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Annual intercropping suppresses weeds: A meta-analysis

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ABSTRACT

Intercropping has been advocated as an environmentally benign method to suppress weeds in agriculture. However, it is not evident from the literature what size of weed suppressive effect is achieved on average by intercropping, and how species choice and crop management affect this effect. We conducted a global meta-analysis of published data to quantify the effect of intercropping on weed biomass in annual arable intercrops grown for their final product. We searched the literature to identify all papers reporting usable experimental data and extracted 339 data records from 39 publications containing data from 76 independent experiments. Two metrics of weed suppression were defined to assess the weed suppressive effect of intercropping: the ratio of observed weed biomass in an intercrop to weed biomass in the less weed suppressive sole crop (R_{weak}), and the ratio of weed biomass in the intercrop to weed biomass in the more weed suppressive sole crop (R_{strong}). On average, weed biomass in the intercrop was substantially and significantly (58%) lower ($R_{weak} = 0.42$) than in the less suppressive sole crop. No significant difference was found between weed biomass in the intercrop and weed biomass in the more weed suppressive sole crop, even though weed biomass tended to be slightly larger in the intercrop than in the more weed suppressive sole crop ($R_{strong} = 1.08$). Findings were consistent across different groups of species combinations, such as maize/legume and small-grain cereal/legume intercrops. Intercrops with an additive design had stronger weed suppression than intercrops with a replacement design. In the latter, a mixed arrangement gave stronger weed suppression than a row design, while spatial arrangement did not affect weed suppressive ability in additive designs. No significant effects on weed biomass were found of simultaneous vs. relay intercropping, and of nitrogen fertilizer input. The R_{weak} decreased significantly with the land equivalent ratio in additive intercrops but not in replacement intercrops, while R_{strong} was unrelated to LER in both designs. The results confirm that intercropping is generally a useful approach for suppressing weeds in annual crop cultivation. Further work is needed to disentangle the contributions of species density, species traits and mixing ratio to weed suppression in intercropping.

1. Introduction

Weeds are an important growth reducing factor in arable crop production due to competition with the crop for light, water and nutrients. Weed induced crop yield losses are variable (Sheng and Zhang, 2001), and can even reach up to 100% in case of a poorly established crop. Weeds are commonly controlled with chemical herbicides, but chemical weed control is costly for farmers and is associated with negative side-effects on the environment and human health (WHO report, 2019). Hand-weeding and mechanical weeding are widely used in organic agriculture, but both are time consuming and therefore expensive. Soil tillage is often effective in controlling weeds, but this practice is fuel intensive and an important source of CO_2 emissions (Sauerbeck, 2001). Furthermore, frequent tillage may exacerbate soil losses due to erosion (Paustian et al., 2000). There is therefore an increasing interest in alternative methods to manage weeds (Bastiaans et al., 2008; Benaragama and Shirtliffe, 2013).

Diversification of cropping systems has been proposed as a promising way to improve resilience to environmental and biotic stresses (Bommarco et al., 2013; Wood et al., 2015). Intercropping is a diversification measure entailing the cultivation of multiple crop species on the same field for a significant part of their growing periods (Willey, 1990). It is

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has long been known that intercropping can increase yield and lower production risks (Vandermeer et al., 1992). Among the different types of intercropping currently used by farmers, systems combining two annual cash crops are widespread and of economic benefit (Lithourgidis et al., 2011; Martin-Guay et al., 2018). The positive impacts of this type of intercropping on yield (Kiær et al., 2009; Lithourgidis et al., 2011; Iverson et al., 2014; Raseduzzaman and Jensen, 2017; Li et al., 2020; Tilman, 2020), land utilization efficiency (Pelzer et al., 2014; Yu et al., 2015; Martin-Guay et al., 2018; Xu et al., 2020), resource use efficiency (Zhang et al., 2017; Hauggaard-Nielsen et al., 2009; Xu et al., 2020), crop disease and pest suppression (Boudreau, 2013; Zhang et al., 2019) have already been demonstrated in several meta-analyses and reviews. Intercropping, as a pathway for ecological intensification of agriculture, is also believed to improve weed suppression (e.g. Mohler, 2001; Jamshidi et al., 2013; Suter et al., 2017). It is often suggested that resource complementarity between the component crops of an intercrop allows for a higher resource capture compared to sole crops, thereby leaving less resources for weeds and hampering their growth (e.g. Liebman and Dyck, 1993; Banik et al., 2006; Corre-Hellou et al., 2011). Nevertheless, no overarching meta-analysis has been done on the weed suppressive effect of intercrops composed of two annual cash crops.

In a recent overview of benefits of intercropping, intercrops were found to suppress weeds more than either of the sole crops in 86% of the cases (Stomph et al., 2020). In a review, Liebman and Dyck (1993) found that weed biomass in intercrops was lower than that in the pure stands of both component crops in 50% of the studies, intermediate between component crops in 42%, while in 8% it was higher than in both component crops. Although these vote counting analyses gave insight in the frequency of weed suppressive effects in intercropping, they did not estimate the effect size of intercropping and thus did not provide a robust quantification of intercropping weed suppression. To derive possible management guidelines for designing weed suppressive intercrops in practice, it is important to characterize the effects of different mixtures on weed suppression quantitatively.

Many factors related to design and crop management can potentially influence weed suppression. Possible factors influencing the weed suppressive effect of crop mixtures include, for instance, the choice of crop species (e.g. Bilalis et al., 2010; Sharma and Banik, 2013), the spatial arrangement such as fully mixed or planted in rows (e.g. Eskandari and Ghanbari, 2010; Sharma and Banik, 2013; Campiglia et al., 2014), the sowing density or relative frequency of component species in a mixture (e.g. Banik et al., 2006; Njoku et al., 2010; Ekpo and Ndaeyo, 2011), the extent to which the component crops are temporally separated as a result of differences in sowing and harvesting dates, fertilizer input rate (Corre-Hellou et al., 2006; Hauggaard-Nielsen et al., 2008) as well as the use of additional weed control measures such as herbicides (Gronle et al., 2014). In this study, we conducted a meta-analysis to synthesize the results of 76 experiments published in literature. The aim of the study was to: (1) quantify the effect of intercrops consisting of two annual cash crops on weed suppression compared to the respective sole crops, (2) assess how different design and management factors influence the weed suppressive effect of intercrops, and (3) analyze the relationship between resource complementarity between component species and weed suppressive ability.

2. Materials and methods

2.1. Data collection from published articles

A literature search was conducted on the Web of Science Core Collection (WoSCC) in April, 2019. We used the Science Citation Index Expanded over the time period 1945-present. We searched for: ("intercrop*" or "mixed crop*" or "crop mix*" or "mixed cult*" or "polycultur*") AND ("weed*") NOT (vineyard or pasture or grassland or orchard or agroforestry) in the topic field. The search yielded 809 publications. The titles and abstracts of these publications were screened to select those that contained primary empirical information on weeds in intercrops. A total of 98 publications were retained based on the title and the abstract. Then we screened the full texts of the 98 articles. Articles were selected if the three following criteria were satisfied: (1) the paper reported data from field experiments, (2) the intercrop consisted of two annual cash crops, and (3) the paper reported weed biomass for both intercrop and sole crop treatments. If data from the same experiment were reported in several papers, the data were included from the paper that reported the data in the greatest degree of detail. The references cited in the studies were reviewed to identify additional papers. Eventually, a total of 39 articles were included in the analysis, with 339 records from 76 experiments (Methods A1). The procedure of paper screening and selection is presented in a prisma diagram (Fig. A1).

We defined an experiment as a unique combination of site and year in which at least one intercrop treatment and two corresponding sole crops were studied under the same management (sowing and harvesting dates, spatial arrangement, weed control measures and fertilizer rate). Some experiments included multiple species combinations and their corresponding sole crops. All suitable combinations were extracted as separate records. A record was defined as a unique combination of site-year and management for a combination of two crop species grown as an intercrop and in pure stands. An article could provide data for two or more experiments if more than one site or year was considered. Data from different experiments were extracted separately and a unique identifier was associated with each experiment. The number of blocks or replicates included in each experiment was noted.

We extracted the weed biomass and crop yield/biomass data expressed as dry matter or fresh biomass per unit area (g/m^2). All articles except one reported biomass of a mixture of weed species, while one article reported biomass of a single weed species. Both were included. Most articles only measured total weed biomass at crop harvest, while in nine articles weed biomass was measured at several crop stages. In case of multiple biomass measurements, we extracted the data of the last sampling date only. In a few cases (14%, 47 out of 339 records), weeding measures (e.g. herbicides) applied either as a pre-application before crop emergence or as a sub-plot treatment within all crop treatments. No statistically significant effect of weed control measures on the effect of intercropping on weed biomass was found. We therefore did not further consider weed control measures as an explanatory variable in the study. For each record, both the intercrop and the sole crops received the same management practices. Several records with herbicide application reported weed biomass values equal to zero in either the sole crops or intercrop, they were not used in the analysis as they did not elucidate the intercropping effect on weed biomass.

2.2. Response variables

Two metrics (R_{weak} and R_{strong}) were calculated to compare the weed biomass in intercrops (B_{ic}) with the weed biomass in the pure stands of the less ($B_{sc,weak}$) and more ($B_{sc,strong}$) weed suppressive crop species for each record of each experiment:

$$\ln(R_{weak}) = \ln\left(\frac{B_{ic}}{B_{sc,weak}}\right) \tag{1}$$

$$\ln(R_{strong}) = \ln\left(\frac{B_{ic}}{B_{sc,strong}}\right) \tag{2}$$

We also determined the ratio of weed biomasses in the pure stands of the stronger and the weaker weed suppressive component crop species (R_{sw}) as an indicator for the difference in weed suppressive ability between the two component species:

$$\ln(R_{sw}) = \ln\left(\frac{B_{sc,strong}}{B_{sc,weak}}\right) \tag{3}$$

A large number of data records (248/339) concerned mixtures of a cereal and a legume. To characterize whether in such mixtures the cereal or the legume was the more strongly weed suppressive component, we calculated a metric $\ln(R_{cl})$:

$$\ln(R_{cl}) = \ln(\frac{B_{sc,cereal}}{B_{sc,legume}}) \quad (4)$$

where $B_{sc,cereal}$ is the weed biomass in cereal pure stand and $B_{sc,legume}$ is the weed biomass in the legume pure stand. For this type of intercrops, two additional ratios ($R_{ic,cereal}$ and $R_{ic,legume}$) were calculated to compare weed control in the intercrop to that in the pure stands of the cereal and legume and study the effect of nitrogen fertilizer input:

$$\ln\left(R_{ic,cereal}\right) = \ln\left(\frac{B_{ic}}{B_{sc,cereal}}\right) \quad (5)$$

$$\ln\left(R_{ic,legume}\right) = \ln\left(\frac{B_{ic}}{B_{sc,legume}}\right) \quad (6)$$

2.3. Explanatory variables

Six explanatory variables were considered to explain the variability of the response variables related to weed suppression: (1) species composition, (2) temporal niche differentiation (TND), (3) intercrop design, (4) spatial arrangement, (5) nitrogen fertilizer input and (6) land equivalent ratio (LER) (Table 1).

Species composition was defined as a categorical variable with three levels: maize/legume, small-grain cereal/legume, and other intercrops. Cereal/legume intercrops represented 248 out of 339 records (248/339). Since there were large differences in the design between cereal/legume intercrops with maize or small-grain cereals (see Results), we distinguished two categories named “maize/legume” (75 cases) and “small-grain cereal/legume” intercrops (173 cases). The remaining intercrops were classified in the category “other intercrops”.

Differences in growing period between species, as in relay intercropping, might affect weed suppression in intercrops. We calculated an index for temporal niche differentiation between the crop species (TND) to characterize the extent to which the growing periods of the component species were non-overlapping in time (Yu et al., 2015):

Table 1
Variables used to explain the weed suppressive ability of intercrops composed of two cash crops.

Variable	Definition
Intercrop composition	Three groups were distinguished: (1) maize/legume, (2) small-grain cereal/legume and (3) other intercrops.
TND	Temporal niche differentiation (TND) was calculated following Eq. (7), ranging from 0 (both species sown and harvested at the same time) to 1 (double cropping).
RDT and intercrop design	Relative density total (RDT) was calculated following Eq. (9). Intercrop design was classified into two groups based on RDT: replacement (RDT = 1) and additive design (RDT > 1).
Intercrop spatial arrangement	Three groups were defined: (1) Fully mixed intercropping: two species are cultivated in a completely mixed random pattern or in rows with the species mixed within the rows; (2) Row intercropping: two species are cultivated in alternate rows; (3) Strip intercropping: two species are cultivated in alternating strips or rows, with at least for one crop species a strip comprising more than one row.
N fertilizer input	The amount of nitrogen applied in the sole crops and the intercrop (unit: kg ha^{-1}). Five strategies for N input were distinguished: (1) equal rate of N in the intercrop and the sole crops, (2) N in the intercrop intermediate between the sole crops, (3) N in the intercrop equal to the highest N input in the sole crop, (4) N in the intercrop larger than the highest N input in the sole crop, and (5) N in the intercrop smaller than the lowest N input in the sole crop.
LER	Land equivalent ratio (LER) was calculated following Eq. (10).

$$\text{TND} = \frac{P_{system} - P_{overlap}}{P_{system}} \quad (7)$$

where P_{system} represents the duration of the whole intercrop in days, while $P_{overlap}$ represents the overlap in growing period of the intercropped species in days. Both periods are based on the sowing and harvest dates. An intercrop is simultaneous if TND is zero, while relay intercrops have TND greater than zero but smaller than one. TND would be one in the case of double cropping, which is not considered here.

Intercrop design refers to species densities in the intercrop as compared to the sole crops. We calculated the relative density (RD) for each species in the intercrop. RD is defined as:

$$RD_1 = \frac{D_{1,ic}}{D_{1,sc}} \quad \text{and} \quad RD_2 = \frac{D_{2,ic}}{D_{2,sc}} \quad (8)$$

where $D_{1,ic}$ and $D_{2,ic}$ are the densities of crop species 1 and 2 in the intercrop, and $D_{1,sc}$ and $D_{2,sc}$ are their densities in the sole crops. Density of a crop species in an intercrop is defined as the number of plants per unit land area of the whole intercrop (i.e. including the area occupied by other species). The relative density total (RDT) is then a useful measure for the overall crowding of species in the intercrop:

$$RDT = RD_1 + RD_2 \quad (9)$$

Based on RDT, intercrop design was classified as replacement (RDT = 1) or additive (RDT >1).

Three types of spatial arrangement in intercrops were distinguished: fully mixed, row and strip configuration (Yu et al., 2015). Mixed intercropping comprised both full mixtures without any row patterns and row intercropping with species mixed within the rows. Row intercropping was defined as two species cultivated in alternate rows. Strip intercropping was defined as two species in alternating strips or rows, whereby at least one of the species was grown in strips that include more than one row (row configurations see Table A1). In the selected articles, an association was observed between intercrop design and spatial arrangement (see Results; Effect of either of the factors see Methods A2). To account for a possible confounding effect between the two factors, they were combined into a six-level (2×3) explanatory factor that was used in all comparisons.

Nutrient availability can affect the competitive balance between plant species (crop-crop and crop-weed) (Naudin et al., 2010). Additionally, weedy species in general respond positively to nitrogen fertilizer (Corre-Hellou and Crozat, 2005), while legumes have a competitive advantage to non-legumes at low N input. Therefore, two questions related to nitrogen input were addressed: (i) How is the effect of intercropping on weed biomass influenced by nitrogen input? (ii) Is the effect of nitrogen input (if it exists) different for intercrops with and without legumes? A subset of 325 records from 72 experiments reported information on N input. Of these, 234 records from 63 experiments were cereal/legume intercrops. We distinguished five different strategies for N input rate in sole crops and intercrops (Table 1, Table A2). In maize/legume intercrops, N input in the intercrop was most cases (46/52) intermediate between that in sole maize (high) and the sole legume (low) (Table A2). In small-grain cereal/legume intercrops, usually equal rates of N were used in sole crops and intercrops (147/158). These two N input strategies were considered when analysing the effect of N input in the mixture on the competitiveness of the intercrop to weeds when comparing to the pure stands of the cereal ($R_{ic,cereal}$) and the legume ($R_{ic,legume}$).

It is often assumed that intercrops are better at suppressing weeds due to niche differentiation. The combined component crops are thought to occupy a broader niche and capture resources more completely, leaving less resource space for weeds to grow (Liebman and Dyck, 1993; Banik et al., 2006). Another result of resource complementarity is the relative overyielding of the intercrops, which is expressed by the land equivalent ratio (LER) (Mead and Willey, 1980; Yu et al., 2015). The LER is defined as:

$$LER = \frac{Y_{1,ic}}{Y_{1,sc}} + \frac{Y_{2,ic}}{Y_{2,sc}} \quad (10)$$

where Y_i is the biomass or yield of species 1 or 2 in intercrop (ic) or sole crop (sc). An LER > 1 indicates overyielding of the intercropping, which may be due to complementarity between crop species in their patterns of resource use and/or facilitative effects (Vandermeer, 1992). We assumed the increases in LER fully came from resource complementarity, and used the LER as a sixth explanatory factor to test whether resource complementarity between crop species can predict weed suppression. A covariable that indicated the type of LER (calculated from biomass or yield) did not affect the analysis, therefore the result was reported without this covariable (Methods A3). We also determined how LER as a response variable was related to other explanatory variables (species composition, TND, intercrop design, spatial arrangement and N input) (Methods A4). A subset of 279 records from 66 experiments reporting the data on crop productivity was used.

2.4. Statistical analysis

Linear regression with mixed-effects models was used to estimate the mean value of R_{weak}, R_{strong}, as well as the relationships between these response variables and the explanatory variables. In the selected articles, there were 209 out of 339 records without standard error or standard deviation reported, we therefore did an unweighted analysis in which all studies had an assumed equal variance (Yu et al., 2015; Martin-Guay et al., 2018; Li et al., 2020; Xu et al., 2020). We used the function lme() from the package nlme to fit the mixed models (Pinheiro et al., 2015; R Core Team, 2014). Parameters were estimated by restricted maximum likelihood (REML). Publication and experiment (unique site * year) were defined as random effects, with experiment nested in publication. The random effects structure was simplified based on Akaike's information criterion (R functions anova() and AIC()) if it did not contribute to a lower AIC. The assumptions of heterogeneity and normality were checked using histograms of model residuals and plot of residuals against fitted values, respectively (Zuur et al., 2009). Finally, we selected twelve mixed effect models to report the results (Table 2).

Publication bias is a concern in meta-analysis since studies with more favorable effect sizes may be more easily published. Here publication bias was evaluated using funnel plots (Koricheva et al., 2013) for ln(R_{weak}) and ln(R_{strong}) (Methods A5). A sensitivity analysis was performed to check the sensitivity of the estimated effect sizes to omitting studies (Methods A6). As within-study standard deviations were missing in most cases, we plotted the average response variable in each article against the total number of experimental units (replicates) over experiments and treatments within the article as a proxy for accuracy (Yu et al., 2015).

Table 2
Mixed effect models fitted to analyse the data. The indices *i*, *j* and *k* represent publication, experiment and treatment, respectively. In all mixed models, a_i is a random publication effect and b_{ij} is a random experiment effect nested within the i^{th} publication. a_i and b_{ij} are assumed normally distributed with constant variances. ε_{ijk} is a residual random error assumed normally distributed with constant variance. The variance terms a_i, b_{ij} and ε_{ijk} are all assumed independent.

Model	Equations	Data
1	$TND_{ijk} = \beta_{IC}(IC_{ijk}) + a_i + b_{ij} + \varepsilon_{ijk}$	All data
2	$(lnR_{weak}, lnR_{strong})_{ijk} = u + a_i + b_{ij} + \varepsilon_{ijk}$	All data
3	$(lnR_{sw})_{ijk} = \beta_{IC}(IC_{ijk}) + a_i + b_{ij} + \varepsilon_{ijk}$	All data
4	$(lnR_{cl})_{ijk} = \beta_{IC}(IC_{ijk}) + a_i + b_{ij} + \varepsilon_{ijk}$	All cereal/legume intercrops
5	$(lnR_{weak}, lnR_{strong})_{ijk} = \beta_{IC}(IC_{ijk}) + a_i + b_{ij} + \varepsilon_{ijk}$	All data
6	$(lnR_{weak}, lnR_{strong})_{ijk} = \beta_0 + \beta_{TND} * TND_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	All data
7	$(lnR_{weak}, lnR_{strong})_{ijk} = \beta_{ED}(IA_{ijk}) + a_i + b_{ij} + \varepsilon_{ijk}$	All records with information on intercrop design and spatial arrangement
8	$(lnR_{weak}, lnR_{strong})_{ijk} = \beta_0 + \beta_{RDT} * RDT_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	All data
9	$(\ln R_{weak}, \ln R_{strong})_{ijk} = \beta_0 + \beta_N * N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	All records with information on N fertilizer input
10	$(lnR_{ic,cereak}, lnR_{ic,legume})_{ijk} = \beta_0 + \beta_N * N_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	All cereal/legume intercrops within N input strategy 1 or N input strategy 2
11	$LER_{ijk} = u + a_i + b_{ij} + \varepsilon_{ijk}$	All records with information on crop productivity; and records with information on crop within intercrops with replacement or additive design
12	$(lnR_{weak}, lnR_{strong})_{ijk} = \beta_0 + \beta_{LER} * LER_{ijk} + a_i + b_{ij} + \varepsilon_{ijk}$	All records with information on crop productivity within replacement or additive design

Note: Model 1 is used to extract information on temporal niche differentiation (TND) of intercrops. IC (Intercrop composition) is a three-level categorical variable for all intercrops: maize/legume, small-grain cereal/legume and other intercrops, or a two-level categorical variable for cereal/legume intercrops: maize/legume and small-grain cereal/legume. Therefore, the intercept β_{IC} (IC_{ijk}) can take three (for model 1, 3, 5) or two values (for model 2), depending on different IC levels. IA (Intercrop arrangement) is a six-level categorical variable for all possible combinations of intercrop design (i.e. replacement and additive design) and spatial arrangement (i.e. mixed, row and strip). For model 2,11, *u* is the mean value.

3. Results

3.1. Characteristics of intercropping systems

3.1.1. Intercrop species composition

In the selected articles, three main categories of crop species were distinguished: cereals (seven species), legumes (twelve species) and other crop species (seven species). The cereal species were maize (*Zea mays*), barley (*Hordeum vulgare*), oats (*Avena sativa*), rice (*Oryza sativa*), sorghum (*Sorghum bicolor*), triticale (*x Triticosecale*) and wheat (*Triticum aestivum*). The legumes were blackgram (*Vigna mungo*), chick pea (*Cicer arietinum*), common bean (*Phaseolus vulgaris*), common vetch (*Vicia sativa*), cowpea (*Vigna unguiculata*), faba bean (*Vicia faba*), fenugreek (*Trigonella foenumgraecum*), field pea (*Pisum sativum*), groundnut (*Arachis hypogaea*), lentil (*Lens esculenta*), lupin (*Lupinus angustifolius*) and soybean (*Glycine max*). The other species were cassava (*Manihot esculenta*), buckwheat (*Fagopyrum esculentum*), canola (*Brassica napus*), linseed (*Linum usitatissimum*), pumpkin (*Cucurbita maxima*), yam (*Dioscorea rotundata*), and chilli peppers (*Capsicum annuum*). These 26 crop species made up a total of 35 intercrop combinations (Fig. 1). Of these, maize/legume systems represented 22% of the records (75 out of 339 records, 11 studies), including four frequently studied mixtures with more than 10 records, i.e. maize with common bean, blackgram, soybean or cowpea. Small-grain cereal/legume systems made up 51% of the records (173/339, 23 studies), including six frequently studied mixtures, i.e. wheat with lentil, pea or faba bean; barley with faba bean or pea; and oat with pea. The other intercrops made up 27% of the records (91/339, 8 studies), including four frequently studied mixtures, i.e. wheat with barley or canola; canola with pea; and chilli with common bean.

3.1.2. Intercrop design and management

Most maize/legume intercrops originated from Asian experiments (55/75), while most of the small-grain cereal/legume intercrops originated from European experiments (121/173). The category "other intercrops" most frequently originated from North America (55/91) (Fig. 2a). Maize/legume intercrops were often laid out as simultaneous

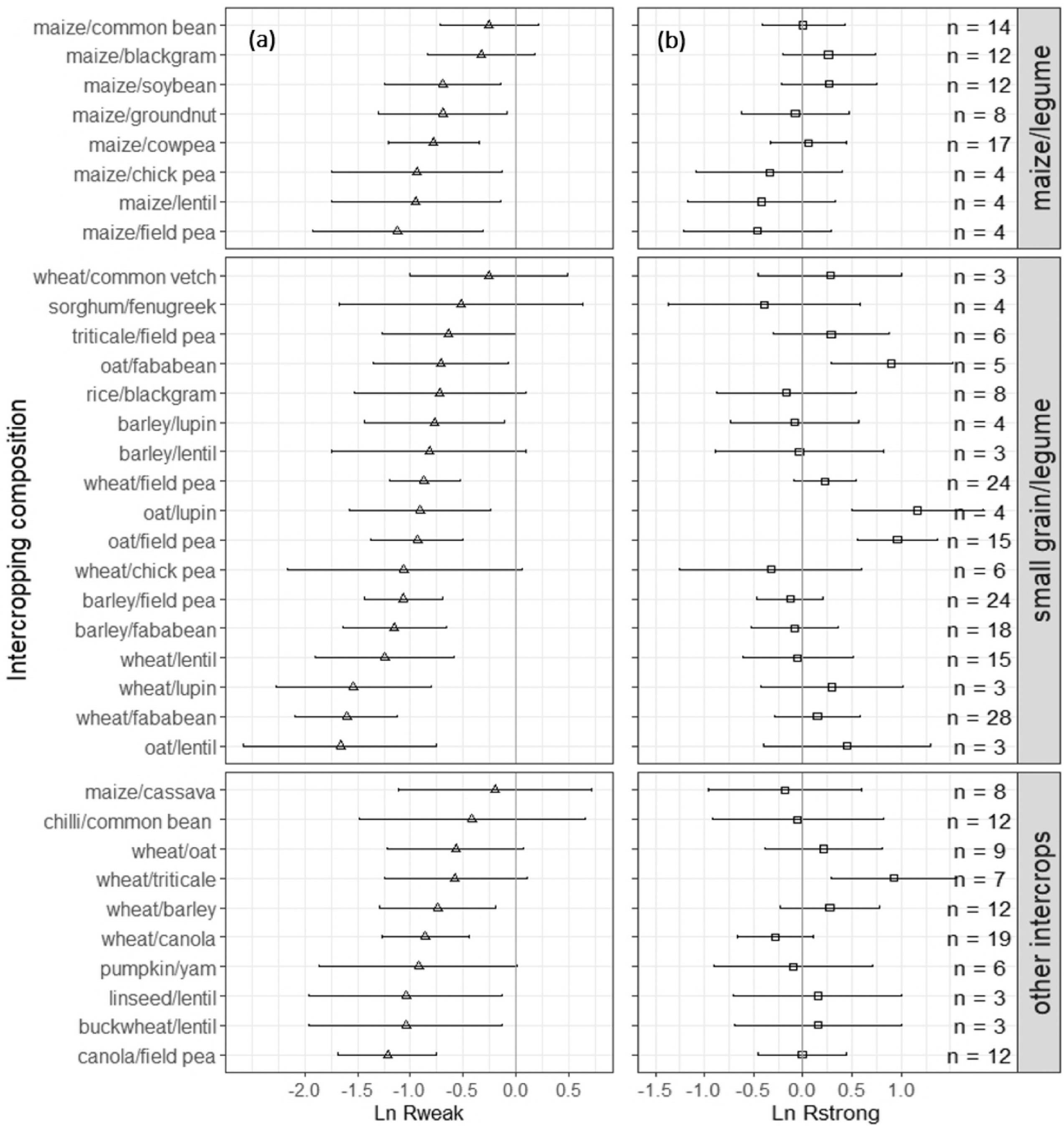

Fig. 1. An overview of 35 species combinations included in the meta-analysis. The log-ratio of the weed biomass in intercrops relative to that of (a) the weaker competitive sole crops ($\ln(R_{weak})$), and (b) the stronger competitive sole crops ($\ln(R_{strong})$) in different species combinations. Vertical lines indicate a value of 0, which corresponds to an equal weed biomass in the intercrop and the sole crops. Points and bars indicate the mean effect sizes and their 95% confidential intervals, respectively. *n* indicates the number of records for each intercrop combination.

systems (39/75) and as relay systems (36/75), while most small-grain cereal/legume intercrops (165/173) and other intercrops (77/91) were simultaneous systems. Accordingly, the TND in maize/legume systems (0.17 ± 0.04, mean ± standard error) was significantly higher than in small-grain cereal/legume systems (0.03 ± 0.03) and other intercrops (0.03 ± 0.03) (model 1, $P < 0.05$ for both comparisons). Maize/legume intercrops usually had an additive design (67/75) and they were most frequently arranged in row (35/75) or strip configuration (37/75). Maize was mostly sown at the same density in mixture as in the sole crop. Small-grain cereal/legume intercrops were equally laid out in replacement (88/173) and additive design (85/173) and mostly in a mixed arrangement (109/173). The other intercrops were most often laid out in a replacement design (61/91) and with a mixed spatial arrangement (62/91) (Figs. 2b, 2c).

In summary, maize/legume intercrops were characterized by a high TND, an additive design and a row or strip arrangement, while small-grain cereal/legume intercrops and other intercrops were characterized by lower TND and a mixed arrangement, either equally distributed over replacement and additive design (small-grain cereal/legume) or predominantly in replacement design (other intercrops) (Observations of records, see Table A3).

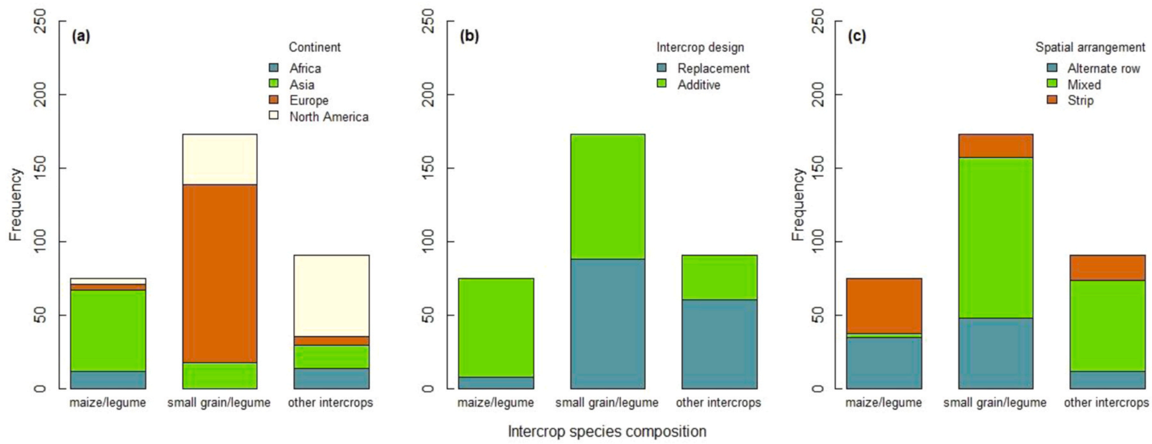

Fig. 2. Number of data records by (a) continent, (b) intercrop design and (c) spatial arrangement across three intercrop compositions.

3.2. Comparison on weed biomass between intercrop and sole crops

Across all records, the mean R_{weak} was 0.42 ($n = 339$; 95%CI:[0.35, 0.50]) with a median value of 0.52 (model 2, Fig. 3a). The mean R_{strong} was 1.08 ($n = 339$; 95%CI:[0.91, 1.28]) with a median value of 1.07 (Fig. 3b). In 45% of the records (152/339), both R_{weak} and R_{strong} were lower than one, indicating that weed biomass was in 45% of the cases lower in the intercrop than in both sole crops. In 46% of the records (157/339), the R_{weak} was lower than one while the R_{strong} was greater than one, meaning that in those records weed biomass was intermediate between that in the sole crops. On average, weed suppressive ability of intercrops was similar to that of pure stands of the more competitive species in the mixture and substantially stronger than that of pure stands of the less competitive species in the mixture.

3.3. Effect of intercrop composition on weed suppression

The ratio of weed biomass in the stronger and weaker component sole crop, R_{sw}, was significantly lower in small-grain cereal/legume (0.32, 95%CI:[0.25, 0.39]) than in maize/legume (0.51, 95%CI:[0.35, 0.73]) and other intercrops (0.42, 95%CI:[0.32, 0.56]) (model 3, both $P < 0.05$, Fig. 4a). This reflected that the relative difference in weed suppressive ability of component crops was larger in small-grain cereal/legume intercrops than in the other two types of intercrops. The ratio of weed biomass in the pure stands of component cereal or legume crops, R_{cl}, was on average above one (1.47, 95%CI:[0.80, 2.70]) in maize/legume intercrops and significantly below one in small-grain cereal/legume intercrops (0.46, 95%CI:[0.30, 0.70]) (model 4, $P = 0.003$, Fig. 4b). Thus, in maize/legume intercrops, maize tended to be the weaker competitor against weeds, whereas in small-grain cereal/legume intercrops, the small-grain cereal was on average the stronger competitor towards weeds.

Across 35 species combinations, weed biomass was lower in intercrops than in the weaker components (Fig. 1a). The average R_{weak} values were consistently lower than one in all three types of intercrops (model 5, $P < 0.001$, Fig. 5a). Weed biomass in intercrops and in the stronger component crops were not significantly different in most of the considered crop mixtures (Fig. 1b). The average R_{strong} was not significantly different from one in any of the three types of species combinations (model 5, Fig. 5b).

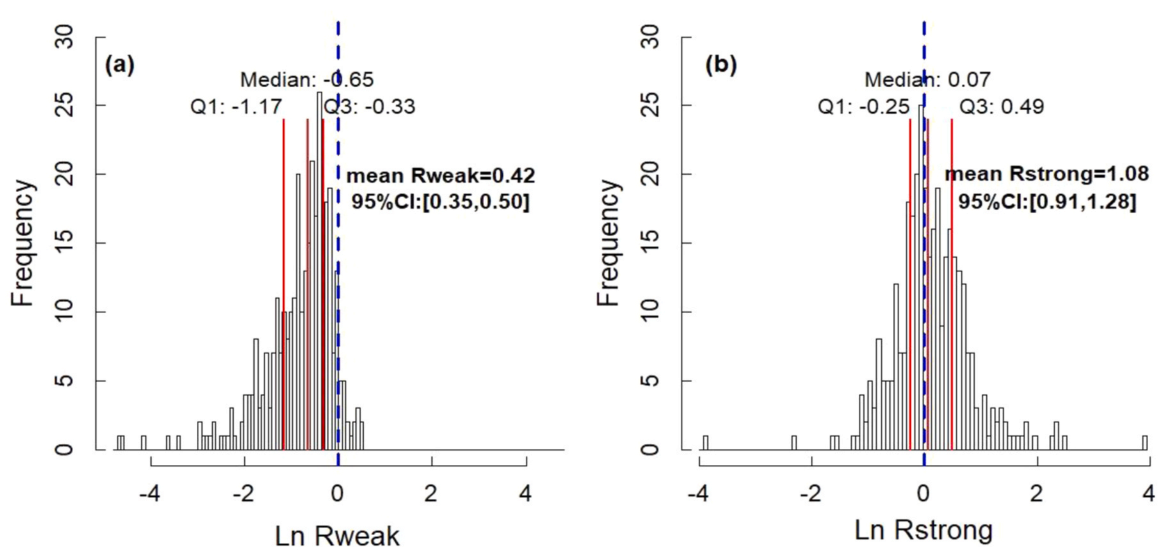

Fig. 3. Frequency distribution of (a) ln(R_{weak}) and (b) ln(R_{strong}). Vertical red lines in panels a and b indicate the first quartile (Q1), median and the third (Q3) quartile of ln(R_{weak}) and ln(R_{strong}). The vertical blue lines indicate a value of 0 (log scale), which corresponds to an equal weed biomass in intercrop and sole crop. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

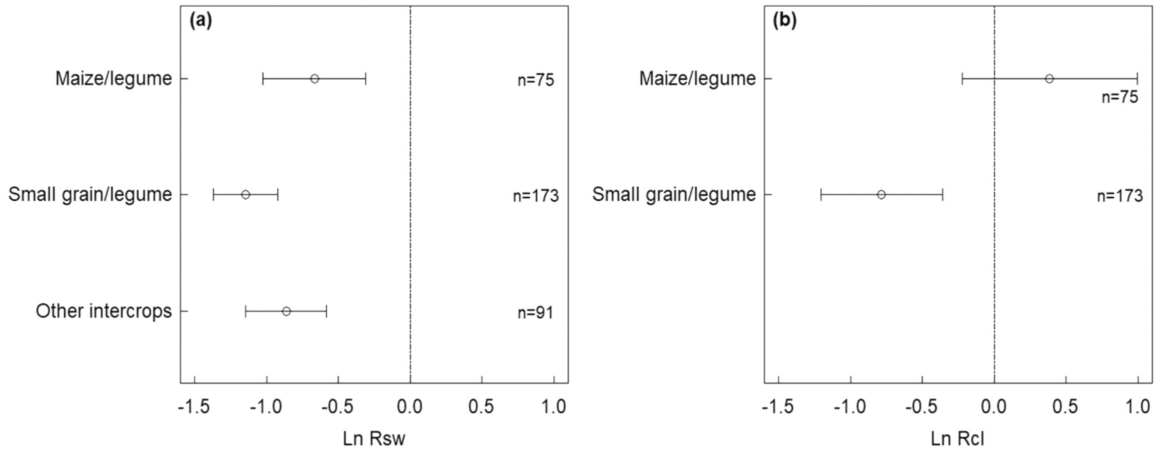

Fig. 4. (a) ln(R_{sw}) (ratio of weed biomass in pure stands of the stronger and weaker component crop) for three intercrop compositions, and (b) the ln(R_{cl}) (ratio of weed biomass in pure stands of the small-grain cereal and legume component crop) for small-grain cereal/legume intercrops. Vertical lines indicate a value of 0, corresponding to an equal weed biomass in both component crops. Points and bars indicate the mean effect sizes and their 95% confidential intervals, respectively. *n* indicates the number of observations.

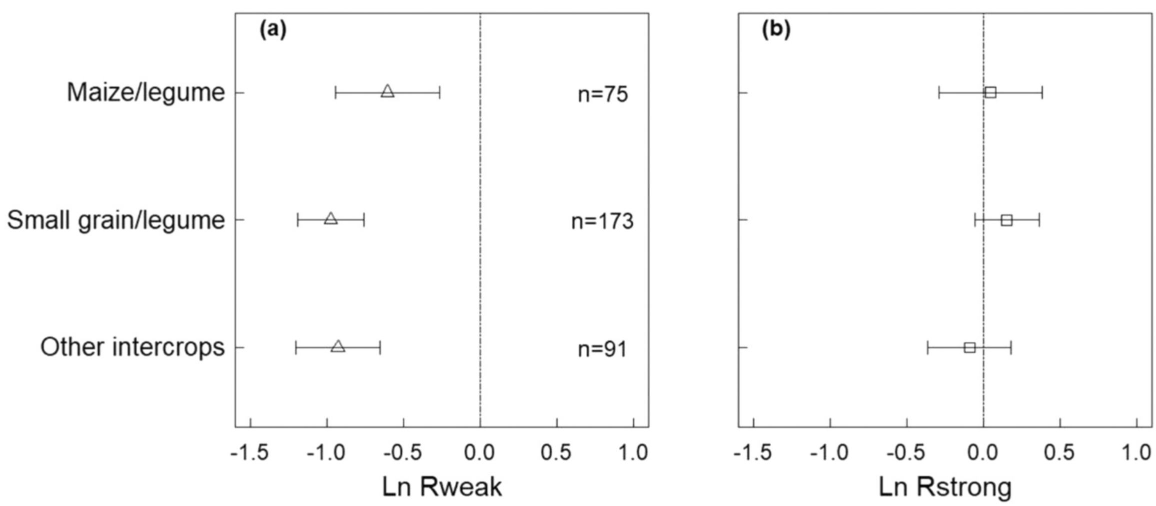

Fig. 5. (a) ln(R_{weak}) (weed biomass in intercrops compared to that of the weaker component crops) and (b) ln(R_{strong}) (weed biomass in intercrops compared to that of the stronger component crops) across the three distinguished species compositions. Vertical lines indicate a value of 0, corresponding to an equal weed biomass in intercrop and sole crops. Points and bars indicate the mean effect sizes and their 95% confidential intervals, respectively. *n* indicates the number of observations.

3.4. Effect of temporal niche differentiation, intercrop design and spatial arrangement on weed suppression

The TND reflects the overlap in growing period between the component species in an intercrop. TND did not significantly affect the R_{weak} and R_{strong}, neither within maize/legume intercrops (model 6, Fig. A2a), the system with the greatest TND, nor across all intercrop systems (Fig. A2b).

Since intercrop design and spatial arrangement were associated, we analysed the effect by using a categorical variable that combines both aspects. The R_{weak} was consistently lower than one, except for the replacement - row design (model 7, $P < 0.01$, Fig. 6a). For this design, the R_{weak} (0.75, 95%CI:[0.54, 1.06]) was also significantly higher than for the other four groups (all pairwise comparisons: $P < 0.05$). The R_{strong} was higher than one in both replacement designs (replacement - row: 2.02, 95%CI:[1.45, 2.82], $P < 0.001$; and replacement - mixed: 1.31, 95%CI:[0.98, 1.75], $P = 0.069$), while it was not significantly different from one in the additive designs (model 7, Fig. 6b). The R_{strong} in replacement - row designs was also significantly higher than that of all others (all pairwise comparisons: $P < 0.05$). Besides, the R_{strong} in replacement - mixed designs was higher than in both additive - mixed designs (0.83, 95%CI:[0.65, 1.22], $P = 0.053$) and additive - strip designs (0.81, 95%CI:[0.62, 1.07], $P = 0.016$), while it was not different from the additive - row designs (0.97, 95%CI:[0.76, 1.24], $P = 0.103$). Thus, weed suppression was in general stronger in additive intercrops than in replacement intercrops. For this reason, the influence of relative density total (RDT) on weed suppression was further investigated. The R_{strong} decreased 0.51 per unit RDT (model 8, $P < 0.001$), while there was no relation between R_{weak} and RDT (Fig. 7).

3.5. Effect of N fertilizer input on weed suppression

Increased N input rate did not affect R_{weak} and R_{strong} (model 9, Fig. A3), indicating that the responses of weeds to increased N fertilizer were similar in intercrops and sole crops and the comparative suppressiveness of mixtures to weeds compared to pure stands was not affected by N input. Within each N input strategy, increased N input did not affect the $R_{ic,cereal}$ and $R_{ic,legume}$ (model 10, Fig. A4), indicating that the weed suppression of intercrops compared to the component cereal or legume species was not affected by N input.

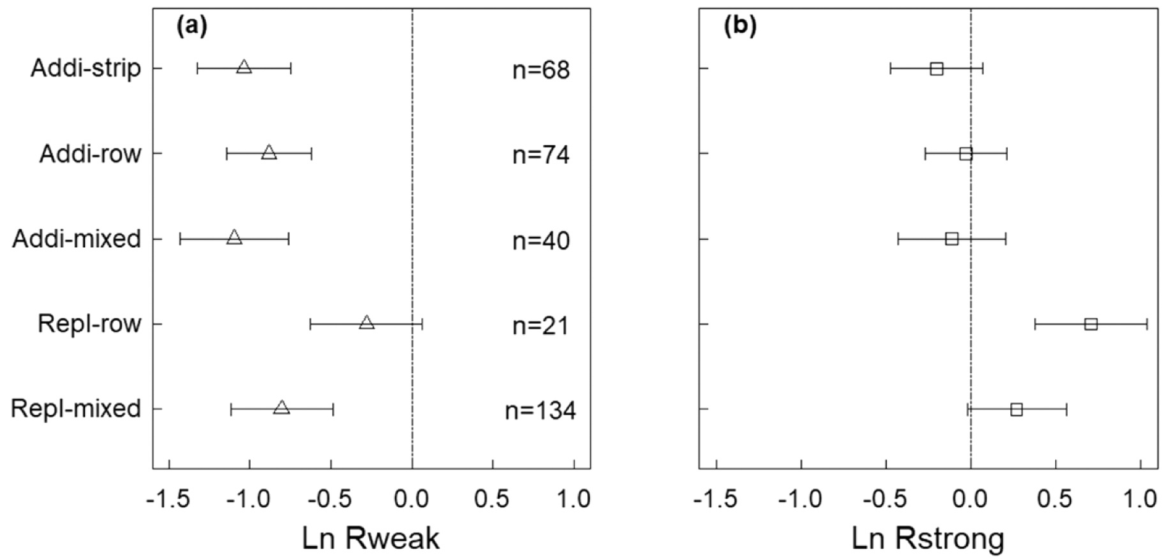

Fig. 6. The (a) ln(R_{weak}) (weed biomass of intercrops compared to that of the weaker component crops) and (b) ln(R_{strong}) (weed biomass of intercrops compared to that of the stronger component crops) across different combinations of intercrop design and spatial arrangement. Strip intercrops with a replacement design ($n = 2$ only) were omitted. Vertical lines indicate a value of 0, corresponding to an equal weed biomass in intercrop and sole crops. Points and bars indicate the mean effect sizes and their 95% confidential intervals, respectively. n indicates the number of observations.

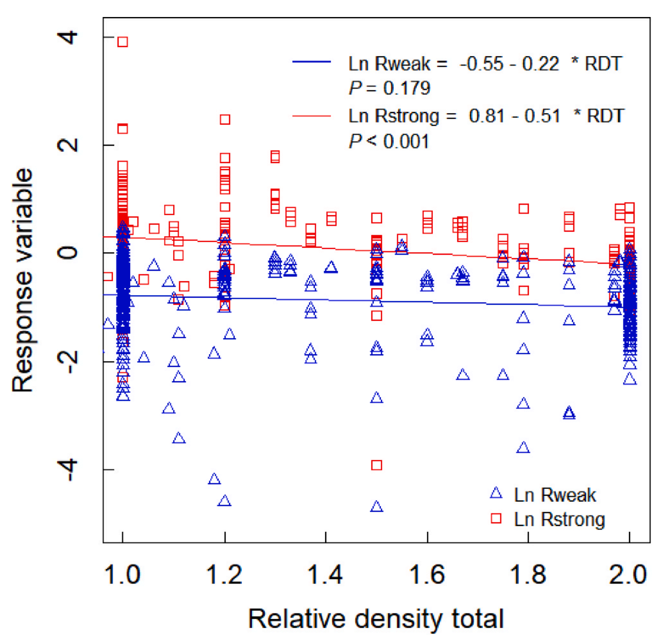

Fig. 7. Effect of relative density total (RDT) on the (a) ln(R_{weak}) (weed biomass of intercrops compared to that of the weaker component crops) and (b) ln (R_{strong}) (weed biomass of intercrops compared to that of the stronger component crops).

3.6. Effect of land equivalent ratio of intercrops on weed suppression

Across all records, the mean LER was 1.32 ($n = 279$, 95%CI:[1.22, 1.42]) with a median value of 1.24 (model 11, Fig. A5). For intercrops with a replacement and additive design, the mean LER was 1.16 ($n = 121$, 95%CI:[1.08, 1.25]) and 1.39 ($n = 158$, 95%CI:[1.27, 1.52]) respectively (model 11). The LER increased 0.28 per unit RDT ($P < 0.001$, Table S3, Fig. S3a) and 0.73 per unit TND ($P < 0.01$, Table S3, Fig. S3b). These results indicate that if LER is used as an index for resource complementarity in the mixtures, substantially greater complementarity was achieved with increasing density or temporal niche differentiation.

In intercrops with a replacement design, the LER did not significantly affect R_{weak} and R_{strong} (model 12, Fig. 8a). In intercrops with an additive design, there was a negative relationship between LER and R_{weak} and R_{strong}. Only the relationship between LER and R_{weak} was significant (Fig. 8b).

4. Discussion

4.1. Weed suppression in intercrop and sole crops

This study aimed to quantify the overall effect of intercropping on weed biomass (weed suppression) in comparison to that in the pure stands of the species making up the intercrop. We also investigated how the weed suppressive effect of intercropping is affected by the design and management of intercrops. We found that the weed suppression in intercrops was better than that in both component crops in 45% of all the cases, and intermediate between the component crops in another 46% of the cases. This counting outcome was consistent with the findings reported in the review of Liebman and Dyck (1993). Moreover, we found that weed biomass was on average 58% lower in intercrops than in the weaker suppressive component crops. At the same time, weed biomass in the intercrop was not significantly different from that of the stronger suppressive component crops (Fig. 3). These findings were consistent across a wide range of crop species combinations, intercrop designs, temporal segregation, spatial arrangement and nitrogen input, confirming the general ability of intercropping to achieve weed suppression as good as the more weed competitive species and substantially better than that of the less competitive species.

4.2. Factors influencing the weed suppressive function of intercrops

Three groups of intercropping systems were distinguished: maize/legume, small-grain cereal/legume and other intercrops. For these three groups, the weed suppressive ability of the component crops differed considerably, and the biggest difference between component species was found in the small-grain cereal/legume systems (Fig. 4a). For all three groups, the general pattern held true that the weed suppressive ability of the intercrop was close to that of the more competitive crop and much stronger than that of the less competitive crops (63/75)

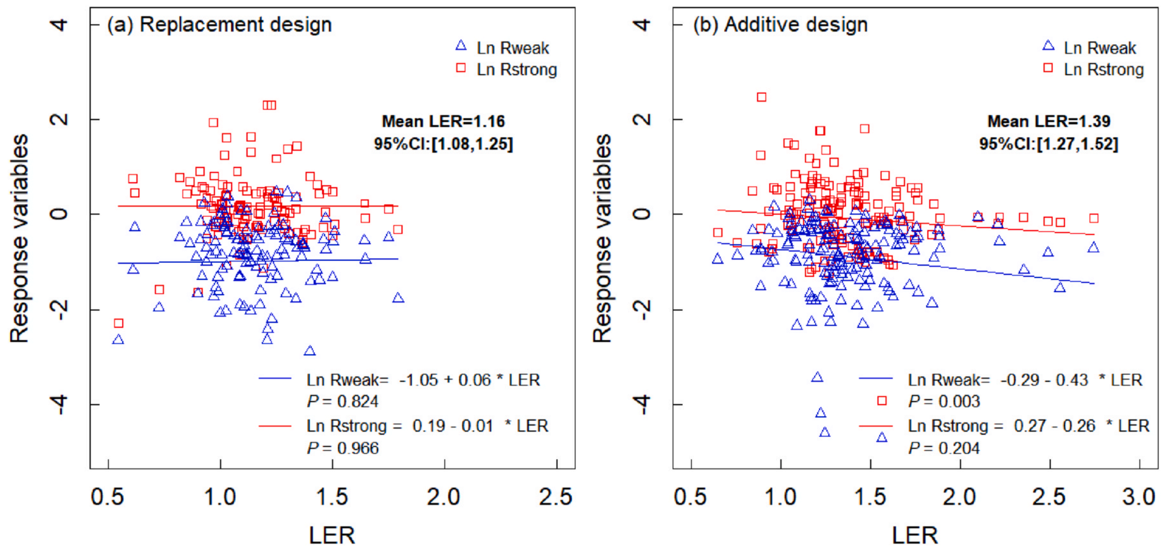

Fig. 8. Effect of land equivalent ratio (LER) on the ln(R_{weak}) (weed biomass in intercrops compared to that of the weaker component crops) and ln(R_{strong}) (weed biomass in intercrops compared to that of the stronger component crops) under different intercrop designs: (a) intercrops with replacement design (n = 121) and (b) intercrops with additive design (n = 158).

(Fig. 5). We found that in maize/legume systems, maize was usually the less weed-suppressive component, while in small-grain cereal/legume intercrops, legumes were often (116/173) the weak weed-suppressive component (Fig. 4b). Both maize and legumes are frequently reported to be weak weed suppressors (Bilalis et al., 2010; Mcdonald, 2003; Rubiales and Fernandez-Aparicio, 2012). Maize, a species with a slow early development, is sown at a wide plant spacing and is therefore not a strong competitor towards weeds, despite being tall and having a dense canopy during the later season. Broadleaved legumes with horizontal leaf orientation cover the soil faster than maize and are therefore more weed suppressive. Since at least half of all annual weeds require light for seed germination (Juroszek and Gerhards, 2004), early soil cover is an important weed suppressing mechanism. In maize/legume intercrops, the early emergence of legumes hinders the growth of weeds through shading, and therefore determines the outcome of competition with weeds to a large degree. In small-grain cereal/legume intercrops, small grains are normally the stronger competitor against weeds, due to their relatively fast initial growth (e.g. earlier germination and tiller ability) and extensive root system (e.g. Hauggaard-Nielsen et al., 2006; Bedoussac and Justes, 2009; Andrew et al., 2015). The relative growth rate at which the component species is able to occupy the space and pre-empt resource is also important for the weed suppression.

Among the design and management factors, we detected that intercrop design had a major effect on the outcome of crop-weed competition. An additive design in intercrops substantially improved weed suppression. The negative relationship between RDT and R_{strong} indicates that this outcome was, at least in part, due to an increased seeding rate in intercrops with additive designs (Fig. 7). The higher plant density increases the relative competitiveness of intercropped species (e.g. Banik et al., 2006; Ekpo and Ndaeyo, 2011; Marin and Weiner, 2014), through enlarging the occupied available space by the components at the beginning of the growing season (Spitters and van den Bergh, 1982). When increasing the plant density, the distance between individual plants narrows and this might well explain why spatial arrangement was found to be hardly important with intercrops in additive design (Fig. 6). In intercrops with a replacement design, spatial arrangement was important for weed suppression. A fully mixed configuration had stronger weed suppression than an alternate row design (Fig. 6). The more even spatial pattern of species created by a mixed arrangement resulted in a more complete competition from intercropped species towards weeds, and a lower weed biomass was thus observed. In pure stands, a more spatially uniform distribution of crop plants is also known to be better at reducing weeds (Weiner et al., 2001; Olsen et al., 2017). In both situations the intraspecific competition is reduced, resulting in a situation in which individuals (pure stand), or individuals of the more competitive component species (intercrops) are able to occupy the space and to preempt resources more successfully.

A longer overlap in growth period between component species was expected to enhance the competitive effect of intercrops on weeds. However, we found no evidence to support this hypothesis (Fig. A2). Another meta-analysis that focused on intercropping of a cash crop and a leguminous service crop also found that the level of temporal segregation was not an important factor in weed suppression (Verret et al., 2017). Here the establishment method of the service crop (i.e. living mulch, synchronized sowing and relay sowing) represented different levels of overlap. But also in this case the period of overlap did not affect weed control. Increased nitrogen input did not affect the competitive effect of intercrops as compared to pure stands on weeds (Fig. A3). And we did not find evidence that the competitive effect of cereal/legume mixtures on weeds, as compared to sole cereals or legumes was affected by N input (Fig. A4). These results suggest that the nitrogen capture and consumption may not be the first critical competitive process affecting weed productivity.

Identifying which factors influence the weed suppressive ability of intercrops was one objective for this meta-analysis. This analysis was however hindered by confounding between individual design and management factors. We found that maize/legume intercrops were mainly laid out in additive designs with a row or strip arrangement, of which most of the intercrops with a strip design were composed of a row of one species combined with a strip of the other species. Small-grain cereal/legume intercrops were equally found in replacement and additive design, but a strip arrangement of small-grain cereals and legumes was only found in additive design. These strip arrangements were always a combination of two strips. Among the other intercrops, the combination of replacement design and mixed arrangement was the most common (Fig. 2, Table A3).

Intercrops with a TND > 0 were exclusively found among intercrops in additive design with a row or strip arrangement. Intercrops in replacement design were exclusively found in a mixed spatial arrangement (Table A3). Such confounding among explanatory factors was also found in other meta-analysis studies on intercropping systems (Yu et al., 2015; Li et al., 2020). The implication of the association between explanatory factors is that it is not possible to identify in a meta-analysis unique factors driving weed suppressiveness. The main driving force for weed suppression might be a combination of factors that co-occur rather than a single factor. At the same time, it might also not be necessary to uncouple all factors, as there might be agronomic reasons for preferentially combining certain design and management factors (Li et al., 2020). For instance, in maize intercrops the sowing density and spatial positioning of maize plants is usually maintained and a second crop is simply added. This automatically results in an additive design in row or strip arrangement.

4.3. No indication that resource complementarity in intercrops contributes to weed suppression

It has often been suggested that the niche differentiation between component crops, resulting in a more complete resource capture, is an important mechanism for improved weed suppression in intercrops. However, our analysis provided equivocal support for this hypothesis. On the one hand, we found that additive intercrops generally had higher LER and suppressed weeds better than replacement intercrops. This supports the notion that density increase in intercropping increases resource capture and yield, and suppresses weeds through stronger resource competition. Within additive intercrops, we found that a greater LER was associated with a smaller value of the R_{weak} (Fig. 8b), indicating that additive intercrops with a comparatively higher resource capture and yield (i.e. high LER) have lower weed biomass when compared to the pure stand of the weaker competitive species. However, we did not find significant relationships between LER in the intercrop and R_{strong} in additive intercrops or R_{strong} and R_{weak} in replacement intercrops (Fig. 8). Thus, the overall evidence supporting relationships between weed suppression and LER as an index for complementarity was less strong than the evidence supporting relationships between weed suppression and species density. For the analysis of the possible effect of species complementarity, the relationship between LER and weed suppression in replacement design is more meaningful, since the confounding effect of plant density is absent from replacement designs. In intercrops with a replacement design, the LER was also significantly larger than one, suggesting a more complete resource capture than in the sole crops. However, no significant association between LER and weed suppressive ability was detected (Fig. 8a). This suggests that species complementarity, despite the conceptual logic of the idea, is not a key driver for the weed suppression in intercrops.

Increased plant density has already been reported to result in stronger weed suppression in pure stands (e.g. Weiner et al., 2001; Zhao et al., 2007; Olsen et al., 2017). Hence, the positive influence of relative density total on weed suppression metrics in intercropping found in our study (Fig. 7) is consistent with previous work, confirming that increased plant density is an important cause for good weed suppression. Overall, we therefore infer that species competitiveness rather than species complementarity is the leading principle in achieving weed competitive intercrops, though it cannot be entirely ruled out that niche differentiation between crop species helped to allow for the higher density additive mixtures to be sown. Thereby, plant density is a key driver for both crop competitiveness to weeds and yielding ability in the intercropping. On the other hand, the close agreement between the weed suppressive ability of the intercrop and that of the stronger weed suppressive component crop points at another mechanism. It might well be that the stronger weed suppressive species becomes better at suppressing weeds in intercrops as compared to its pure stand. In other words, the more strongly weed suppressive crop may be partly released from intraspecific competition by planting it together with a less competitive species, allowing individuals of the competitive species to proliferate and become more competitive against weeds. To test this hypothesis, a methodology is needed that is able to disentangle the effect of species, density and mixing ratio.

4.4. Implication for practice

The main practical implication is that, for crops with poorly weed suppressive ability, the combination with a more competitive crop in an intercrop is an ecological method to alleviate the weed pressure. Although intercrops and the stronger competitive crops show similar weed suppressive ability, the better tolerance to weed competition increases the advantage of intercrops over sole crops in the case of excessive weed infestation (Corre-Hellou et al., 2011). This beneficial effect of intercropping would come in addition to potential improvements in agroecosystem services such as achieving better returns on fertilizer, pesticide, energy and manpower resources (Willey and Osiru, 1972; Lithourgidis et al., 2011).

The better weed suppressive ability of intercrops seems to originate from the stronger weed suppressive component. The weaker competitive crops may, however, suffer from the presence of this more suppressive species. Thus, while using a competitive species to suppress weeds in a mixture, it must be prevented that this competitive species overgrows the other, less competitive crop species. In several studies that focused on intercropping to protect the poorly suppressive crop from weeds, this optimization aspect was the main research objective (e.g. Baumann et al., 2002). In order to obtain a satisfying harvestable yield and weed reduction in intercrops, the challenge is to find a proper competitive balance between the two component crops. Competition might be managed through planting density and relative time of introduction of the two crops (Yu et al., 2016).

5. Conclusion

This study showed that intercropping improves weed suppression compared to arable crop species with poor weed suppressive ability, but showed similar level of weed control as the strongly weed suppressive crops. Intercrops with additive designs were better at suppressing weeds than intercrops with replacement designs. The weed suppressive ability of replacement intercrops was better in a mixed configuration than in a row configuration. No indications were found that resource complementarity between component crops contributed substantially to improved weed suppression in the intercrop.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107658.

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