additive and independent from each other.

For a given cover crop species or mixture composition, there will be variation in yield between site-years, due to differences in soil and weather conditions, and management, including sowing and harvesting date. This "between site-years" variance is very important for practice. Farmers prefer a cover crop that combines a high yield with low variability "between site-years", i.e. it will do well regardless of environmental circumstances and management.

The second type of variance to compare between pure stands and mixtures is that between individual entries of each group; that is the variation between different species within the group of pure stands and between different mixture compositions within the group of species mixtures. If mixtures reduce variability in performance as a result of "regression to the mean", we expect this "between treatments" variance component to be smaller for the group of mixtures than for the group of pure stands. Moreover, if variability within pure stands is higher than variability in mixtures, it means that the risk of choosing a sub-optimal pure stand species is greater than the risk of choosing a sub-optimal mixture.

The third relevant type of variance is the variation in yield between different spots in the same field. This variation is supposedly reduced in mixtures due to different responses of species to within-field variability in growing conditions, due to differences in, e.g., soil humidity, organic matter content, or available nitrogen. Variance between plots in a given pure stand or mixture in a given site-year relates to the ability of the pure stand or mixture to accommodate to micro-variation in growing conditions within the field. A low variance indicates that the species shows consistent performance across the field. In mixtures, this could mean that the species are compensating for a poor performance of the companion species. However, this was not observed in earlier studies (Wortman et al., 2012; Smith et al., 2014; Florence et al., 2019).

Species that are known to be highly productive, such as oil-seed radish and black oats are often present in mixtures, while pure stands also comprise species that provide ancillary services such as nematode control (*Tagetes* spp.) but are not necessarily high yielding. To eliminate the potential bias of low yielding sole crops in the dataset, we compared productivity and yield variability of the highest yielding pure stands with productivity and yield variability of the highest yielding mixtures.

Thus, we made a quantitative comparison between pure stands and mixtures of cover crops in terms of biomass, N yield, and the variability in these traits, using data from four sites and two years. Variability among site-years was first examined by investigating yield response to site productivity. Thereafter mixed effects models were used, to quantify for both pure stands and mixtures the average productivity and the variability at three levels: 1) between site-years, 2) between treatments within site-years, and 3) between plots (replicates) within treatments within site-year. Estimation of variance components with mixed models allows to simultaneously quantify these three different types of variance and thus reveals at which level the variability among mixtures deviates from the variability among pure stands. We tested two hypotheses: 1) average biomass and N uptake is higher in cover crop mixtures than in pure stands, 2) at all three levels (between site-years, between treatments and between plots) the variability in biomass and N uptake is smaller in mixtures than in pure stands. Finally, the same hypotheses were tested using the five most productive pure stands and the five most productive mixtures to eliminate the effect of low yielding species in the group of pure stands.

Table 1
Site description, field operations and prevailing weather conditions in 2017 and 2018 at four sites; Grundhof (Germany), Neer, Scheemda and Wageningen (all three in the Netherlands).

Site characteristics	2017				2018			
	Grundhof 54°46′42″N 9°39′29″E	Neer 51°15′34″N 5°57′24″E	Scheemda 53°09′15″N 6°57′38″E	Wageningen 51°59′31″N 5°39′15″E	Grundhof 54°42′33″N 9°37′48″E	Neer 51°15′35″N 5°57′45″E	Scheemda 53°09′04″N 6°57′44″E	Wageningen 51°59′28″N 5°39′09″E
Soil type	Sandy clay	Sandy	Sandy	Sandy	Sandy clay	Sandy	Clay	Sandy
Soil organic matter (%)	2.1	2.5	8.0	3.4	3.4	2.5	6.9	3.1
Soil mineral N (kg ha^{-1}) in July	25	46	71	20	22	13	33	18
Soil pH ($CaCl_2$)	6.0	5.8	5.7	5.2	6.2	5.9	7.5	5.2
Previous crop	Winter wheat	Carrots	Italian rye-grass	Winter wheat	Winter wheat	Carrots	Oats	Summer barley
Sowing date	8th August	2nd August	17th August	23rd August	8th August	31st July	22nd August	23rd August
Harvesting date	2nd November	26th October	30th October	16th November	6th November	23rd October	14th November	21st November
Nitrogen application	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}	30 kg N ha^{-1}
Plot size (m^2)	12.5	7.5	7.5	15	12.5	7.5	7.5	15
Sampled area (m^2)	1.0	6.6	5.0	4.5	12.5	7.5	5.0	15.0
Sum of Precipitation (mm) during the growth period.	421	181	201	133	144	107	123	142
Global radiation sum (MJ m^{-2})	761	925	679	679	801	1103	723	774
Accumulated growing degree days (base temperature: 4 °C)	825	1022	731	688	905	1077	799	779

2. Materials and methods

2.1. Site description

Field experiments were conducted in two consecutive years (2017–2018) at four locations, three in the Netherlands (Neer, Wageningen and Scheemda) and one in northern Germany (Grundhof). Different fields were used in the two years to avoid cumulative effects of growing the same mixture at the same site in subsequent years. Soil type was sandy in Neer and Wageningen, clay in Scheemda and sandy clay in Grundhof (Table 1). Soil organic matter content ranged from 2.1 % in Grundhof in 2017 to 8.0 % in Scheemda in 2017. The distance between the two furthest sites (Neer and Grundhof) was approximately 450 km. In all cases, the seedbed was prepared to a depth of 8 cm with a power harrow. Cover crops were sown at the end of summer and harvested 11–13 weeks later. Immediately after sowing, 30 kg N ha^{-1} was applied as slow release fertilizer (calcium ammonium nitrate, 27 % N). This application of nitrogenous fertilizer is a common practice in the Netherlands that aims to promote rapid cover crop development. Sowing and harvesting dates of winter cover crops varied across site-years due to variation in harvest date of the preceding cash crop and rainfall at the site. The difference between the earliest (Neer) and the latest (Wageningen) sowing date of cover crops was approximately three weeks. Details of all sites, including field operations and weather conditions, are summarized in Table 1.

2.2. Experimental design

At all sites, we used a randomized complete block design. The number of replicates was four in Wageningen and three at the other locations. In 2017, each experiment comprised 10 pure stands and 10 mixtures, while in 2018, each experiment comprised 12 pure stands and 11 mixtures. Pure stands comprised the most common species used as cover crops across the experimental regions. From a pilot experiment with 25 pure stands of cover crops, we selected the most productive species from different botanical groups (data not shown). The selected species in the current study belonged to six plant families: Brassicaceae, Poaceae, Fabaceae, Boraginaceae, Asteraceae, and Linaceae. Based on these species, 2-, 3- and 4-species mixtures were composed in collaboration with stakeholders (seed companies). To maximize the potential advantages of mixtures, species were mixed that differ in architecture and belong to different plant families (Table 2). Some species such as oilseed radish were present in more mixtures than other species, representing the interest of stakeholders to test particular mixture compositions with expected complementarities. Cover crops were sown in rows with 12.5 cm between rows using a 3 m wide seed planter in Wageningen (Rabe Turbo drill, Germany) and a 1.5 m wide seed planter in the other sites (Hege, belt cone planter, Germany). For each species, we used the seeding rate recommended by the seed supplier (Table 2). In plots with mixtures, seeds were mixed within the row, to create 2-, 3- and 4-species mixtures, using 50 %, 33 % and 25 % of the full seeding rate of the component species.

2.3. Soil sampling

Five random soil samples were collected from each plot at sowing of the cover crops using a 20 cm long soil probe with a diameter of 2 cm. Soil samples from the same block were mixed to create three or four (Wageningen) replicate samples. Total mineral N in the samples was determined using calcium chloride extraction ($CaCl_2$). In all samples, soil organic matter was determined by loss on ignition. All samples were oven dried at 105 °C for 24 h, then the dried weight of each sample was recorded. From the dried soil, approximately 10 g from each sample was placed in a Nabertherm oven to ignite at 550 for 3 h. Dry weight before and after the ignition was recorded and the difference is assumed to represent organic matter (Table 1).

Table 2
Seeding rate and thousand seed weight of winter cover crops grown in pure stands and mixtures.

Botanical family	Latin name	Common name	Cultivar	Seeding rate (kg ha^{-1})	Thousand seed weight (g)
Brassicaceae	*Eruca sativa*	Salad rocket	Garden rocket	10	1.97
	Raphanus sativus	Oilseed radish	Valencia	30	10.5
	Raphanus sativus	Oilseed radish	Angus	30	10.2
	Sinapis alba	White mustard	Master	25	5.06
Poaceae	*Avena strigosa*	Black oats	Exito	90	19.9
	Avena strigosa	Black oats	PRATEX	90	21.5
Fabaceae	**Vicia faba*	Field beans	Avalon	130	326
	Vicia sativa L.	Common vetch	Jose	110	53.7
	Triflolum alexandrinum	Berseem clover	Laura	35	2.71
Boraginaceae	*Phacelia tanacetifolia*	Phacelia	Factotum	16	1.80
Asteraceae	*Tagetes patula*	French Marigold	Ground control	5	3.00
Linaceae	**Linum usitatissimum*	Linseed	Juliet	35	6.67
2-species mixtures	Black oats 'Exito' + Oilseed radish 'Angus'				50 % of each species
	Black oats 'PRATEX' + Oilseed radish 'Valencia'				
	Black oats 'PRATEX' + Common vetch				
	Oilseed radish 'Valencia' + Common vetch				
	Black oats 'PRATEX' + French marigold				
	Oilseed radish 'Valencia' + Phacelia				
3-species mixtures	Oilseed radish 'Valencia' + Phacelia + Berseem clover				33 % of each species
	Oilseed radish 'Valencia' + Phacelia + Salad rocket				
4-species mixtures	White mustard + Phacelia + Black oats 'PRATEX' + Berseem clover				
	Oilseed radish 'Valencia' + Phacelia + Black oats 'PRATEX' + Berseem clover				25 % of each species
	*Oilseed radish 'Valencia' + Black oats 'PRATEX' + Field beans + Linseed				

* Treatments used in 2018 only.

2.4. Biomass harvest

Aboveground plant mass was harvested at approximately 12 weeks after sowing using a 1.5 m wide harvesting machine (Haldrup F-55). Plants were cut at 1−2 cm aboveground. Weeds were separated from the sampled material. The harvested area differed between site-years and ranged between 4.5 and 15 m^2 (Table 1). Total plot fresh weight was recorded by the harvesting machine while a randomly selected and shredded sub-sample was also obtained from the harvesting machine. Sub-samples were oven dried at 70 °C for 48 h. Subsequently, dry weight of all species was calculated. Use of machinery was not possible in Grundhof in 2017, due to extremely wet conditions. In this case, an area of one m^2 per plot was harvested by hand and dry weight was measured for the total harvested biomass. From the dried samples in all site-years, C and N concentration was determined, using a dynamic flash combustion in a C:N elemental analyser (EA 1108: Fisons Instrument). The product of biomass and N concentration was referred to as N yield.

2.5. Data analysis

2.5.1. Analysis of mean biomass and N yield

Two sets of linear mixed effect models (three models in each set) were used to analyse biomass and N yield in different cover crop species, to compare biomass and N yield between pure stands and mixtures, and to compare the different plant families. Cropping system (either pure stands or species mixtures), Treatment (each uniqe pure stand or species mixture composition) and plant families (six levels) were defined as fixed effects in this analysis. Within pure stands, there were 12 levels (species) for the factor treatment while within mixtures, there were 11 levels (mixture compositions). In all models, we included site-year and block as nested random factors. Models were fitted using the function lmer of the package lme4 (Bates et al., 2014) in R version 3.4.3 (R Core Team, 2018). Biomass and N yield were analysed separately. Significance of fixed effects was determined with analysis of variance (ANOVA). Pairwise comparisons were made using Tukey HSD test. The assumptions of normality and homogeneity of variances were checked graphically (Zuur et al., 2009). To investigate the changes in biomass and N yield in response to the number of component species, we used a linear mixed effect model with the number of component species as a fixed effect.

2.5.2. Variation in yield of cover crop treatments across site-years

A linear regression was fitted between biomass (or N yield) and the mean biomass per site-year (or mean site-year N yield) to investigate the response to site productivity in different mixtures and pure stands. A separate linear regression was fitted for each pure stand and mixture. Mean site-year biomass or mean site-year N yield were calculated as the average biomass or N yield of all pure stands and mixtures in a site-year for eight site-years. Treatments that were only included in 2018 were omitted from this analysis.

2.5.3. Analysis of yield variances between site-years, treatments and plots

A mixed model with three variance components was developed to quantify differences in variability of biomass and N yield between pure stands and mixtures. Variance components were estimated separately for the pure stands and the mixtures. The first variance component, $\sigma^2_{\text{site year}}$, characterizes the variance between site years. Superimposed on the random site year effect is a random effect for treatment $\sigma^2_{\text{treatment}}$ where treatment denotes species identity among the pure stands or mixture composition amongst the mixtures. This variance characterizes the variation in biomass or N-yield between different species among the pure stands and between different species combinations among the mixtures, within the site years. The third variance component describes the variation between plots in the same treatment and site-year. All variances were estimated simultaneously using a Bayesian linear mixed model, defined as:

$$Y_{sti} = \beta_0 + \beta_1 x + a_s + b_t + \varepsilon_{sti} \quad (1)$$

where Y_{sti} is the biomass or N yield measured in the s^{th} site-year, t^{th} pure stand or species mixture, and i^{th} replicate, β_0 is the overall mean biomass or N yield in a pure stand, and β_1 is the difference in biomass or N yield between pure stands and mixtures. The variable x is an indicator variable which is 0 for pure stands and 1 for mixtures. a_s is a random site-year effect which is normally distributed with mean zero and variance $\sigma^2_{\text{site year}}$, b_t is a random pure stand or mixture effect which is normally distributed with variance $\sigma^2_{\text{treatment}}$, and ε_{sti} is a random residual term describing the between-plots variability, including the measurement error. The variance of ε_{sti} is σ^2_{plot}. All random variables were assumed normally and independently distributed with zero mean. Models were fitted using the package MCMCglmm (Hadfield, 2010) in R

Table 3
Mean biomass, N yield and CN ratio of all cover crops species. Presented means were averaged over eight site-years. sd = standard deviation. CV = coefficient of variation in percentage calculated as (sd/mean)*100. Highlighted rows refer to the five highest yielding (biomass and N yield) pure stands and mixtures. Species used in 2018 only was excluded from the selection process.

Botanical family	Latin name	Common name	Cultivar	Biomass t ha^{-1}	sd	CV	N-yield kg N ha^{-1}	sd	CV	CN ratio
Brassicaceae	*Eruca sativa*	Salad rocket	Garden rocket	3.09	2.11	68%	81	57	70%	14.2
	Raphanus sativus	Oilseed radish	Valencia	4.74	2.58	55%	109	50	46%	17.8
	Raphanus sativus	Oilseed radish	Angus	4.85	2.48	51%	104	54	52%	18.4
	Sinapis alba	White mustard	Master	4.50	1.86	41%	79	34	43%	24.4
Poaceae	*Avena strigosa*	Black oats	Exito	5.26	2.64	50 %	80	31	39%	26.0
	Avena strigosa	Black oats	PRATEX	5.84	3.10	53%	90	36	40%	27.2
Fabaceae	**Vicia faba*	Field beans	Avalon	2.80	2.55	91%	57	41	72%	19.1
	Vicia sativa L.	Common vetch	Jose	1.90	1.46	77%	62	43	69%	11.4
	Triflolum alexandrinum	Berseem clover	Laura	1.37	1.42	103%	36	34	95 %	13.5
Boraginaceae	*Phacelia tanacetifolia*	Phacelia	Factotum	3.44	1.65	48%	74	38	51%	17.7
Asteraceae	*Tagetes patula*	French Marigold	Ground control	2.68	2.67	100%	42	38	89%	23.0
Linaceae	**Linum usitatissimum*	Linseed	Juliet	3.14	1.99	63%	56	24	42%	22.5
2-species mixtures	Black oats 'Exito' + Oilseed radish 'Angus'			5.28	2.59	49%	107	50	47%	19.2
	Black oats 'PRATEX' + Oilseed radish 'Valencia'			5.36	2.67	50 %	101	34	33 %	21.7
	Black oats 'PRATEX' + Common vetch			4.98	2.31	46%	84	30	35%	23.2
	Oilseed radish 'Valencia' + Common vetch			4.41	2.16	49%	101	41	40%	17.0
	Black oats 'PRATEX' + French marigold			5.39	2.62	49%	92	43	47%	25.2
	Oilseed radish 'Valencia' + Phacelia			4.76	2.88	60%	106	49	46%	17.8
3-species mixtures	Oilseed radish 'Valencia' + Phacelia + Berseem clover			4.41	2.45	56%	104	47	45%	16.8
	Oilseed radish 'Valencia' + Phacelia + Salad rocket			4.35	2.56	59%	101	45	45%	16.4
	White mustard + Phacelia + Black oats 'PRATEX' + Berseem clover			4.81	2.00	42%	97	42	43%	20.8
4-species mixtures	Oilseed radish 'Valencia' + Phacelia + Black oats 'PRATEX' + Berseem clover			4.87	2.27	46%	97	40	41%	19.8
	*Oilseed radish 'Valencia' + Black oats 'PRATEX' + Field beans + Linseed			5.43	1.49	27 %	102	17	17%	21.7

* Treatments used in 2018 only.

version 3.4.3 (R Core Team, 2018). Markov Chain Monte Carlo (MCMC) chains were run with 50,000 iterations (3000 iterations for burn-in) and a thinning interval of 10. The MCMC outputs were used to approximate the posterior distributions of the ratio of the variance in mixture to the variance in the pure stands at all three levels of variability (between site-years, between treatments, between plots), for biomass and N yield, separately. Results were used to compute the posterior mean and median of the variance ratio, its 95 % credible interval, and the probability of a variance ratio smaller than one, i.e., the probability that mixtures are more stable in yield than pure stands. At any level of variability, if the variance ratio was significantly smaller than one, we would have concluded a higher stability in mixtures yield as compared to pure stands and vice versa.

2.5.4. Analysis of productivity and yield variability of the most productive treatments

Highly productive species, such as crucifers and black oats are often present in mixtures, while pure stands also comprise species that are less productive such as legumes and some flowering forbs. The average yield of mixtures may turn out to be higher than that of pure stands, simply because low yielding species were overgrown by their high yielding companion species. This may result in a biased comparison of yields in pure stands and mixtures. To prevent such bias, we made a comparison of yield and yield variability of the five most productive pure stands and mixtures across the eight site-years, thus effectively excluding the influence of low yielding treatments (Table 3). Biomass and N yield were compared for the five most productive mixtures and the five most productive pure stands, using linear mixed effect models including biomass and N yield as fixed effects and block nested within site-years as random effects. Differences in yield variability between the most productive mixtures and pure stands were analysed using the Bayesian linear mixed model (Eq. 1).

3. Results

Site-year had a significant effect on cover crop biomass yield ($p < 0.001$), N concentration ($p < 0.001$) and N yield ($p < 0.001$). This effect was particularly due to the difference in biomass yield between Neer (on average 8.2 t ha^{-1} in 2017 and 7.3 t ha^{-1} in 2018) and the other sites (with averages ranging from 2.0 to 4.1 t ha^{-1}; Fig. 1). The higher productivity in Neer was associated with an earlier sowing date than at the other sites. As a result, there was a big difference in the accumulated growing degree days between Neer (1022–1077 °C d from emergence to harvest) and the other three sites (ranging from 688 to 905 °C d; Table 1). In addition, cumulative global radiation over the growth period of cover crops was higher in Neer (from 925 to 1103 MJ m^{-2} from emergence to harvest) than in the other sites (from 679 to 801 MJ m^{-2}). Mixtures tended to have a higher average yield than pure stands in each site-year.

In six of the eight site-years, the highest biomass was produced by black oats, whereas oil-seed radish and white mustard each realized the highest production in one of the other two site-years (Supplementary Fig. 1 and 2). Black oats had the lowest N concentration (on average 1.65 % ± 0.54 %) and the highest C:N ratio among all species (on average 26.6 ± 8.6; Table 3). Thus, while black oats produced a large amount of biomass, it accumulated a low amount of N relative to its biomass (Supplementary Fig. 3 and 4). Crucifers produced large amounts of biomass with high nitrogen concentration (N concentration = 2.26 % ± 0.74 %), and therefore had a significantly lower C:N ratio than found in black oats (on average 18.7 ± 7.3; $p < 0.001$). Crucifers accumulated on average the highest amount of nitrogen (averaged over site-years 90.5 kg N ha^{-1}). Across crucifers, oil-seed radish accumulated the most nitrogen (ranging from 73.0 to 159.2 kg N ha^{-1}) followed by white mustard (ranging from 103.2 to 117.2 kg N ha^{-1}; Supplementary Fig. 3 and 4). Salad rocket was the crucifer species with the lowest biomass (on average 3.1 t ha^{-1}) but it captured a relatively large amount of N (on average 81 kg N ha^{-1}), thus it had a low C:N ratio (on average 14.2).

Legumes combined low biomass with a high N concentration (2.86 % ± 0.67 %) and they had the lowest C:N ratio of all plant families (on average 14.2). Phacelia, French marigold and linseed, three forb species included in the experiments, produced, on average, 3.09 t ha^{-1} biomass which was below that of black oats and crucifers but higher than that of the legumes. These three forb species captured moderate amounts of N (on average 57.6 kg N ha^{-1}). Plots with low yielding species were characterized by higher levels of weed density, but no quantitative data are available.

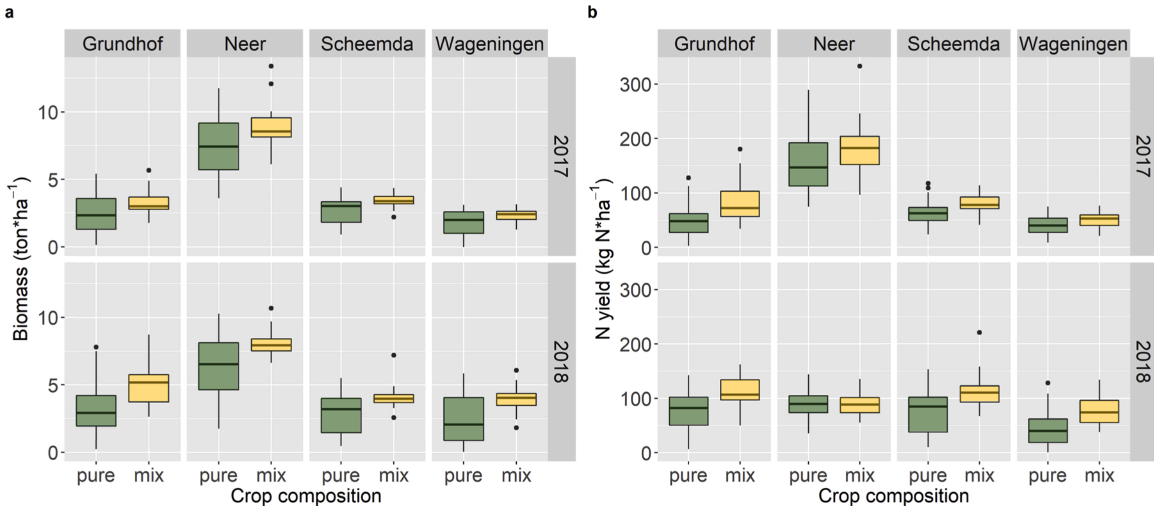

Fig. 1. Average biomass (a) and N yield (b) of winter cover crops grown as pure stands (pure) or mixtures (mix) in 2017 and 2018 at four sites; Grundhof (Germany), Neer, Scheemda and Wageningen (all three in the Netherlands).

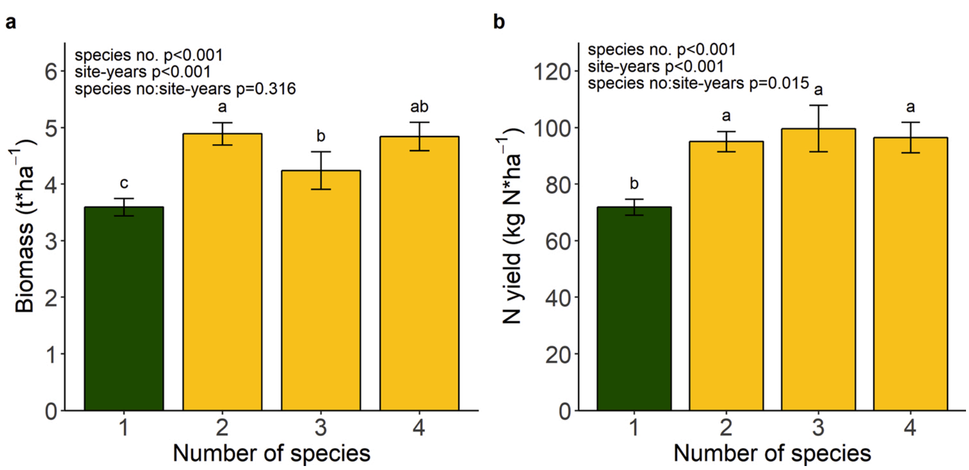

Fig. 2. Response of biomass (a) and N yield (b) of winter cover crops to the number of component species within mixtures in 2017 and 2018 at four sites: Grundhof (Germany), and Neer, Scheemda and Wageningen (all three in the Netherlands). Results of a linear mixed effects model with number of species as a categorical covariate. Green bars represent pure stands (n = 12), yellow bars represent 2-species mixtures (n = 6), 3-species mixtures (n = 2) and 4-species mixtures (n = 3). Error bars represent ±1×standard error. Different letters denote significant differences at P ≤ 0.05; Tukey HSD test. (For interpretation of the references to colour in the Figure, the reader is referred to the web version of this article).

Averaged over site-years, species mixtures produced a 1.27 t ha^{-1} higher amount of biomass ($p < 0.001$) and accumulated 27 kg N ha^{-1} more nitrogen than pure stands ($p = 0.014$). Two-species mixtures had 1.30 t ha^{-1} greater biomass than pure stands, but three-species mixtures produced 0.63 t ha^{-1} less biomass than 2-species mixtures while production of 4-species mixtures was intermediate between 2- and 3-species mixtures. Thus, there was no consistent increase of productivity with the number of species in mixtures (Fig. 2). Mixtures accumulated more nitrogen than pure stands, irrespective of the number of component species. There were no significant differences in N yield between mixtures with 2, 3 or 4 species.

For each species and species mixture, a linear regression was fitted between crop productivity (biomass or N yield) and the mean site productivity (Fig. 3a and b). Pure stands varied more in the rate of response to site productivity than mixtures. Among the pure stands, biomass of black oats showed the greatest response (measured as ton ton^{-1}) to site mean biomass with slopes ranging from 1.14 to 1.36. Crucifers mostly had lower slopes than black oats, ranging from 0.76 to 1.20. The smallest slope was observed for legumes ranging between 0.56 and 0.60. Mixtures had a similar response as crucifers with slopes ranging between 0.84 and 1.29.

N yield of pure stands varied more than that of mixtures in their response to site productivity, expressed in terms of N-yield (Fig. 3c and d). Crucifers showed the steepest increase in N yield, with slopes (measured in kg N kg^{-1} N) ranging between 1.28 and 1.48, but a very low slope (0.54) was observed for white mustard, the species with the lower slope also for biomass. Slopes of legumes, black oats and forbs (French marigold and phacelia) were mostly smaller than those of crucifers, ranging from 0.72 to 0.98. Slopes of mixtures were similar to those of crucifers and black oats and ranged between 0.71 and 1.25.

As shown in the previous analysis, site-year had a great effect on the yield of all treatments. This finding is confirmed by the results of the mixed model with the three variance components: mixing species did not substantially reduce the variability of biomass and N yield across site-years (Fig. 4). The ratio of the between-site-year variance for mixtures and for pure stands was not statistically different from one. The ratio of the between-site-year variances of mixtures and pure stands had a wide credible interval, indicating large uncertainty. These results also held when Neer, the site with the higher biomass production, was removed from the analysis (data not shown).

For both biomass and N yield, the ratio of the between-treatments variance of mixtures and pure stands was significantly smaller than one. The 95 % credible interval of the variance ratio of the between-species variance for biomass yield was [0.01, 0.23]. Similarly, for N yield, mixtures had a significantly smaller between-treatments variance as compared to pure stands, resulting in a variance ratio with a credible interval [<0.01, 0.1]. These results show that variability of biomass and N yield between different mixtures was smaller than the variability

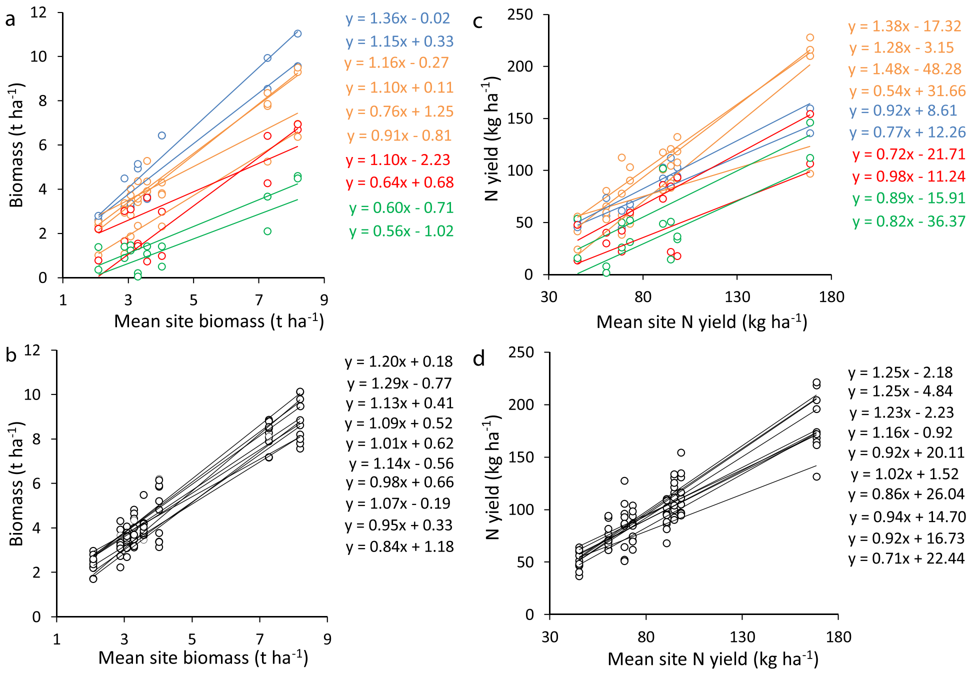

Fig. 3. Response of biomass (a and b) and N yield (c and d) of winter cover crops to the site productivity calculated as the average biomass or N yield of all pure stands (a and c) and mixtures (b and d) at each site-year. Blue lines represent black oats, orange lines represent crucifers, green lines represent legumes, and red lines represent other forbs. Black lines represent mixtures. (For interpretation of the references to colour in the Figure, the reader is referred to the web version of this article).

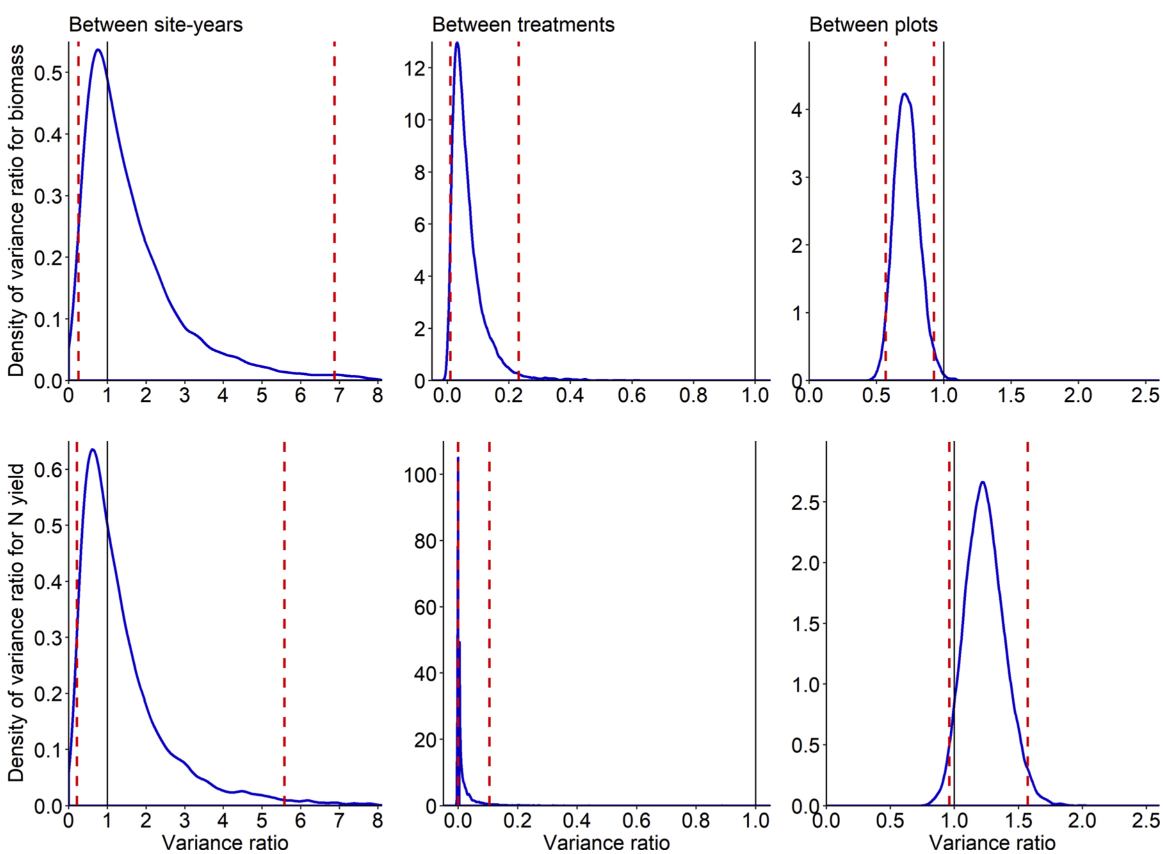

Fig. 4. Variance ratios of cover crop mixtures over pure stands, calculated for biomass (top three panels) and N yield (lower panels). The calculated variance ratios reflect three different sources of variability; between-site-years (left panels), between species or mixture compositions within site years (middle panels), and between plots within species or mixture compositions within site-years (right panels). Each panel shows the estimated posterior probability density (blue curve) of the variance ratio, based on a Bayesian estimation of parameters in a generalized linear mixed effects model using Markov Chain Monte Carlo estimation. The vertical black line refers to the null hypothesis variance ratio of one. The two dotted red lines represent the 2.5 % and 97.5 % credible limits of the estimated variance ratio. Variance ratio < 1 means that variance of mixtures is smaller than variance of pure stands, and vice versa. (For interpretation of the references to colour in the Figure, the reader is referred to the web version of this article).

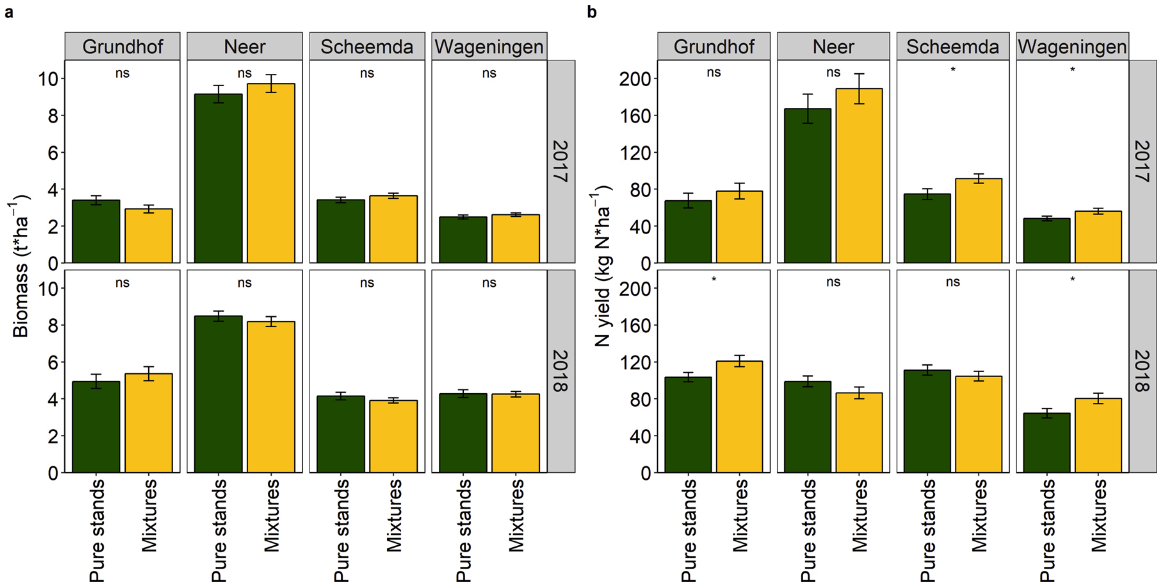

Fig. 5. Average biomass (a) and N yield (b) of the five best pure stand treatments of cover crops (green bars) compared to the five best mixture treatments (yellow bars) in eight site-years, estimated with mixed effect models. Error bars represent ±1×standard error. * = P ≤ 0.05; ns = P > 0.05. (For interpretation of the references to colour in the Figure, the reader is referred to the web version of this article).

between different pure stands.

Mixing species of cover crops also reduced between-plots (within field) variability of biomass production. The credible interval of the ratio of between-plots variance in mixtures and pure stands was [0.56, 0.91] for biomass yield. Such a reduced between plots variability was not observed for N yield with a credible interval of [0.96, 1.57] for the variance ratio for between plots variance in N yield of mixtures and pure stands.

In a final analysis, we compared the average biomass and N yield of the five best performing pure stands with that of the five best performing mixtures, thus excluding an effect of the less well performing pure stands (Fig. 5). In this analysis, there was no difference in biomass of the five best performing species in pure stand and the best mixtures in any of the eight site-years of the study (Fig. 5a). However, mixtures had a higher N yield than pure stands in 4 out of 8 site-years (Fig. 5b). Averaged over site years, the best mixtures accumulated 8.5 kg N ha^{-1} (9%) more nitrogen than the best performing pure stands ($p = 0.028$).

When only the five best performing treatments for mixtures and pure stands were considered, differences in yield variability disappeared. For this selection of treatments, the variance estimates at the three levels of variability were similar in pure stands and mixtures, both for biomass and N yield (Supplementary Table 1 and 2).

4. Discussion

Results of this study give a nuanced perspective on the effect of species mixtures on biomass and N yield in cover cropping. The overall average biomass and N yield were greater in mixtures than in pure stands. However, when low yielding pure stands were excluded and the analysis was restricted to the highest yielding pure stands and species mixtures, no difference in biomass production between the mixtures and the pure stands was found. This implies that farmers obtain comparable levels of production whether they choose to grow the best species alone or in a mixture. There was, however, a higher N yield in mixtures in four of the eight site-years of the study, with an average increase of 8.02 kg N ha^{-1} (9%).

Several recent studies found higher average biomass production in cover crop mixtures than in pure stands (Finney et al., 2016; Murrell et al., 2017; Blesh, 2018; Elhakeem et al., 2019; Florence et al., 2019). In these studies, as in our study, yield of mixtures was equivalent to that of the best performing pure stands, indicating that the lower average yield of pure stands was related to inclusion of species with low productivity. Including less productive species in mixtures is of less importance, as their low performance is compensated through gap filling by better performing species. For instance, in a previous study, we found that gaps in the canopy created by poorly growing winter vetch was compensated by more productive companion species such as black oats and oil-seed radish (Elhakeem et al., 2019).

The average C:N ratio of the five best mixtures (C:N = 20.6) was lower than that of the five best pure stands (C:N = 22.7; $p < 0.001$). Thus, while biomass of the best mixtures and best pure stands was similar, a better mineralization from residues of mixtures is to be expected due to higher N concentration (Trinsoutrot et al., 2000; Li et al., 2013). The better capture of nutrients by cover crop mixtures, as compared to pure stands, was also reported by Couedel et al. (2018a) and Couedel et al. (2018b). Root architecture and strategies for nutrient acquisition vary among species of cover crops (Wendling et al., 2016). Perhaps, the higher N yield of mixtures is due to complementarity in rooting patterns that might have increased the capture of mineral N from the soil (Blesh et al., 2019).

Differences in responsiveness to diverse growth conditions were smaller between mixture treatments than between pure stands. Legumes were less responsive to the improvement in growth conditions than black oats and crucifers. These findings are in agreement with those reported by Wendling et al. (2019). Moreover, in an earlier food crop study, cereal yield was more responsive to differences in site productivity than legume yield, whereas intercrops of cereals and legumes had the same responsiveness to site productivity as cereals (Faris et al., 1983). Thus, high yielding species benefit more from better growing conditions than low yielding species, resulting in a large variation in responsiveness between pure stands. Mixtures showed similar responsiveness as high yielding pure stands. It is yet not clear why the low yielding species are less responsive to the changes in growing conditions. One explanation could be the differences in resource capture and resource use efficiency of the different species. Elhakeem et al. (2021) recently reported that high yielding species, such as crucifers and black oats, are more efficient than legumes in intercepting and converting radiation into biomass.

Using species mixtures did not reduce variation in biomass and N yield between sites and years, contradicting the initial hypothesis that mixing species would contribute to stabilization of yield under uncertain and variable environmental conditions. There was a high variability in biomass and N yield of cover crops between site-years, regardless whether the crop was mixed or sown in pure stand. This finding was also reported by Wendling et al. (2019). The site-year effect has many possible causes, such as differences in soil type, precipitation, temperature, radiation and sowing/harvesting dates. In this study, there was approximately a three weeks difference between the earliest and latest sowing date. Consequently, global radiation and growing degree days were dramatically different across sites, particularly between Neer and the other three sites. In Neer (the site with the highest productivity) cover crops were following carrots, a high input crop, while at the other sites, cover crops were following cereals. The similarity of the variance between site-years of mixtures and pure stands indicates that using mixtures will not overcome adverse growing conditions related to late sowing and adverse weather. When growing conditions are less favourable in autumn, e.g. due to low temperatures, low radiation levels, or excessive rain and water logging of the soil, mixtures suffer as much as pure stands. In our experiments this was the case in the site-year Grundhof-2017. On the other hand, favourable growth conditions as in site Neer (in 2017 and 2018) resulted in enhanced growth in both pure stands and mixtures.

In other field studies, contrary to our findings, mixtures of cash crop species (i.e. intercrops) were found to produce less variable yield across site-years as compared to sole crops. From 51 field experiments, in spite of the large difference in yield levels across site-years, yield variability of pigeonpea-sorghum intercrop was found to be 11 % lower than that of sole pigeonpea and 20 % lower than sole sorghum (Rao and Willey, 1980). Moreover, a global meta-analysis showed that yield variability of cereal-grain legumes intercrop was 25 % lower than that of sole cereals and 37 % lower than that of sole grain-legumes (Raseduzzaman and Jensen, 2017). These different findings on yield stability between the studies on cash crops and cover crops may be related to the fact that cash crops are usually grown under more favourable conditions than cover crops. Cash crops are sown when growing conditions are favourable whereas sowing of cover crops is dependent on the harvesting date of the preceding cash crop. Depending on this harvesting date, cover crops can grow under colder or warmer conditions. Further work is needed to elucidate why mixing food crops would stabilize productivity whereas mixing cover crops would not.

The between-treatment variation in biomass and N yield was lower for mixtures than for pure stands, which was in agreement with the second hypothesis. It indicates that in mixtures there is some degree of "regression towards the mean". The between-treatments variation in productivity is relevant for growers when they make their decision on what to sow. The high variability within the group of pure stands means that some candidate species are poor performers when it comes to accumulation of biomass or N, while other species or varieties perform much better. Our results indicate that certain species, e.g. berseem clover, common vetch, salad rocket and French marigold, are consistently low yielding (Supplementary Fig. 1 and 2). Such species may be useful for specific purposes, e.g. nematode control or provision of flower resources to beneficial insects, but if the aim is to improve the soil by incorporation of organic material, such species may be avoided as pure stands. On the other hand, black oats and crucifers are good candidates if the purpose is to accumulate high biomass and capture high amounts of N. The high yield and low variability of yield in mixtures was probably due to the fact that all mixtures comprised at least one productive species (black oats and/or a crucifer). These high yielding species contributed the most to the biomass produced by mixtures, which is known as the selection effect (Loreau and Hector, 2001). This result holds for the different cultivars of black oats and oilseed radish that were used in this study. The performance of the different cultivars of the same species was similar. When the low yielding treatments were eliminated from the analysis, the high between-treatment variation within the group of pure stands became significantly smaller and equivalent to that of mixtures. This result is in line with our conclusion that the inclusion of low yielding pure stands was the reason for the initial high between-treatments variability among pure stands.

Spatial variability in biomass production, estimated as between plots variation within a given field and year was reduced in species mixtures as compared to pure stands. Conversely, previous studies on biomass variability of cover crops across plots showed no decrease in yield variability from growing mixtures (Wortman et al., 2012; Smith et al., 2014; Florence et al., 2019). The significant effect of mixing on between-plots variability in our study may be related to larger harvested plot size in our study compared to previous studies. We used harvested plot sizes of several m^2 in each experiment while previous studies used smaller sample sizes of 0.18 to 1.5 m^{-2}. Sampling a larger area reduces measurement error and would in general tend to increase the power to reject the null hypothesis, which we did in this case. Unlike for biomass, mixtures did not reduce the between-plot variance for N yield. In most mixtures, we found a positive correlation between biomass yield and N concentration; plots with higher biomass had slightly higher N concentration. Moreover, component species within a mixture have different N concentrations, and therefore the compensation mechanism observed for biomass production does not necessarily result in a reduced variability for N yield. Consequently, between-plots variance for N yield did not differ between pure stands and mixtures.

In conclusion, we found that cover crop mixtures that contain productive species have the same biomass and higher nitrogen uptake than the most productive pure stands. We did not find a relationship between the number of component species within a mixture and productivity. Responsiveness to site productivity was more variable between pure stands than between mixtures. Using estimation of variance components with mixed effects models, we compared yield variability between cover crop mixtures and pure stands at three levels: between site-years, between treatments, and between plots within site-years. The site-year effect on biomass was similar for pure stands and mixtures, implying that mixtures do not even out the variation that is due to variation in growing conditions. However, within each site year, mixtures of cover crops had considerably lower variation across treatments and slightly lower variation across plots than pure stands. These differences in variation between mixtures and pure stands disappeared when only the most productive treatments were used in the analysis. Overall, these results highlight that some complementarity between species did occur, but agronomic consequences in terms of yield increase and yield variability were less prominent than expected. The implication for practical farming is that productivity of mixtures that contain high yielding species is similar to that of pure stands of those high yielding species. Evidence was obtained that N yield is higher in mixtures than in pure stands. Whether mixtures can consistently reduce yield variability in cover cropping would require longer data series than we obtained in these trials. Data from large number of experiments is needed to assess yield and yield variability in different species and species compositions.

Author statement

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Wopke van der Werf: Conceptualization, Methodology, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fcr.2021.108217.

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