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The productive performance of intercropping

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Crop diversification has been put forward as a way to reduce the environmental impact of agriculture without penalizing its productivity. In this context, intercropping, the planned combination of two or more crop species in one field, is a promising practice. On an average, intercropping saves land compared with the component sole crops, but it remains unclear whether intercropping produces a higher yield than the most productive single crop per unit area, i.e., whether intercropping achieves transgressive overyielding. Here, we quantified the performance of intercropping for the production of grain, calories, and protein in a global meta-analysis of several production indices. The results show that intercrops outperform sole crops when the objective is to achieve a diversity of crop products on a given land area. However, when intercropping is evaluated for its ability to produce raw products without concern for diversity, intercrops on average generate a small loss in grain or calorie yield compared with the most productive sole crop (−4%) but achieve similar or higher protein yield, especially with maize/legume combinations grown at moderate N supply. Overall, although intercropping does not achieve transgressive overyielding on average, our results show that intercropping performs well in producing a diverse set of crop products and performs almost similar to the most productive component sole crop to produce raw products, while improving crop resilience, enhancing ecosystem services, and improving nutrient use efficiency. Our study, therefore, confirms the great interest of intercropping for the development of a more sustainable agricultural production, supporting diversified diets.

intercropping | productivity | land-use efficiency | transgressive overyielding | food security

Higher agricultural production and lower environmental footprint are required to meet the global demand for food and feed in a sustainable manner (1, 2). Furthermore, the world's food supply is increasingly homogeneous in composition and less species rich (3). Loss of crop species diversity may make global food production less sustainable and less stable (4, 5) and increase the need for crop protection against pests, diseases, and weeds due to lower resilience (6–9). Intercropping, i.e., the mixed cultivation of two (or more) crop species on the same field (10, 11), is a crop diversification strategy which allows lowering inputs while achieving higher crop yields than expected based on the sole crop yields of the constituent species (12, 13). Due to its contribution to efficient use of resources and diversification of crop species, intercropping provides a compelling opportunity for the sustainable intensification of agriculture. Nevertheless, worldwide adoption of intercropping is lagging, particularly in the global North, while its adoption in the global South could be challenged by the movement of labor to the cities. An in-depth analysis of the productive performance of intercropping is required to assess its potential in modern agriculture and inform policymakers.

Overyielding of intercrops, when compared with sole crop yields, is usually ascribed to resource complementarities between species (14, 15) and may also be due to increased resilience to pests, diseases, and weeds (6–8). Overyielding may be defined in different ways, and there are several metrics to quantify the benefits of growing intercrops instead of sole crops (Table 1). These metrics should be interpreted carefully in line with their definitions (16). The land equivalent ratio (LER) is the most commonly used index to assess the land use of intercrops compared with sole crops (17). It is by definition the same as the relative yield total (18). The LER represents the land area required by sole crops to produce the yields of component species obtained in a unit area of intercrop. An LER larger than one means that intercropping is more efficient in land use than sole cropping. Based on the values of LER estimated from large databases, previous meta-analyses have shown that intercropping saves on average 18 to 23% of the required land compared with production of the same species in sole crops (13, 19–21). That means intercropping allows to obtain the same crop outputs on a smaller land area.

Another measure of intercropping performance is provided by the net effect (22). The net effect is defined as the difference between the actual intercrop yield (defined in a common unit for the constituent species, e.g., grain or protein yield) and the expected intercrop yield based on sole crop yields and species proportions in the mixture (22, 23) (Box 1, Figure).

Significance

Agricultural diversification is useful for agronomic, environmental, and dietary reasons. Here, we confirm, based on a meta-analysis of 226 field experiments, that the simultaneous cultivation of two species in the same plot (intercropping) leads to substantial land savings over single crops when the objective is to produce a diversified set of crop products. While intercropping leads on average to a small yield penalty for grains and calories compared with the most productive single crop species comprised in the mixture, it can provide similar or even higher protein yields, especially with modest N fertilizer application. In addition, it provides further ecological services. Intercropping thus has the potential to diversify crop production and make cropping systems more sustainable.

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Table 1. Comparison of metrics assessing intercropping productive performance

Metrics	LER	TOI	NER
Definition	Sum of the relative yields of intercropped species compared with the respective sole crops.	The ratio of total intercrop yield and the highest sole crop yield among the component species.	The ratio of the sum of observed yields to the sum of expected yields calculated according to the proportions of each crop in the mixture.
Formula*	LER = $Y_1/M_1 + Y_2/M_2$	TOI = $(Y_1 + Y_2)/\max(M_1, M_2)$	NER = $(Y_1 + Y_2)/(P_1M_1 + P_2M_2)$
Interpretation	The relative land area needed for sole crops to obtain the same crop outputs as obtained in a unit area of intercropping.	The relative yield obtained when shifting from the most productive sole crop to the intercrop. Also, the area of land needed for the most productive sole crop to get the same yield as the total yield obtained in intercropping.	The relative yield when intercropping two crop species compared with the weighted average of the sole crop yields where the species proportions in the mixture serve as weights.
Mean effect size for grain yield†	1.23 [1.20, 1.27]	0.96 [0.93, 0.98]	1.28 [1.25, 1.32]
Mean effect size for protein yield	1.23 [1.20, 1.27]	1.02 [0.99, 1.06]	1.23 [1.20, 1.26]

*Y_1, Y_2, M_1, and M_2 are the intercrop (Y) and monocrop (M) yields of species 1 and 2, respectively. See Materials and Methods, Eqs. 1, 2, and 4, and associated explanation and definitions.
†Mean effect size and 95% CI (in brackets) for grain yield and protein yield were estimated from the dataset considered in this study. A mean effect size higher than one indicates that intercrops perform better than sole crops. For an example calculation of metric values, see Box 1.

Contrary to the LER, which is a sum of dimensionless ratios, the net effect of intercropping is expressed in terms of a yield difference per unit area (16). Using global data on crop yields in intercropping, Li et al. (13) showed that intercropping produces 1.5 t grain yield per hectare more than expected on the basis of the sole crop yields, confirming that on average intercrops outperform the mean of the component sole crops. Here, following Cardinale et al. (19), we will express the net effect as a yield ratio (total yield observed)/(total yield expected) to make it more easily comparable to the LER (Table 1 and Box 1). This net effect ratio (NER) reflects the relative yield when intercropping two crop species, compared with the weighted average of the sole crop yields where the species proportions in the mixture serve as weights.

Producing a diversity of agricultural products is necessary to meet demands from the society and the market, but for an individual farm, it may be more interesting to produce as high a total amount of raw material as possible. In practice, farmers may be inclined to grow only the most productive species in their fields without consideration for crop species diversity, aiming to maximize total yield of grain, calories, or protein per unit of land, regardless of diversity. This aim is particularly relevant if the product is used as bulk, for instance to feed animals or to serve as raw material for the food industry or as feedstock for biofuels. When the production objective is to maximize the total biomass or yield of grain, calories or proteins, growing the most productive single crop species per unit of land would be more efficient than also including a crop species with a lower productivity in the cropping system, unless there is such strong complementarity in mixtures that total intercrop yield would exceed the yield of the highest yielding sole crop. In this context of maximum bulk production, a relevant benchmark for assessing the production efficiency of intercrops would be the yield of the single most productive species. An intercrop shows transgressive overyielding if its total yield is greater than that of the highest yielding species comprised in the mixture (24). Transgressive overyielding is relevant when the objective is to maximize the production of calories, protein, forage, biomass, or bioenergy per unit area (25–28). As a metric for transgressive overyielding, we propose the ratio of total intercrop yield over the highest sole crop yield of the component species (i.e., TOI, Table 1 and Box 1) (29). The TOI is never larger than the LER or NER, i.e., it is at most equal to the smallest of LER and NER (see *Materials and Methods*) (29).

Previous studies showed that in natural ecosystems, although species mixtures produced more biomass than expected as measured by the net biodiversity effect, transgressive overyielding was often not achieved, i.e., TOI < 1 (30, 31). In only 35% of the observed plots, species mixtures produced greater biomass than that of the single most productive species (30, 32). While the LER and net biodiversity effect of intercropping have been analyzed in several global meta-analyses (9, 14–17), no such analysis has been conducted for transgressive overyielding in mixtures of crop species.

Maize/legume mixtures are characterized by high LER and they allow reducing nitrogen (N) fertilizer input without loss of productivity (13). High N use efficiency is of paramount importance for lowering N fertilizer input and lowering N losses to the environment, to make crop systems more sustainable (33). We, therefore, also analyzed a TOI for N fertilizer use (TOI^{N}). This index measures to what extent intercropping produces greater output per unit of N fertilizer than the most productive sole crop does (Eq. 6, see *Materials and Methods*). It is unknown what species combinations and which management are able to improve N fertilizer efficiency compared with the most productive sole crop species.

An important quality trait of grain crops is the protein content of the grain. Legumes have high protein contents and are the world's primary source of plant dietary protein, offering a diversity of amino acids, complementing the profiles of cereals (34). Previous studies have shown enhanced cereal grain protein content in cereal/legume mixtures compared with sole grain cereal crops, especially at low N fertilizer input (35, 36). However, legumes have in general lower grain yields than cereal crops (37), potentially affecting the benefit of cereal/legume intercrops for protein yield as it depends both on total production and the N content of the grain. Cereal/legume mixtures show positive net effects when compared with the expected yield per unit area (13, 23); however, it is not known whether such mixtures achieve transgressive overyielding, i.e., higher grain yield, calorie yield, or protein yield, when compared with the sole cereal or legume with the highest grain, calorie or protein yield. Furthermore, we do not know whether cereal/legume intercrops show contrasting performance when considering grain yields or protein yields. It is thus important to assess overyielding in intercropping not only using metrics for grain yield but using, in addition, metrics for calorie or protein yield.

Box 1 Calculation of productivity metrics in intercropping

Assume an intercrop with 50% maize (P_1 = 0.5) and 50% soybean (P_2 = 0.5). Sole maize grain yield is M_1 = 10 t ha^{-1}, while sole soybean grain yield is M_2 = 4 t ha^{-1}. Fertilizer input in maize is $Nfert_1$ = 250 kg ha^{-1} and in soybean $Nfert_2$ = 50 kg ha^{-1}. $Nfert_{IC}$ = 150 kg ha^{-1} in the intercrop (i.e., the average of the sole crop inputs). Grain yields in the intercrop are Y_1 = 8 t ha^{-1} for maize and Y_2 = 2 t ha^{-1} for soybean. Expected yields (EY) are calculated by multiplying sole crop yields by their corresponding land shares, i.e., $EY_1 = P_1M_1$ = 5 t ha^{-1} for maize and $EY_2 = P_2M_2$ = 2 t ha^{-1} for soybean.

LER

$$\mathrm{LER} = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} = \frac{8}{10} + \frac{2}{4} = 0.8 + 0.5 = 1.3$$

Transgressive overyielding index (TOI)

$$\mathrm{TOI} = \frac{(Y_1 + Y_2)}{\max\,(M_1,\ M_2)} = \frac{8+2}{10} = 1$$

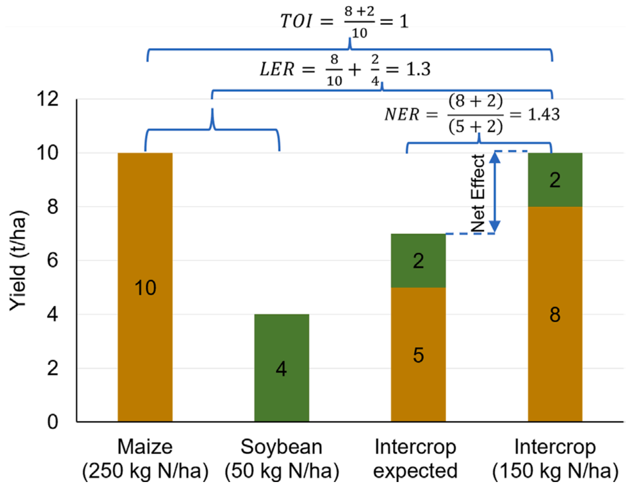
NER

$$\mathrm{NER} = \frac{Y_1 + Y_2}{EY_1 + EY_2} = \frac{Y_1 + Y_2}{P_1M_1 + P_2M_2} = \frac{8+2}{0.5\times 10 + 0.5\times 4} = \frac{10}{7} = 1.43$$

TOI for N fertilizer use efficiency (TOI^{N})

$$\mathrm{TOI}^{N} = \frac{(Y_1 + Y_2)/Nfert_{IC}}{M_1/Nfert_1} = \frac{(8+2)/150}{10/250} = \frac{5}{3} = 1.67$$

In this example, intercropping produces 8 t ha^{-1} of maize and 2 t ha^{-1} of soybean with 23% less land than sole crops, produces 43% more yield than expected, is as productive as the most productive sole crop (maize), and is 67% more N use efficient than the most productive species, maize.



Graphical illustration of the calculation of different metrics. The yields in sole crops and intercrop are shown as orange bars (maize) and green bars (soybean).

In this paper, we used a large global dataset comprising results of 226 experiments to assess the different types of productive performance of intercropping, considering land area and N fertilizer input as production resources. After having analyzed grain yield data, we further made use of data on calorie and protein concentrations in grain (38) to assess the performance of intercropping for producing food and feed calories and protein. We explored which kind of species combinations and management achieved transgressive overyielding in the production of grain, calorie, and protein yield.

Results

Intercrops showed 19% higher average land-use efficiency than sole crops for the production of grain with a mean LER_{grain} of 1.23 (95% CI: [1.20, 1.27], n = 934, land-saving proportion = (1.23-1)/1.23 = 0.19 (39)) and a 28% higher grain yield than expected from single crops, with a mean NER_{grain} of 1.28 (95% CI: [1.25, 1.32], n = 934), but intercropping produced on average 4% less grain yield per unit area than the most productive sole crop species comprised in the mixture (mean TOI_{grain} = 0.96, 95% CI: [0.93, 0.98], n = 934) (Fig. 1). The LER_{grain} and NER_{grain} were larger than one for 84% and 87% of data records, respectively, but TOI_{grain} was larger than one for only 36% of the data records. The results were similar for calorie production. For protein production, however, the average intercrop productivity was not significantly different from that of the most protein-productive sole crop (mean $\mathrm{TOI}_{protein}$= 1.02, 95% CI: [0.99, 1.06], n = 934) (Fig. 1), and $\mathrm{TOI}_{protein}$ was greater than one for nearly half of the data records (47%).

We found a higher N use efficiency in intercrops compared with the most productive component sole crop for production of grain or calories (TOI^{N}_{grain} = 1.11, 95% CI: [1.02, 1.20], n = 638, $\mathrm{TOI}^{N}_{calorie}$ = 1.11, 95% CI: [1.01, 1.21], n = 638, Fig. 2). However, N use efficiency for protein production was not significantly higher for the intercrop than for the most protein-productive sole crop (mean $\mathrm{TOI}^{N}_{protein}$= 1.06, 95% CI: [0.97, 1.15], n = 638, Fig. 2).

TOI values are by definition at most equal to the smallest of the LER and the NER (Fig. 3 and *SI Appendix*, Fig. S1; see also *Materials and Methods*), because the NER and LER compare the intercrop yield with, respectively, the weighted total or species-specific sole crop yield, while the TOI compares the intercrop yield with the higher of these sole crop yields. However, there were strong correlations between each two of the three metrics (Fig. 3). TOI for grain yield increased with LER and NER for grain yield, suggesting there is no trade-off between producing more bulk commodities and increasing a diversity of crop products. Therefore, the search for transgressive overyielding in intercropping would likely favor similar crop species and management choices as the search for high land-use efficiency or high relative yield gain.

The three most frequent species combinations in the data set (i.e., maize/legume, maize/nonlegume, and nonmaize/legume intercrops, *SI Appendix*, Table S1) showed differences in performance. The proportion of LER_{grain} values larger than one was higher in maize/legume intercrops (estimated proportion 0.88, 95% CI: [0.85, 0.91], n = 436) and maize/nonlegume intercrops (0.92, 95% CI: [0.79, 0.91], n = 132) than in nonmaize/legume intercrops (0.77, 95% CI: [0.73, 0.81], n = 352). On the contrary, the

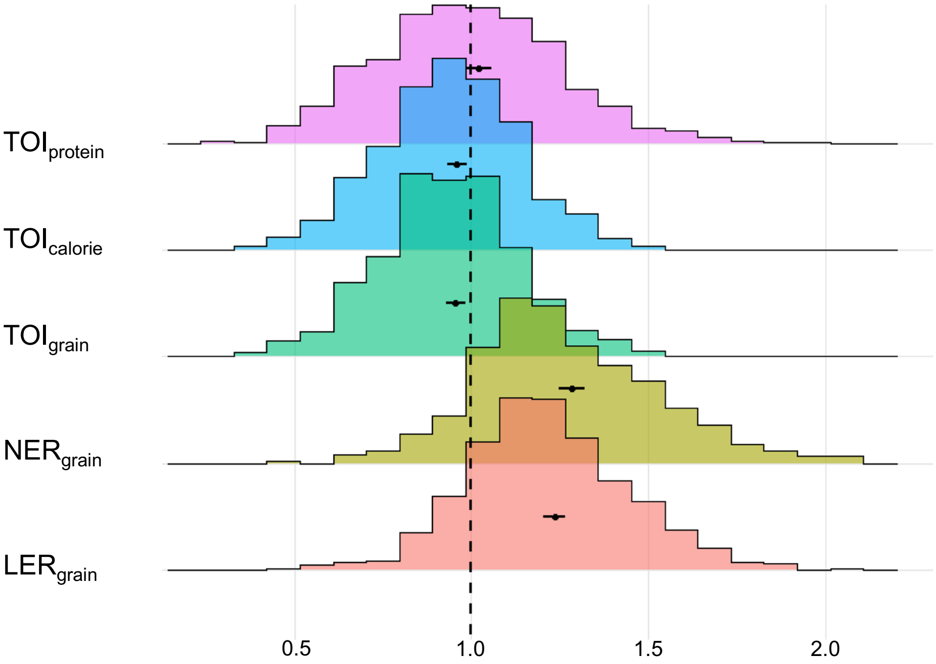


Fig. 1. Values of metrics for assessing the productive performance of intercropping. LER, NER, and TOI based on grain yield ($\mathrm{LER}_{\mathrm{grain}}$, $\mathrm{NER}_{\mathrm{grain}}$, $\mathrm{TOI}_{\mathrm{grain}}$), and TOI based on calorie yield ($\mathrm{TOI}_{\mathrm{calorie}}$) and protein yield ($\mathrm{TOI}_{\mathrm{protein}}$). Histograms show the distribution of the data for each metric. The small black points and error bars represent the mean metric values and their 95% CIs. The vertical dashed line at 1.0 represents the reference value for the index if intercropping is equivalent in production efficiency to sole crops.

proportion of $\mathrm{TOI}_{\mathrm{grain}}$ larger than one was lower in maize/legume intercrops (estimated proportion 0.29, 95% CI: [0.24, 0.33], n = 436) than in maize/nonlegume (0.41, 95% CI: [0.33, 0.49], n = 132) and nonmaize/legume intercrops (0.43, 95% CI: [0.38, 0.48], n = 352). While $\mathrm{TOI}_{\mathrm{grain}}$ was lower than one in most cases for maize/legume intercrops, TOI for protein yield was larger than one in 55% of the maize/legume data with a mean $\mathrm{TOI}_{\mathrm{protein}}$ of 1.10 (95% CI: [1.05, 1.15], n = 436, *SI Appendix*, Fig. S2). Thus, maize/legume intercropping produced on average 10% more protein per ha than the most protein-productive sole crop. Furthermore, the mean $\mathrm{TOI}^{\mathrm{N}}_{\mathrm{protein}}$ was 1.18 (95% CI: [1.07, 1.30], n = 436) in maize/legume intercrops, indicating that maize/legume intercrops are much more N-use efficient than the most protein-productive sole crop (often maize, 253 out of 436 data records of maize/legume intercrops). $\mathrm{TOI}_{\mathrm{protein}}$ exceeded one in 65% of maize/nonlegume intercrops and 30% of nonmaize/legume intercrops, but the mean TOI value was not significantly higher than one for these two types of intercrops, whether expressed per unit land or per unit N fertilizer (*SI Appendix*, Fig. S2). Only few data were available for legume/legume intercrops. Within this group, the TOIs for grain yield and calorie yield were largest for pigeon pea/soybean intercrops (mean $\mathrm{TOI}_{\mathrm{grain}}$ = 1.32, 95% CI: [1.11, 1.52], n = 11; mean $\mathrm{TOI}_{\mathrm{calorie}}$ = 1.22, 95% CI: [1.02, 1.42], n = 11) (*SI Appendix*, Fig. S3).

Component species in mixtures may differ substantially in yielding ability. The probability of achieving transgressive overyielding increased as the grain yield of the lower yielding species approached that of the higher yielding species, i.e., when the yields of the two species are similar (Fig. 4*A*). This trend was found in all the three main species combinations (Fig. 4 *A* and *B*). In maize/legume and maize/nonlegume intercrops, there was a greater than 50% chance of transgressive overyielding when the grain yield ratio exceeded 0.5 (i.e., when sole crop yield of the low yielding species exceeded 50% of the sole crop yield of the high yielding species). In nonmaize/legume intercrops, there was a greater than 50% chance of getting transgressive overyielding when the yield ratio exceeded 0.7. The results suggest that similar yield levels in sole crops result in a large TOI (*SI Appendix*, Figs. S4 and S5) in combination with a small selection effect [i.e., no strong dominance by species with particular traits (22)] (*SI Appendix*, Fig. S6). Likewise, the probability of obtaining transgressive overyielding for protein production increased with the similarity of the protein yields of the component species (Fig. 4*B*). The results thus indicate that transgressive overyielding for protein production in cereal/legume mixtures can be obtained by selecting component species with similar protein yields.

Maize/legume intercrops provided significant transgressive overyielding in terms of protein yield in the absence of N fertilization (intercept of 1.15, 95% CI: [1.07, 1.23], n = 363) (Fig. 4*D*), while intercrops with maize but without legumes had higher values of TOI when N fertilizer input was high (Fig. 4 *C* and *D*). Both calorie TOI and protein TOI of nonmaize/legume intercrops were independent of N fertilizer input (P = 0.77, Fig. 4*D*, and P = 0.17, *SI Appendix*, Fig. S5*D*, respectively).

Discussion

In this study, we analyzed transgressive overyielding in intercropping and compared it with performance metrics related to land saving (LER) and relative yield gain (NER). We found that intercropping resulted in substantial (19%) land savings compared with sole crops to produce a diverse set of crop outputs. Furthermore, based on an average grand mean NER of 1.28, intercrops had on average 28% greater yield than expected from monocultures. In addition, although our results showed that intercropping did not guarantee transgressive overyielding (TOI) for grain production (on average 4% lower yield than the most productive species), we found that intercropping achieved the same average level of protein production as the most protein-productive single crop. Thus, our results indicate that intercropping is an efficient cropping system to produce diverse crop outputs on a limited area of land (as shown by high LER and NER) while it had higher protein production than the most protein-productive sole crop in 47% of the cases. The positive correlation between

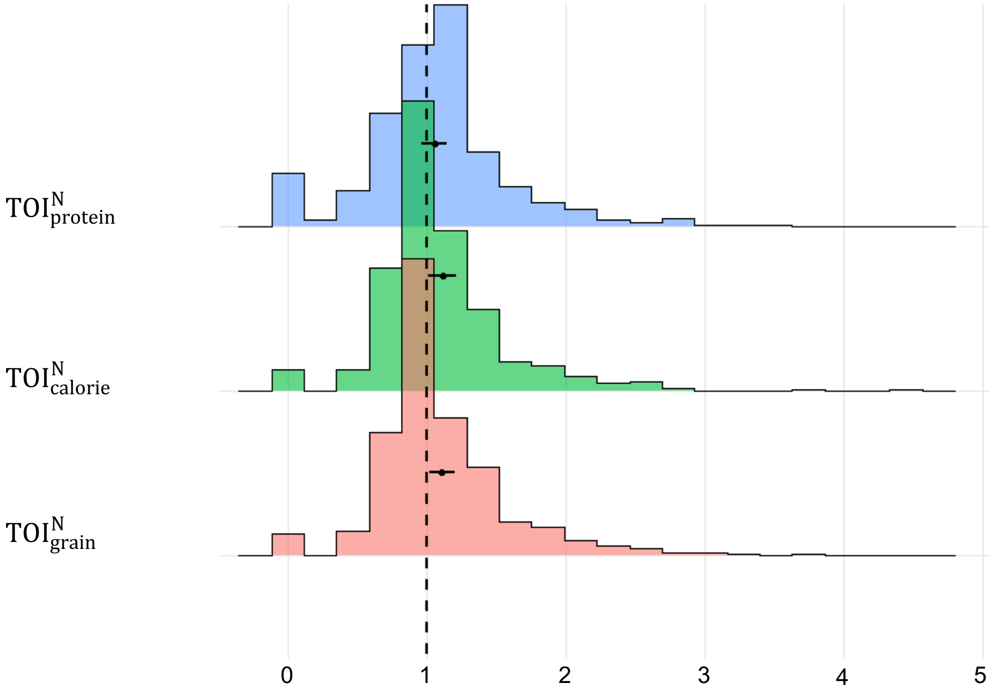


Fig. 2. Values of N fertilizer TOI (i.e., TOI^N). N fertilizer TOI for grain yield (TOI^N_{grain}), calorie yield ($TOI^N_{calorie}$), and protein yield ($TOI^N_{protein}$). These indices express the extent to which the PFP of N fertilizer on intercrop grain yield, calories, or protein exceeds that of the sole crop species with the highest grain yield, calorie yield, or protein yield, respectively. The small black points and error bars represent the mean metric values and their 95% CIs. The vertical dashed line at 1 represents the reference value for the index if intercropping is equivalent in production efficiency to sole crops.

the different measures of excess yield suggests that there is no trade-off between producing more bulk products and producing a diversity of crop products.

Although transgressive overyielding for grain production was on average not achieved, maize/legume intercrops produced on average 10% higher protein yield than the most protein-productive sole crop and a 18% higher protein yield than the most protein-productive sole crop per unit N fertilizer, indicating strong species complementarities and options for increased efficiency of fertilizer use for the production of food and feed protein by using maize/legume intercropping.

The absence of systematic transgressive overyielding for grain production must be put into perspective, given the limitations of this criterion. Indeed, societies and markets often (but not always) require a diversity of foods and feeds and do not just require the output of the highest yielding crop species, i.e., populations cannot be fed on maize alone. Moreover, diversification of agriculture may be required to allow crop rotations and diverse landscapes not focusing on a single crop to reduce crop vulnerability to pests, pathogens, and weeds (40). Diversified cropping systems can reduce the risk of crop failure associated with drought or erratic rainfall (9) and show greater yield stability than monocultures (41). Therefore, TOI as a concept has an intrinsic limitation due to its lack of recognition of these benefits of diversity that go beyond single season production efficiency. Also, TOI shares with LER and NER the limitation that it ignores differences in market prices between crop species. Another limitation of TOI is its reliance on a posthoc choice of the high yielding sole crop while, in practice, farmers do not always know in advance which crop species will be the most productive, especially in the case of strong year-to-year variation in the performance of sole crops (32). Nevertheless, maize is usually the most productive crop compared with small grains and legumes across a broad range of conditions, making the use of TOI relevant in this case. Given the results of our multicriteria evaluation and all its additional well-known benefits [pest, disease, and weed control (6, 8, 42), improved drought resistance (9), and soil carbon accumulation (43)], intercropping should be considered a promising alternative to sole cropping.

Our study shows transgressive overyielding in intercropping for 36% of data records and land saving and relative yield gain in intercropping for 84 to 87% of data records, where each record comprises metric values that compare the performance of intercrops and sole crops for a certain species combination and management in an experiment. These results are comparable to the results of ecological studies on grassland species mixtures (30, 31), where 35% of the species mixture plots of natural plant communities produced higher biomass than achieved by the most productive component species when grown alone (30, 31). On the contrary, only 2% of cover crop mixtures achieved transgressive overyielding based on 243 comparisons (44).

A lack of transgressive overyielding is not necessarily in conflict with positive species complementarity and facilitation that enhance resource capture. Species differ intrinsically in productivity due to the length of the growth duration, water use efficiency, harvest index, or the resources necessary for grain production (higher for grains with a high oil or protein content) (45). Interestingly, our analysis reveals that transgressive overyielding (i.e., TOI > 1) is more likely to occur when intercropping combines species with similar yields. In this case, a moderate species complementarity effect is able to increase the yields of the species in the mixture to a level high enough to compensate for the intrinsically lower yield of one of the components. On the contrary, when the two species have very different yield levels, complementarity is generally not high enough to give a productive advantage to intercropping compared with the most productive sole crop. Transgressive overyielding requires strong niche differentiation to make up for replacement of individuals of the highest yielding species with individuals of a lower yielding species (46). A high probability to achieve transgressive overyielding is obtained

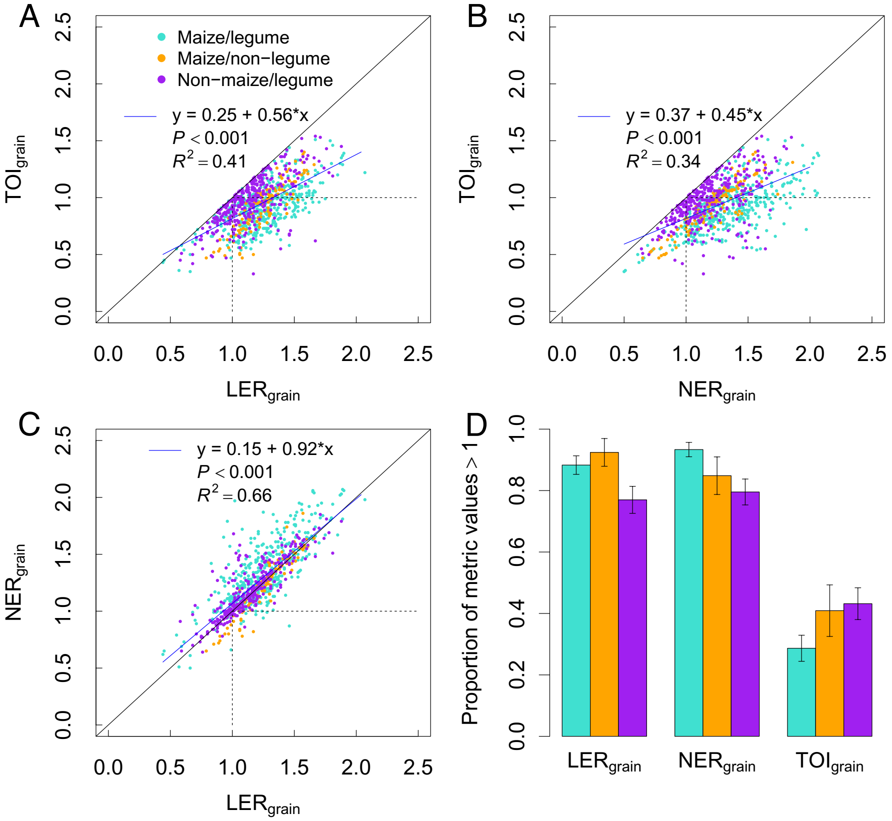


Fig. 3. Bivariate scatter plots illustrating relationships between LER, NER, and TOI (*A*–*C*) and proportions of data records with performance metrics larger than one for three types of species combinations in intercropping (*D*). Metric values are based on grain yield in maize/legume (turquoise), maize/nonlegume (orange), and nonmaize/legume intercrops (purple). A 1:1 line is shown in panels *A*–*C* for reference. The horizontal lines represent TOI = 1 or NER = 1, and the vertical lines represent NER = 1 or LER = 1. Blue lines in panels *A*–*C* are regressions fitted using linear models based on data of the three types of species combinations. Bars in panel *D* represent the proportions of data records with metric values larger than one and their approximate 95% CIs, calculated as $p \pm 1.96 \times \sqrt{\frac{p(1-p)}{n}}$, where *P* is the observed proportion of data records with the metric value greater than one, and *n* is the number of observations.

when species combinations with similar yielding abilities are grown together.

The cultivation of the most productive species as sole crops can be relevant when the production objective is gross energy, and when there is no need for crop rotation or spatial diversity of crop species to control pests and diseases and maintain productivity. Maize production is an example of this production orientation in many parts of the world. However, maize/legume intercrops have the potential to combine high yields (including protein yields) and high production efficiency per unit fertilizer [e.g., Xu et al. (21)], especially when including legumes with high protein yield. Converting existing large areas of corn, wheat, and soybeans, currently grown as single crops, to intercrops could improve land-use and fertilizer-use efficiency, with additional nonproduction benefits, including increased resource use efficiency (21); dietary diversity (47); pest, disease, and weed control (6, 8, 42); and improved organic soil carbon and N content (43). Such a transition to intercropping practices could be made both in systems with a production orientation toward improved sustainability (low input–low output–high efficiency) and a production orientation toward high productivity (moderate inputs–high outputs–high efficiency) (13).

Optimizing plant densities, spatial plant arrangement, and crop varieties could enhance transgressive overyielding in intercrops in the future. We found that TOI increased with relative density total (*SI Appendix*, Fig. S7). This finding is consistent with the results of grassland biodiversity studies showing that increased plant density contributed to positive effects of biodiversity on plant productivity (48). Such a positive effect of plant density on total intercrop productivity could be the logical consequence of complementary resource use between companion species, allowing for higher densities. However, it may indicate that sole crop densities in experiments were suboptimal (49, 50). It is also possible that monocultures cannot be grown at the optimal density for yield because high density would increase the risks of crop failure. This is for instance the case for maize in China, which reaches highest yield at densities of about nine plants per m^2, whereas farmers prefer using lower densities, e.g., six plants per m^2, to reduce the risk of stem lodging (51). In strip intercropping, spatial arrangement may be optimized to allow strong maize stems that are not prone to lodging such that additive designs, as compared with the monostands, become possible (52). In China, maize/soybean strip intercropping was found to perform better with an additive intercropping design (53). Breeding research is ongoing to find resource foraging traits of species to maximize niche complementarity and intercrop performance (54), which could be suitable for additive intercropping. Further research is needed to ascertain whether high TOIs in systems with high relative density total reflect strong complementarity, allowing such density increases or improper low densities in the sole crop treatments.

A meta-analysis of published experimental data is necessarily constrained by the densities and configurations tested in experiments, and reported LERs may be inflated due to suboptimal monostands (49, 55) or a suboptimal LER outcome may be obtained due to suboptimal mixture designs. The available field experiments on intercropping cover only a relatively small number of all the possible spatiotemporal crop arrangements. There are many more possible spatiotemporal arrangements than those tested in the field experiments published in the literature, in part because current mechanization techniques do not allow for the

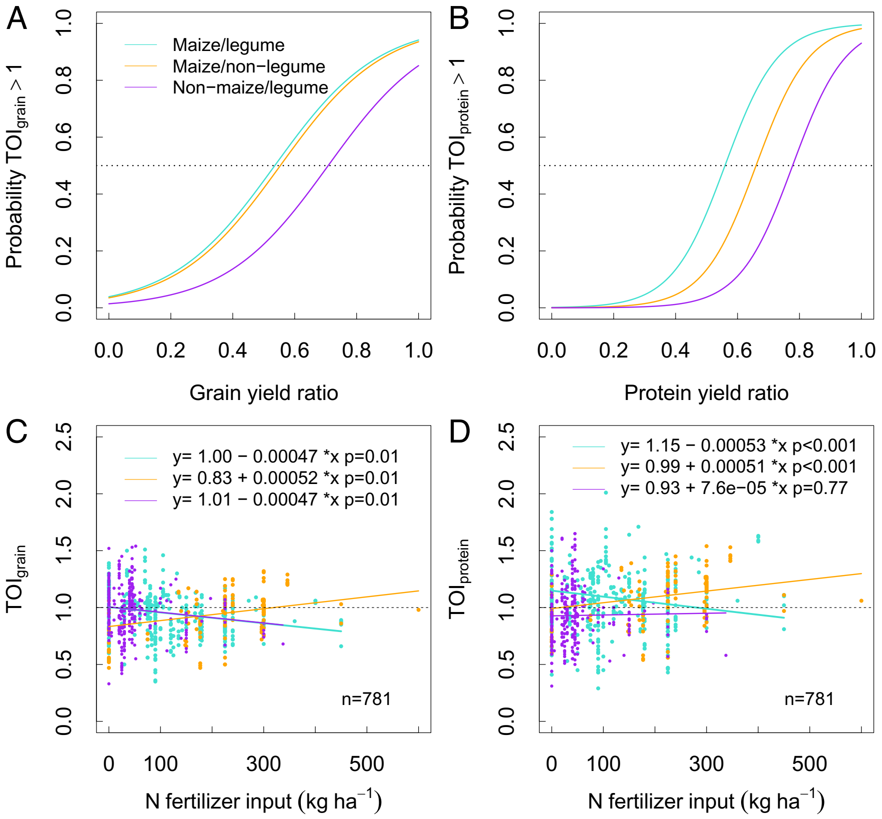


Fig. 4. Probability of a TOI larger than one (TOI > 1) as a function of the ratio of the grain yields (*A*) or protein yields of the sole crops (*B*) and value of TOI in response to N fertilizer input (*C* and *D*). Metric values are based on grain yield in maize/legume (turquoise), maize/nonlegume (orange), and nonmaize/legume intercrops (purple). Yield ratio is defined as the ratio of the sole crop yield of the lowest yielding species to the sole crop yield of the highest yielding species. A yield ratio of one indicates that the two sole crop yields are equal. The dashed lines in panels (*A* and *B*) represent a probability of TOI > 1 equal to 0.5, and the dashed lines in panels (*C* and *D*) represent TOI = 1.

implementation of diversified arrangements and because conducting experiments to compare a large number of spatiotemporal crop arrangements is resource intensive. Spatially explicit mechanistic models (56, 57) could facilitate the exploration of alternative crop arrangements in order to identify optimal crop association modalities. Such models may assist in identifying optimal trait complementarities in mixtures, tailored to the growing conditions and management.

Maize/legume intercrops on average produced 10% higher protein yield than the sole crop with the highest protein yield, and they produced 18% higher protein yield per unit of N fertilizer than the species with the highest protein yield (Fig. 2). Maize/legume intercrops gave 15% higher protein yield than the component sole crop with the highest protein yield under no fertilizer input (Fig. 4). However, transgressive overyielding in protein production of maize/legume intercrops decreased with N fertilizer input and the intercrop advantage with respect to protein production disappeared entirely at N fertilizer inputs above 283 kg ha^{-1} (Fig. 4). This finding is consistent with that of previous studies showing that the yield advantage of cereal/legume intercrops was greatest with no N fertilizer input but was reduced when N fertilizer was applied (25, 58). Thus, maize/legume intercrops offer potential particularly if the objective is the production of grain or protein while environmental impacts from nutrient spillovers need to be mitigated by lowering N fertilizer inputs. The protein production performance of cereal/legume intercrops could be even higher than estimated in the present analysis since we estimated protein yields assuming a constant protein concentration of crops, but a higher cereal grain protein and N concentration has been found when cereals were grown in mixtures with legumes (36, 47).

Greater adoption of intercropping in practical farming needs advances in many domains. Demonstrations of intercropping practices are needed to give farmers a chance to learn and appreciate the opportunities. Ideally, farmers and researchers explore opportunities for intercropping jointly in a cocreation setting (59). The Wageningen University research farm, for example, hosts a large experiment with diversification strategies including strip cropping (with wide strips of 3 m) and, within strips, species mixtures (e.g., wheat/faba bean) or variety mixtures (e.g., in potato) (60). This experiment is visited yearly by hundreds of farmers. While such 3 m strips allow cultivation with standard implements, these do not enable optimal complementarity between mixed crop species (61). Hence, developments in technology are needed to allow cultivation with narrower strips (62). Efforts are ongoing to build implements for cultivation in narrower strips (53), but much greater efforts are needed. Robotization and miniaturization may be enabling technologies for intercropping adoption (53, 63). Likewise, technology for postharvest separation of grains and adaptation of supply chains may greatly favor intercropping adoption (64).

It is also not likely that current varieties are already optimally suited for intercropping (54, 65, 66). Research is needed to elucidate whether and how the performance of intercropping systems may be further optimized by breeding “plant teams” that optimize complementary resource capture (54). The management of intercrops needs to be fine-tuned to local climate and soil conditions, available varieties, and the production orientation, calling for a reorientation of agronomy to embrace diversity. As intercrops consist of multiple species, the challenge of optimizing genotype by environment by management interactions is greatly aggravated for intercropping as compared with that of sole crops (54). Finally, in-depth insight into mechanisms underlying high performance of intercrops is needed to support technology development in breeding and agronomy (67).

Governments can do much to promote intercropping as a diversification strategy for yield increase. The Chinese government has issued a policy in 2022 promoting maize/soybean intercropping to boost national maize and soybean yields and allow a transition toward more efficient use of N in farming (68). The European Union has consistently made resources available for research and cocreation on intercropping through its Horizon 2020 and Horizon Europe research programs to accelerate the development and acceptance of intercropping and fostering both research and cocreation between farmers and researchers. While diversification of agriculture is challenging, both in the global North and the global South, the potential of intercropping to make agriculture more sustainable should provide continued incentive for societies and policymakers to invest in its development and adoption and overcome the lock-in on monostands.

In conclusion, intercropping performs well in producing a diverse set of crop products and performs almost similar to the most productive component sole crop to produce raw products. Furthermore, intercrops provide additional advantages for making agriculture more sustainable by suppressing diseases, pests (67, 69), and weeds (6, 8), and using N more efficiently (21). Intercrops with legumes, especially maize/legume intercrops, showed transgressive overyielding under low N fertilizer input, indicating their potential for developing more sustainable low N input cropping systems, particularly for producing dietary protein. All in all, this analysis therefore supports the great potential of intercropping for diversifying cropping systems to contribute to sustainable intensification of agriculture.

Materials and Methods

Data Collection. We used the database described in the study by Li et al. (13), which includes field experiments on grain-producing intercrops consisting of two crop species from three crop types: cereals, legumes, and oilseed crops. The data set includes 934 observation records, representing data from 226 field experiments described in 132 publications (*SI Appendix*, Method S1). Each record contained data on the intercrop and monocrop yields and all associated management in the intercrop and monocrop treatments. "Experiment" was defined as a unique combination of site and year. Within experiments, different data records represent different combinations of species, densities, pattern, N fertilizer, and other agronomic management factors in intercropping and monocropping, whereby the management in intercrops and sole crops was similar or the same such that monocrop treatments provided a valid reference for the intercrop treatment. During data extraction, particular attention was given to data records with large LER in order to check that the monocultures and intercrops were conducted under the same or similar management. It was assumed that monocultures achieved optimal yields. This could not be formally verified because source publications did not report this information, but many publications mention that monostands are grown in accordance with local recommendations or farmer practice. Monocultures and intercrops were always replicated and averages across replicates were extracted for monoculture and intercrop treatments from the selected studies. Metric values (LER, NER, TOI, and $\mathrm{TOI^N}$) were calculated from these treatment means for each record. The data set includes several descriptors such as the publication title, year and author, species combination, the yield and N fertilizer rate of both sole crops and intercrops, intercrop design (*SI Appendix,* Table S3), intercropping pattern (*SI Appendix,* Table S4), and number of replicates. As most of the studies did not report calorie and protein data, grain calorie content and protein content were calculated for all data records using crop-specific standard values from the United States Department of Agriculture (USDA) Nutrient Database (38).

Conceptualization. Three metrics were used for comparing the production efficiency of intercrops and sole crops, as follows (Table 1).

LER. The LER is defined as the sum of the relative yields of intercropped species compared with their respective sole crops (Eq. 1) (17).

$$\mathrm{LER} = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} = \mathrm{pLER}_1 + \mathrm{pLER}_2, \qquad [1]$$

where Y_1 and Y_2 are the yields (per unit of total area of the intercrop) of species 1 and 2 in an intercrop, M_1 and M_2 are the yields of species 1 and 2 in the sole crops, and pLER_1 and pLER_2 are the partial land equivalent ratios (relative yields) of species 1 and 2, respectively. Partial LERs are calculated as the ratio of the yields of a species in the intercrop and the sole crop. The LER indicates the relative land area required under sole crops to obtain the same yield of the component species as a unit area of the intercrop begets under the same or comparable management (17). An LER greater than one indicates that a larger area is needed to produce the output quantities of species 1 and 2 with sole crops than with an intercrop. The partial LERs represent the relative areas of the component crop species required to produce the yield obtained in a unit area of the intercrop.

TOI. The TOI is defined as the ratio of total intercrop yield over the highest sole crop yield of the component species (Eq. 2) (29).

$$\mathrm{TOI} = \frac{(Y_1 + Y_2)}{\max(M_1,\ M_2)} = \frac{Y_1}{\max(M_1,\ M_2)} + \frac{Y_2}{\max(M_1,\ M_2)}. \qquad [2]$$

To calculate TOI, the yields of the species need to be expressed in the same units, e.g., ton grain $\mathrm{ha^{-1}}$, calories yield $\mathrm{ha^{-1}}$, or protein yield $\mathrm{ha^{-1}}$. Depending on the chosen units, different variants of TOI can be defined, e.g., for grain yield, calorie yield, or protein yield. For instance, $\mathrm{TOI_{grain}}$ is calculated using for Y_1, Y_2, M_1, and M_2 the grain yields, while $\mathrm{TOI_{protein}}$ is calculated using for Y_1, Y_2, M_1 and M_2 the protein yields.

The relationship between the LER and the TOI can be easily expressed mathematically. Without loss of generality, assume that $M_1 \geq M_2$ (i.e., by definition, crop species 1 is taken as the most productive species in sole cropping). Then:

$$\mathrm{TOI} = \frac{Y_1 + Y_2}{M_1} = \frac{Y_1}{M_1} + R \times \frac{Y_2}{M_2}, \qquad [3]$$

where $R = \frac{M_2}{M_1}$ is the sole crop yield of the lower yielding species expressed as a proportion of the sole crop yield of the higher yielding species. Equivalently, $\mathrm{TOI} = \mathrm{pLER}_1 + R \times \mathrm{pLER}_2$. Because $R \leq 1$, $\mathrm{TOI} \leq \mathrm{pLER}_1 + \mathrm{pLER}_2$, and thus $\mathrm{TOI} \leq \mathrm{LER}$. Thus, TOI cannot be larger than LER, and TOI equals LER only if the two sole crops have equal sole crop yields ($R = 1$). The practical consequence is that the sum of the pLERs should exceed a threshold that depends on the yield ratio R in order to achieve transgressive overyielding, as illustrated in Fig. 5. The lower the yield of the less productive species, the greater the sum of the pLERs should be to achieve transgressive overyielding (Fig. 5).

NER. The NER is defined as the ratio of the observed yield to the expected yield expressed as a weighted average of the component crop yields according to the proportions of the crop species in the mixture (Eq. 4) (22, 30).

$$\begin{aligned} \mathrm{NER} &= \frac{Y_1 + Y_2}{EY_1 + EY_2} = \frac{Y_1}{EY_1 + EY_2} + \frac{Y_2}{EY_1 + EY_2} \\ &= \frac{Y_1}{P_1M_1 + P_2M_2} + \frac{Y_2}{P_1M_1 + P_2M_2}. \end{aligned} \qquad [4]$$

Here, EY_1 and EY_2 are the expected intercrop yields of the two species, which are calculated as the product of the respective sole crop yields and the corresponding land shares (23), i.e., $EY_1 = P_1M_1$ and $EY_2 = P_2M_2$, where P_1 and P_2 are the proportions of species 1 and 2 in the intercrop, respectively. These proportions represent (by approximation) the proportion of the intercrop area covered with both species with $P_1 + P_2 = 1$. They are calculated on the basis of the densities of a species in the intercrop and the sole crop [the relative density total was scaled to 1 for additive designs (392 data records)] or on the basis of row or plant arrangement. Detailed procedures are given by Li et al. (23). The NER expresses by which proportion intercrop yields are per unit area different from the expected

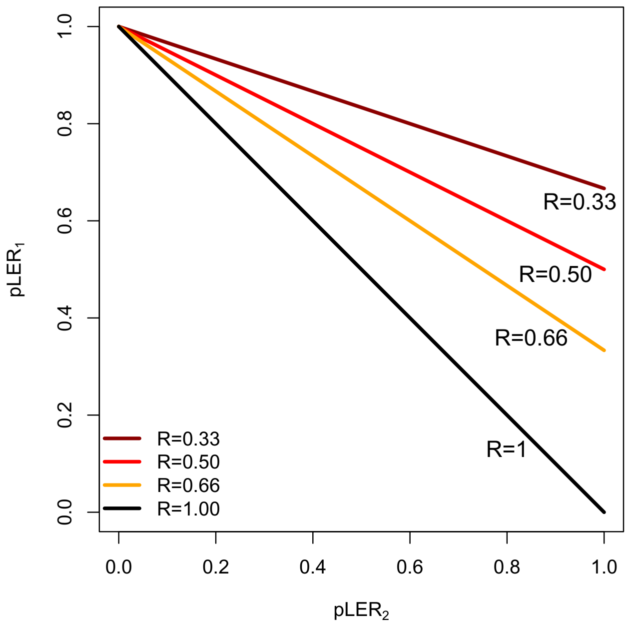


Fig. 5. Lines indicating TOI = 1 (i.e., on the verge of transgressive overyielding) as a function of $pLER_1$ of a high yielding species (y-axis) and $pLER_2$ of a low yielding species (x-axis). If the sum of $pLER_1$ and $pLER_2$ is greater than the limit indicated by the drawn line, the intercrop will show transgressive overyielding. Different lines are characterized by different values of the yield ratio of species 1 and 2 and greater pLERs are required to reach transgressive overyielding if $R = \frac{M_2}{M_1}$ is smaller. When the sole crop yields are equal (R = 1), transgressive overyielding is achieved if LER > 1. However, the condition LER > 1 is not sufficient to achieve transgressive overyielding when one of the two sole crop species has a lower yield than the other, which is generally the case.

(i.e., weighted average) yields of the sole crops when mixed in an area ratio or relative density ratio $P_1 : P_2$ (23). TOI is necessarily smaller than the NER because NER compares the intercrop yields with the weighted sole crops yields, while TOI compares the intercrop yields with the highest sole crop yield.

Whether the NER is larger or smaller than the LER depends on whether the species with the lower or higher sole crop yield has the higher relative yield gain in intercropping compared with sole crops, where relative yield gain is defined as:

$$\Delta RY_i = RY_i - P_i = pLER_i - P_i, \qquad [5]$$

where RY_i is the relative yield of species i, which is equal to $pLER_i$. The difference between the NER and the LER (i.e., NER–LER) equals the ratio of the selection effect (SE) (22) and the weighted average sole crop yield, $P_1M_1 + P_2M_2$ (*SI Appendix*, Method S2). If the species with the higher sole crop yield has the higher relative yield gain in intercropping compared with sole crops, there will be a positive selection effect and the NER will be greater than the LER.

TOI and NER are most easily interpreted as field-level metrics as they compare yields within given unit areas of different cropping systems (Table 1). A value of TOI > 1 indicates that an intercrop produces a greater yield per unit area than growing the highest yielding species as a sole crop. TOI is useful to compare the production efficiency of intercropping with sole crops if the objective is restricted to the production of a single type of product–quantified by a single outcome (i.e., tons of dry matter, calories, protein, euros, yuan, etc.)–and if obtaining a diversity of crop outputs (potentially with diverse uses or different market value) is not necessary and neither is there a need for crop rotation or landscape diversity to maintain productivity. A value of NER > 1 indicates that intercropping produces greater yield per unit area than would be expected if there were no complementarities between the species, such that the relative yields obtained would be equal to the respective land shares, or the absolute yield gain of one species (Y_1-EY_1) would exactly cancel out the absolute yield loss of the other species (Y_2-EY_2) or vice versa. In other words, the NER assesses whether intercropping is a zero-sum game, considering absolute yields. On the contrary, the LER assesses whether intercropping is a zero-sum game, considering relative yields. LER is best interpreted as a measure for land-use efficiency.

TOI for N Fertilizer Use Efficiency. We define the TOI^N as the ratio of the partial factor productivity (PFP) of N fertilizer in an intercrop over the PFP of N fertilizer in the sole crop with the highest yield. PFP is calculated as grain production divided by N fertilizer applied (70).

Assume that $M_1 \geq M_2$ (i.e., species 1 is the most productive species in sole cropping)

$$TOI^N = \frac{(Y_1 + Y_2)/Nfert_{IC}}{M_1/Nfert_1} = \frac{Y_1 + Y_2}{M_1} \times \frac{Nfert_1}{Nfert_{IC}} = TOI \times \frac{Nfert_1}{Nfert_{IC}}, \qquad [6]$$

where $Nfert_{IC}$ is the N fertilizer input per unit area of the intercrop (kg ha^{-1}) and $Nfert_1$ is the N fertilizer input per unit area of the sole crop 1, which is the crop with the highest sole crop yield. In the calculation of TOI^N for grain yield, the yields, Y_1, Y_2, and M_1 are the grain yields per unit area while in the calculation of TOI^N for protein yield, Y_1, Y_2, and M_1 are the protein yields per unit area. TOI^N quantifies by which factor the output of an intercrop per unit of N fertilizer exceeds that of the most productive sole crop. A value of TOI^N greater than one indicates that intercropping is more efficient in N fertilizer use than the most productive sole crop, i.e., the quantity of product (e.g., grain yield, calories, protein) obtained for 1 kg of fertilizer is higher in intercropping than that in the sole crop with the highest grain, protein, or calorie yield. TOI^N is 0 when the species with highest grain, protein, or calorie yield is unfertilized in a sole crop but not in the intercrop. Data records with unfertilized intercropping (157 out of 934) were excluded from the calculation of TOI^N to avoid an undefined fraction.

Statistical Analysis. Linear mixed-effects models were fitted using the function *lme* of the R package *nlme* to estimate the average values of LER, NER, TOI, and TOI^N based on grain yield, calorie yield, and protein yield, and to estimate their relationships with N fertilizer input and with the yield ratio, calorie yield ratio, or protein yield ratio of the sole crops. We used publication and experiment within publications as random effects to account for differences among the studies (publications) and the experiments (sites*years) within studies. Similar to previous meta-analyses on intercropping (19–21), an unweighted meta-analysis was performed in this study because standard errors were not reported and could not be estimated with sufficient confidence for most papers in our data set, due to lack of information. Excluding those papers would be more detrimental to the accuracy of the statistical estimates than the use of unweighted data. Analyses were repeated with the function *lmer* of the more recent *lme4* R package with identical outcomes.

We used funnel plots to assess publication bias in LER_{grain}, NER_{grain}, TOI_{grain}, and $TOI_{protein}$ (71). For each funnel plot, we plotted average LER_{grain}, NER_{grain}, TOI_{grain}, and $TOI_{protein}$ in each of the 132 studies against the total number of experimental units (replicates) in each study as a proxy for study accuracy (19). The funnel plots were symmetrical except the funnel plot of the NER_{grain} (*SI Appendix*, Fig. S8*B*), which was very slightly asymmetrical, with missing values in the bottom left corner representing studies with small study size and low effect size. The very slight asymmetry does not critically affect the conclusions of our study.

Data, Materials, and Software Availability. The datasets and R scripts used in the current study have been archived in Figshare, https://doi.org/10.6084/m9.figshare.20217611.v1 (72).

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