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# Syndromes of production in intercropping impact yield gains

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**Intercropping, the simultaneous production of multiple crops on the same field, provides opportunities for the sustainable intensification of agriculture if it can provide a greater yield per unit land and fertilizer than sole crops. The worldwide absolute yield gain of intercropping as compared with sole crops has not been analysed. We therefore performed a global meta-analysis to quantify the effect of intercropping on the yield gain, exploring the effects of crop species combinations, temporal and spatial arrangements, and fertilizer input. We found that the absolute yield gains, compared with monocultures, were the greatest for mixtures of maize with short-grain cereals or legumes that had substantial temporal niche differentiation from maize, when grown with high nutrient inputs, and using multirow strips of each species. This approach, commonly practised in China, provided yield gains that were (in an absolute sense) about four times as large as those in another, low-input intercropping strategy, commonly practised outside China. The alternative intercropping strategy consisted of growing mixtures of short-stature crop species, often as full mixtures, with the same growing period and with low to moderate nutrient inputs. Both the low- and high-yield intercropping strategies saved 16–29% of the land and 19–36% of the fertilizer compared with monocultures grown under the same management as the intercrop. The two syndromes of production in intercropping uncovered by this meta-analysis show that intercropping offers opportunities for the sustainable intensification of both high- and low-input agriculture.**

With the ongoing increase in the global population and demand for food, improving crop productivity is a pressing challenge<sup>1</sup>. Intensive agriculture provides high yields but comes with serious environmental impacts<sup>2–4</sup>. Intercropping (that is, the mixed cultivation of crop species on the same field<sup>5,6</sup>) is a sustainable way to develop productive agriculture<sup>6–8</sup>: it offers ecological mechanisms for weed suppression<sup>9</sup>, pest and disease control<sup>10,11</sup>, efficient use of light<sup>12</sup> and water<sup>13–15</sup>, conservation of soil resources<sup>16–18</sup>, and yield increase<sup>19–21</sup>. The most obvious advantage of intercropping is land sparing, which is usually quantified by the land equivalent ratio (LER). The LER is defined as the ratio of the area under sole cropping to the area under intercropping needed to give the same yields<sup>22</sup>. An LER greater than one means that intercropping saves land. Previous meta-analyses have shown that the LER of intercropping averages  $1.22 \pm 0.02$  (ref. <sup>23</sup>) or  $1.30 \pm 0.01$  (ref. <sup>8</sup>), depending on the studies selected for meta-analysis. However, the LER is a dimensionless indicator of relative yields in intercropping compared with monocultures. It does not provide information on the absolute yield increase per unit area achieved by intercropping.

The absolute yield gain of species mixtures can be assessed by the net effect (NE) of species mixtures on the yield per unit area<sup>24</sup>. The NE is defined as the difference in yield or biomass between the mixture and the average of the sole crops<sup>24</sup>. The information provided by the NE and the LER is complementary. Both metrics are relevant for assessing the benefit of intercropping. The LER evaluates the comparative land use efficiency of intercropping, while the NE indicates how much more yield is produced per unit area than expected on the basis of sole crop yields and species proportions. The relative yield can be high at low-yield levels, but the NE is not

likely to be substantial at low-yield levels. When issues of global food security are at stake, it is important to not focus solely on the land use efficiency (LER) but to also pay attention to the NE (that is, the absolute yield gain). The absolute yield gain of intercropping at a global scale is unknown.

Intercropping is an ancient cropping system, practised all around the world<sup>25,26</sup> (Supplementary Fig. 1). Various crop combinations have been recognized and utilized in Africa, Asia, Europe and the Americas for centuries and are still prevalent<sup>27</sup>. Crop species may be grown simultaneously or partly so, and in no distinct row arrangement (mixed) or in alternate rows or strips on the same field<sup>25</sup> (Fig. 1). In strip intercropping, the strips are wide enough to permit independent cultivation but narrow enough to allow beneficial interspecific interactions<sup>6</sup> (Fig. 1a,b,e–g).

Maize (*Zea mays*) is a frequently used species in intercropping. This high-yielding C4 species can be sown in strips of several rows, alternating with several rows of a C3 species (for example, a small grain such as wheat (*Triticum aestivum*)<sup>28</sup> or a legume such as soybean (*Glycine max*)<sup>29</sup>). Maize has a late and long growing season and is usually harvested after a C3 species in a system known as relay strip intercropping<sup>25,26,30</sup> (Fig. 1b).

Maize and other cereals can also be sown in alternate rows or mixed in a more or less random pattern with other small grains or legumes (Fig. 1c,d). Alternate-row and mixed intercropping are popular in organic farming with low input in Europe<sup>16,31,32</sup>. Here, mixtures of a legume and a C3 cereal species are the most popular combination (Fig. 1h–j). These intercropping systems have low nitrogen (N) fertilizer input but realize an acceptable protein content in the cereal grain due to N<sub>2</sub> fixation by the legumes.

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**Fig. 1 | Schematic illustrations and examples of alternative intercropping strategies.** **a**, Strip intercropping, with both species grown simultaneously. **b**, Relay strip intercropping, with one species sown and harvested later than the other. **c**, Alternate-row intercropping. **d**, Mixed intercropping. **e**, A mini tractor sowing soybean and applying fertilizer in maize/soybean relay strip intercropping<sup>46</sup>. **f**, Relay strip intercropping of maize and soybean<sup>46</sup>. **g**, A soybean harvester working in a soybean strip in Southwest China<sup>46</sup>. **h**, Alternate-row intercropping of durum wheat and winter pea in France<sup>68</sup>. **i**, Mixed lentil/spring wheat intercropping at harvest<sup>58</sup>. **j**, Mechanical harvest of mixed lentil/spring wheat intercropping in France<sup>58</sup>. Adapted with permission from refs. <sup>46,58,68</sup>.

These systems have the advantages of low input and low emissions<sup>33,34</sup>. However, due to lower inputs, they are also comparatively low yielding. In these systems, the intercropped species are mostly sown in full mixtures that are harvested at the same time<sup>21</sup> (that is, without temporal niche differentiation (TND)).

We previously found that intercrops with maize in China have greater yield gains than intercrops without maize<sup>35</sup>. The LER was increased at greater TND (ref. <sup>23</sup>) and at lower N input<sup>36</sup>. However, the effects of these management factors on the NE of intercropping on yield have not been studied at a global scale. We therefore investigate here the effects of species combinations, temporal and spatial arrangements, and fertilizer input on the yield gain at a global scale.

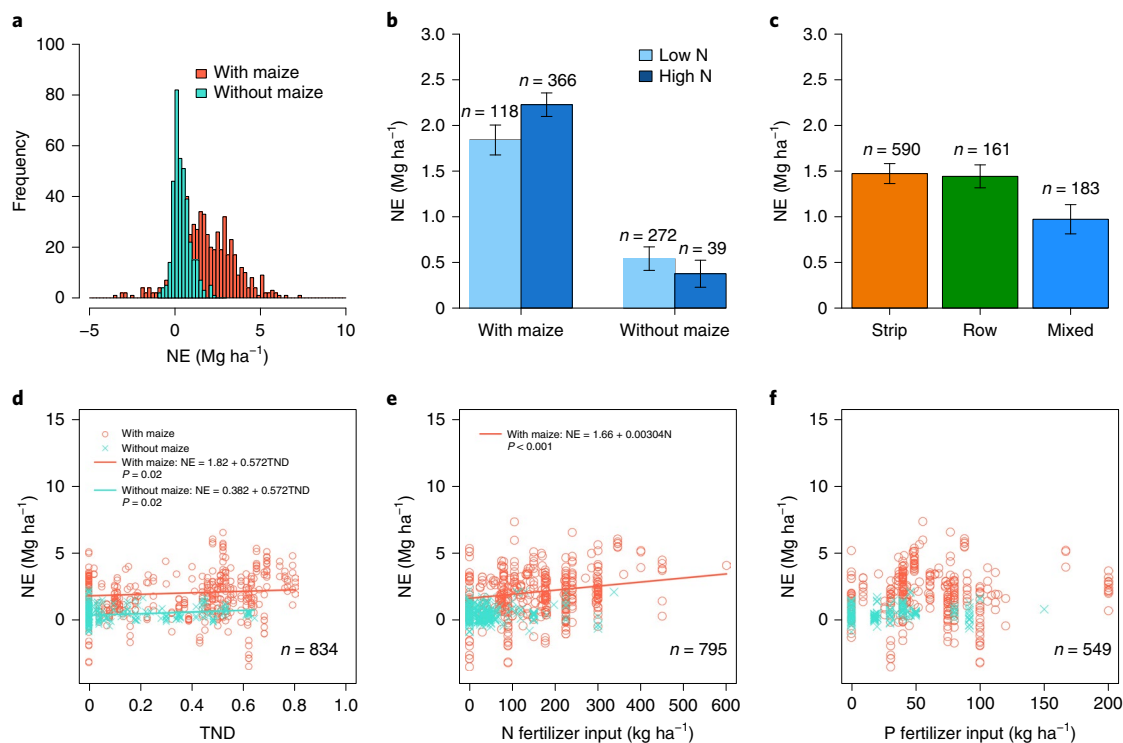
We present here a global meta-analysis to quantify the yield gain for grain-producing intercropping systems with different species combinations (with or without maize), temporal and spatial arrangements, and fertilizer inputs. We also evaluated whether intercropping can save land and fertilizer. The land and fertilizer savings were quantified with relative metrics<sup>8,23,29</sup>, while the yield gains were assessed with an absolute yield metric<sup>24</sup>. We show that the greatest absolute yield gains are achieved when the management factors are coordinated in a high-input, high-output syndrome of production<sup>37,38</sup> in intercropping, with a substantial input of fertilizer, the inclusion of maize in the mixture, cultivation in strips and the use of relay intercropping. Substantially smaller yield gains, but still considerable land and fertilizer savings compared with sole crops under the same management, are obtained in a low-input,

low-output intercropping strategy, without maize, and with fully mixed intercrops without TND.

## Results

The overall yield gain (NE) in intercropping was  $1.5 \pm 0.1 \text{ Mg ha}^{-1}$  (mean  $\pm$  s.e.m.) in this global dataset. The NE was positive in 87% of the data records (Fig. 2a). The yield gains differed between intercrops with or without maize and between intercrops in different spatial arrangements. The NE was  $2.1 \pm 0.1 \text{ Mg ha}^{-1}$  in intercrops with maize, approximately four times as high as in intercrops without maize ( $0.5 \pm 0.1 \text{ Mg ha}^{-1}$ ) (Fig. 2b and Supplementary Fig. 3). When the NE was compared between intercrops with or without maize receiving N input less than the median value of  $75 \text{ kg N ha}^{-1}$  in the dataset, or at least this amount, the overall effect of N input was non-significant ( $P=0.32$ ), but there was a significant interaction ( $P=0.01$ ), indicating contrasting responses to N input in intercrops with or without maize (Fig. 2b). The NEs were similar in strip and alternate-row intercrops ( $1.5 \pm 0.1$  and  $1.4 \pm 0.1 \text{ Mg ha}^{-1}$ , respectively; Fig. 2c), but the NEs were significantly greater in these two spatial arrangements than in fully mixed intercrops ( $1.0 \pm 0.2 \text{ Mg ha}^{-1}$ ). The spatial arrangement effects were confounded with those of the presence of maize, the fertilizer input and the use of relay intercropping.

We used an index for TND to characterize complementarity in growing periods between the intercropped species. TND quantifies the total period of non-overlap as a proportion of the total growing



**Fig. 2 | NEs of various types of intercropping and the associations with TND and fertilizer inputs. a,** Frequency distribution of the NEs of intercroppings with and without maize. **b,** Interaction between the effects of N input (high N input,  $\geq 75 \text{ kg ha}^{-1}$ ; low N input,  $< 75 \text{ kg ha}^{-1}$ ) and maize presence on yield gain. **c,** NEs of intercroppings with different spatial arrangements. The bars represent the estimated means based on a mixed-effects model. The error bars represent the standard error of the mean;  $n$  is the number of data records (this applies to all figures). **d–f,** Relationships between NE and TND (**d**), N fertilizer input (**e**) and P fertilizer input (**f**). Only the regressions with  $P < 0.05$  are presented.

period of the two species on a scale from 0 (simultaneous growth) to 1 (the first species is harvested before the second is sown)<sup>23</sup>. The NE increased  $0.6 \pm 0.2 \text{ Mg ha}^{-1}$  per unit of TND ( $P = 0.02$ , Fig. 2d) in intercroppings both with and without maize. The NE of intercroppings with maize increased  $3.0 \pm 0.5 \text{ kg ha}^{-1}$  per kilogram of N fertilizer per hectare, but the NE of intercroppings without maize was independent of N fertilizer input. There was no response of the NE to phosphorus (P) fertilizer input, irrespective of whether maize was included in the intercrop.

The temporal and spatial arrangements, fertilizer input and species selection differed between intercropping systems with and without maize. TND was significantly larger ( $P < 0.001$ ) in intercroppings with maize ( $0.3 \pm 0.03$ ) than in intercroppings without maize ( $0.1 \pm 0.03$ , Fig. 3a) (that is, the relative cogrowth period of the crop species was shorter in intercropping systems with maize than in systems without maize).

Nitrogen fertilizer input was three times as high in intercroppings with maize ( $155 \pm 10 \text{ kg ha}^{-1}$ ) as in intercroppings without maize ( $46 \pm 10 \text{ kg ha}^{-1}$ ) ( $P < 0.001$ , Fig. 3b). The P fertilizer rate was similar in intercroppings with and without maize ( $P = 0.08$ , Fig. 3b).

The observed yield of intercroppings with maize ( $8.9 \pm 0.3 \text{ Mg ha}^{-1}$ ) was  $5.5 \text{ Mg ha}^{-1}$  higher ( $P < 0.001$ ) than the observed yield of intercroppings without maize ( $3.4 \pm 0.3 \text{ Mg ha}^{-1}$ , Fig. 3c). The expected yield (calculated as the product of the monoculture yield and the land share of component species in intercropping) of intercroppings with maize ( $6.7 \pm 0.2 \text{ Mg ha}^{-1}$ ) was  $3.7 \text{ Mg ha}^{-1}$  higher than the expected yield of intercroppings without maize ( $3.0 \pm 0.2 \text{ Mg ha}^{-1}$ , Fig. 3c).

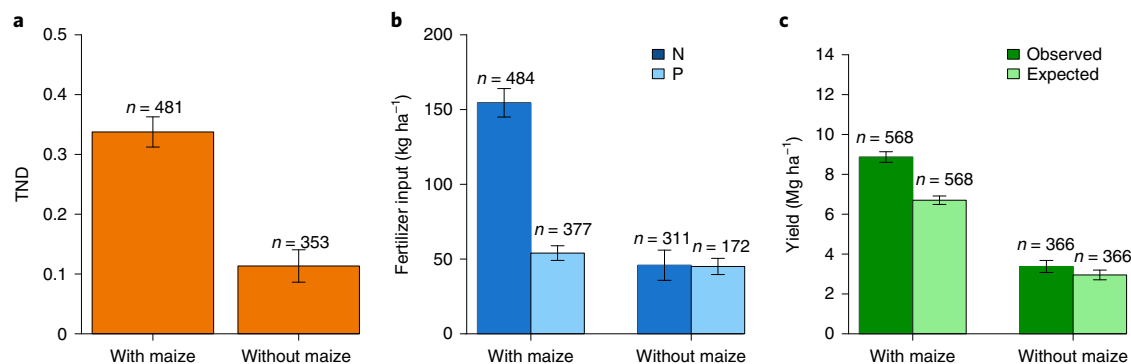
There were marked differences in spatial arrangement and companion species between intercropping systems with and without maize. Most of the intercroppings with maize were arranged in strips (461 out of 568 records, Fig. 4a), and far fewer records represented

intercroppings with maize grown in alternate rows (79 out of 568) or fully mixed with the companion species (28 out of 568). Of the intercroppings without maize, 155 of 366 records were mixed intercropping, 82 records were alternate-row intercropping and 129 records were strip intercropping (Fig. 4a). Legumes such as pea (*Pisum sativum*), faba bean (*Vicia faba*), soybean and peanut (*Arachis hypogaea*) were the most common companion species in intercroppings with maize (436 records, Fig. 4b) (Supplementary Table 1). There was also a substantial number of observations (120 records) of maize intercropped with small grains, such as wheat or barley (*Hordeum vulgare*) (Supplementary Fig. 2). Intercroppings without maize were dominated by legume-based intercroppings (352 out of 366 records, Fig. 4b), such as mixtures of legumes with small grains (wheat, barley, oats (*Avena sativa*) or rice (*Oryza sativa*), 284 records), another legume species (25 records) or another species (43 records), such as oilseed rape (*Brassica napus*) or sesame (*Sesamum indicum*). Only 14 records of intercroppings without maize included a non-legume species (Supplementary Table 1).

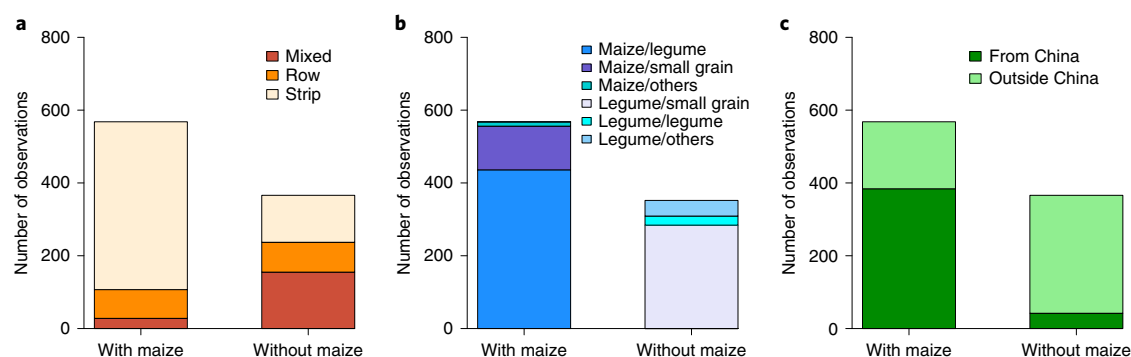
Of a total of 426 records originating from China, 384 records concerned intercropping with maize, whereas a smaller proportion of records originating from studies outside China (184 out of 508 records) concerned intercropping with maize (Fig. 4c). A majority of records (324 out of 508) originating from studies outside China concerned intercropping without maize. These studies originated from Europe (44%), Asia (32%) and Africa (17%) (Supplementary Fig. 4).

The results of a principal component analysis illustrate the existence of two contrasting syndromes of production in intercropping (Fig. 5). On the one hand, there are systems with maize with high yield levels, high N input and strip intercropping with large values of TND (high loadings on principal component 1, Supplementary





**Fig. 3 | TND, fertilizer inputs and yield levels of intercrops with and without maize. a–c,** TND (**a**), N and P fertilizer input (**b**), and observed yield and expected yield (**c**) of intercrops with and without maize.



**Fig. 4 | Spatial arrangements, species selection and geographic origin of intercrops with and without maize. a,** Number of observations (records) for different intercropping patterns. **b,** Species selection (combinations with less than ten observations) are not shown. **c,** Studies on intercropping with or without maize originating from China and outside China.

Table 2). On the other hand, there are systems without maize with substantially lower yield levels, lower N input and often simultaneous alternate-row or mixed intercropping. Studies representing the high-yield intercropping syndrome with maize originated mostly from China, while studies representing the lower-yield intercropping syndrome without maize originated mostly outside China.

Relative metrics—LER, N fertilizer equivalent ratio (NFER) and P fertilizer equivalent ratio (PFER)—were calculated to characterize the relative use efficiency of land (LER), N fertilizer (NFER) and P fertilizer (PFER) in intercropping. The LERs of intercrops with and without maize were both significantly larger than 1, but the average LER of intercrops with maize ( $1.29 \pm 0.02$ ) was significantly greater than the average LER of intercrops without maize ( $1.16 \pm 0.02$ ) ( $P < 0.001$ , Fig. 6a and Supplementary Fig. 5). Averaged over levels of N input, the land savings in intercrops with maize were 13% larger than in intercrops without maize. When N input was added as a categorical variable in this analysis, the effect of maize presence was still highly significant, but in addition there was a small but significant decrease in LER (by  $0.05 \pm 0.02$  units,  $P = 0.004$ ) with higher N input. There was no significant interaction between N input and maize presence ( $P = 0.23$ ) (Fig. 6a).

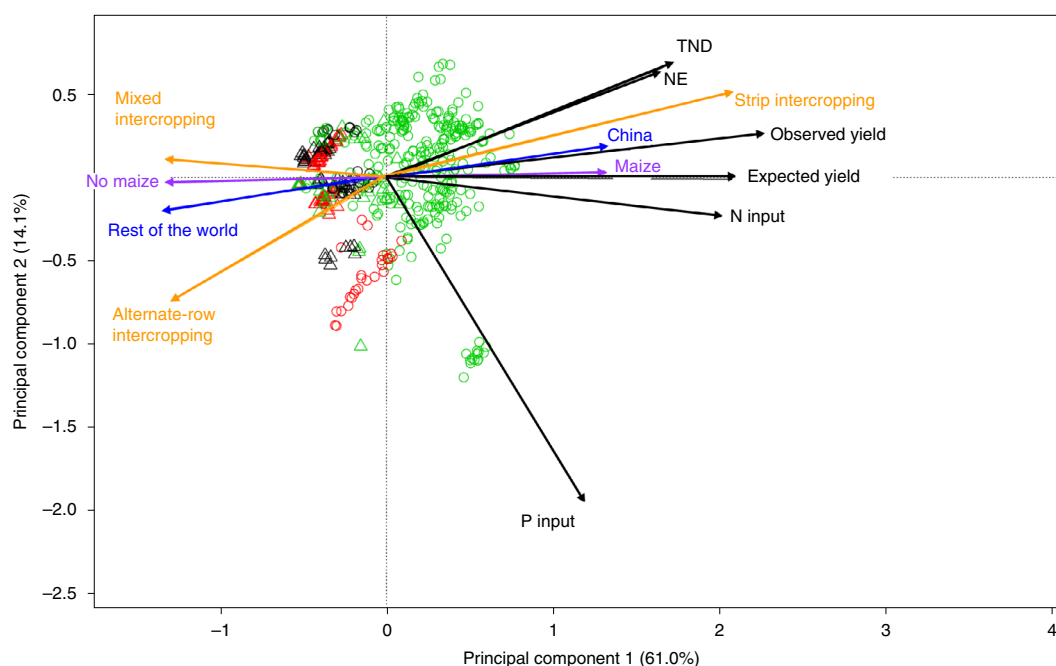
The NFER and PFER indicate the ratio of the fertilizer amounts used in sole cropping to the fertilizer amounts used under intercropping to produce equal amounts of yield. The NFERs of intercrops with and without maize were  $1.33 \pm 0.04$  and  $1.19 \pm 0.05$ , respectively (Fig. 6b). So, to achieve the same yield as intercrops, the sole crops used 19–33% more N fertilizer than the intercrops, indicating increased N use efficiency in intercropping if nutrient use efficiency is expressed as fertilizer used per unit yield produced.

The NFER of intercrops with maize was higher ( $P = 0.01$ ) than that of intercrops without maize, indicating that intercrops with maize save more N fertilizer compared with sole crops than do intercrops without maize. Similarly, the PFER of intercrops with maize ( $1.36 \pm 0.03$ ) was larger than the PFER of intercrops without maize ( $1.19 \pm 0.04$ ) ( $P < 0.001$ , Fig. 6b), indicating that, while both types of intercrops save P fertilizer compared with sole crops, the savings are greater in intercrops with maize than in intercrops without maize.

## Discussion

This paper presents a dichotomy in strategies for intercropping that could be regarded as two syndromes of production<sup>37,38</sup>. These different strategies have probably been developed to address different production objectives. On the one hand, systems with maize (commonly used in China) represent a strategy of intercropping based on high inputs, high outputs and a comparatively large intercropping advantage in terms of absolute yields per hectare. These systems are based on strip intercropping with narrow strips (usually 1–2 m wide) and a relay sequence in the sowing and harvesting of the intercropped species. Due to this relay sequence, the total duration of the intercropping system exceeds that of both component crops, providing the opportunity for increased capture of light, water and nutrient resources, and limiting the period of cogrowth, during which the species compete for resources. These relay systems obtain the greatest possible grain yield under land and resource constraints<sup>28,39,40</sup>.

On the other hand, systems without maize were often cultivated with low inputs, and they had substantially lower intercropping benefits in terms of absolute yield per hectare. These intercropping systems were usually grown as simultaneous intercrops, with



**Fig. 5 | Principal component analysis of the associations between yield gain and intercropping design and management.** The symbols represent mixed intercropping with maize (black circles) or without maize (black triangles), alternate-row intercropping with maize (red circles) or without maize (red triangles), and strip intercropping with maize (green circles) or without maize (green triangles). The arrows represent continuous variables (black) and categorical variables (coloured). The factor loadings are given in Supplementary Table 2.

simultaneous sowing and harvesting of the two species, and with the species grown most often in alternate rows or completely mixed, but rarely in strips. This type of system addresses the aim of developing an agricultural system that exploits species complementarities to drastically lower inputs, but these systems had lower outputs than the systems of the first syndrome. Due to the simultaneous sowing and harvesting, these systems are easier to mechanize than systems with maize, which are usually relay systems. Furthermore, due to the lower inputs, these systems are expected to have lower nutrient losses per hectare than systems managed according to the high-yield syndrome.

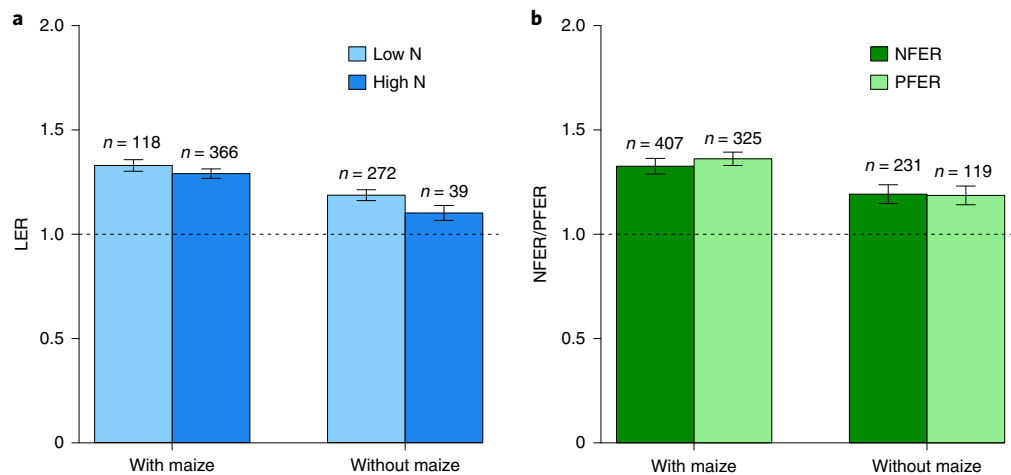
Land and fertilizer equivalent ratios were well above 1 (in the range of 1.16 to 1.36) in both syndromes of production, indicating that compared with sole crops, both strategies of intercropping resulted in considerable savings of land and nutrient resources. The relative efficiencies of intercrops compared with sole crops (LER, NFER and PFER) were greater in the case of the high-input, high-output syndrome than in the case of the low-input, low-output syndrome, leading to the unexpected finding that the benefits of diversifying agriculture are at least as high under high-input conditions as under low-input conditions.

Large intercropping benefits in production systems with high inputs contrast with the established opinion that the stress gradient hypothesis is a key explanation for intercropping benefits<sup>30</sup>. This hypothesis is based on the idea that under stressful conditions, facilitative and complementary species traits support the functioning of mixtures. While there is no doubt that this hypothesis explains many cases of overyielding in intercrops at low input levels, the current analysis shows that the benefits may be even greater if stresses are relieved, and intercropping is exploited to enhance resource capture and mitigate nutrient losses at higher input levels. The findings show that intercropping can be adapted to both low-input and high-input agriculture, on the basis of different production situations and socio-economic conditions with associated constraints and objectives, resulting in two syndromes characterized by a coordinated set of management practices.

In this analysis, we cannot disentangle the effect of maize from the effects of strip intercropping, relay intercropping or fertilizer inputs. Most of the maize intercrops were tall/short combinations, so intercrops were often sown in strips to reduce interspecific competition for light<sup>40,41</sup> and to permit management by hand in smallholder farming. Maize is better adapted to high temperatures than C3 species, which makes a C3/C4 mixture amenable to TND between component species. The spatial and temporal niche differentiation and the differences in plant height, photosynthesis mechanisms<sup>42</sup>, rooting patterns and phenology<sup>43</sup> between maize and C3 species allow the complementary use of light, water and nutrient resources in intercropping. Legume-based intercrops were especially favoured in low-input (organic) agriculture to compensate for low external input and to make use of biological N<sub>2</sub> fixation by legumes to maintain yield<sup>31,44</sup>.

The existence of these syndromes of production suggests different production orientations in different regions: high yield and high land use efficiency in China, and reduced inputs and low nutrient emissions outside China. In China, to achieve a stable food supply with limited land and resources, Chinese farmers developed and practised intercropping for thousands of years<sup>45</sup>. However, to maximize grain yields, fertilizer inputs have been strongly increased over the past few decades in most regions in China<sup>45,46</sup>, contrasting with traditional and circular patterns of low input and low output<sup>25</sup>. Tightened environmental policies may reduce inputs in China in the future<sup>47</sup>, both in intercropping and in sole crops, to diminish nutrient losses per hectare.

The high NFER and PFER of intercropping indicate that a 19% (without maize) to 35% (with maize) reduction in fertilizer input may be achieved in intercropping as compared with sole crops while achieving the same amount of product output. The lower input of nutrients required per unit product in intercropping provides the potential to save fertilizer<sup>29</sup> and reduce losses to the environment<sup>48,49</sup> compared with monocultures that receive high inputs in China<sup>47</sup>. Nevertheless, despite the greater NFER and PFER (relative input per unit product), the high-input, high-output syndrome may still



**Fig. 6 | Land and fertilizer savings of intercropping.** **a**, Interaction between the effects of N input and maize presence on LER. **b**, NFER and PFER of intercrops with and without maize. The dashed lines represent an LER, NFER or PFER equal to 1.

have higher nutrient emissions per hectare than the low-input, low-output syndrome. Further research is needed to assess the environmental benefits of the high-input intercropping strategy compared with sole crops or reduced-input intercrops. A middle way may be found between the low- and high-input strategies, combining the strengths of both, but this will require a further analysis of the trade-offs.

Intercropping is not currently a part of modern industrialized high-input and high-yield agriculture in Western nations. However, intercropping is gaining increasing interest in the context of sustainable agriculture in the West, and innovative farmers are experimenting with it, often using legumes to reduce N fertilizer inputs. Legume-based intercrops are used in organic farming to produce high-quality grain and forage at low N input<sup>21</sup>, to reduce N leaching<sup>48</sup> and to improve overall resilience by reducing pest and disease incidence<sup>10</sup>, weed pressure<sup>9</sup> and the risk of crop failure associated with drought or erratic rainfall<sup>50,51</sup>. Those intercrops are mostly fully mixed to adapt to sowing and harvesting with machinery in countries with high levels of mechanization<sup>21</sup>. Mixed intercropping is also practised by smallholder farmers in shifting cultivation systems with limited use of fertilizer and machinery<sup>6,50</sup>. Combining traits of both syndromes of production in intercropping may enable high food production with a lower environmental footprint than is realized in the currently existing high-input, high-output syndrome.

Our study suggests that intercropping strategies with maize provide an opportunity to design intercropping systems with large TND to adapt to extended growing seasons and higher temperatures due to global warming<sup>52,53</sup>. Furthermore, the temporal arrangement in relay strip intercropping allows better timing of fertilizer application to save fertilizer input. For instance, reduced N fertilizer input at the early cogrowth stage in maize/pea intercropping improves N<sub>2</sub> fixation of intercropped pea, and N fertilization at the late cogrowth stage increases the recovery growth of intercropped maize<sup>54,55</sup>. The relatively high and stable crop productivity and economic benefits of intercropping are attractive to farmers<sup>56–58</sup>. However, the management of two crops in one field is more complex than that of a single crop, and markets may require high purity standards for harvested products that may be difficult to achieve if the crops are harvested simultaneously with existing machinery<sup>21,58</sup>. Strip relay intercropping may be a greater challenge for mechanization than simultaneous intercropping. Limited work on these challenges has been done, and work is currently ongoing to overcome these challenges<sup>46,59</sup> and make mechanized intercropping possible<sup>60</sup>. The remarkable advantages of intercropping, and the possibility of applying intercropping

under high-yield conditions, as shown here, should provide the incentive for stakeholders and policymakers to work on solving the current constraints and introduce much-needed diversity in agricultural systems<sup>2,61</sup>.

The current analysis did not consider water use in intercropping. In many production situations with high inputs and outputs, irrigation water is used. Relay intercropping increases the length of the growing season and thus increases total crop evaporation<sup>15</sup>. Therefore, intercrops need greater amounts of irrigation water than sole crops<sup>14</sup>. Nevertheless, previous work has shown that the increased water consumption in intercropping systems is more than offset by the higher productivity, such that the overall effect of intercropping is still an increase in water use efficiency (calculated per unit product) when compared with sole crops<sup>13,15,62</sup>. We did not include water use efficiency in the current analysis because our literature searches were not tailored to this variable. New systematic literature review and data retrieval are needed to analyse the worldwide water footprint of intercropping. On the basis of current knowledge, the likely outcome is that the high water use efficiency of intercropping can help alleviate water constraints in agriculture<sup>63</sup>. This is primarily due to species complementarities with respect to the location (soil depth) and timing (during the season) of water extraction<sup>13,14</sup>.

In conclusion, this meta-analysis presents two diverging syndromes of agricultural production by intercropping and suggests that these syndromes allow harvesting 16% to 29% more grain per hectare while using 19% to 36% less fertilizer per unit output than conventionally done in the monocrops of modern industrialized agriculture. Higher yields and lower inputs might mean greater profit to farmers<sup>56–58</sup>, lowered environmental impacts<sup>48,56</sup> and a more stable and secure food supply<sup>50,51</sup>. This meta-analysis shows how these advantages may be realized by intercropping in both high- and low-input agriculture. Intercropping therefore provides an important principle for advancing the sustainable intensification of agriculture.

## Methods

**Data selection.** The dataset was built by combining a database built by Yu et al.<sup>23</sup> and a database built by Li et al.<sup>35</sup>. From the original database of Yu et al.<sup>23</sup>, all the data records of grain-producing intercrops (such as cereals, legumes and oilseed crops) that provided data on species densities were extracted (539 records). We removed the duplicate data records (9 publications and 31 data records) in the two datasets. All intercrops in the resulting database were grain-producing intercrops. The dataset included variables such as the publication title, year and author, and the yield of both sole crops and intercrops, species combination, planting density, row distance, fertilizer input, sowing dates and harvest dates. Most of the studies did not report the irrigation frequencies and volumes in the

different treatments. Therefore, irrigation amount was not included in the dataset. The dataset included 934 data records, representing data from 226 experiments described in 132 publications. ‘Experiment’ was defined as a unique combination of site and year. Within experiments, data records were defined by treatment, including species combination, sowing and harvest dates, and fertilizer input.

**Response and explanatory variables.** In the analysis, the response variables are NE, LER, NFER, PFER, rate of N (and P) fertilizer input in intercrops ( $\text{kg ha}^{-1}$ ), observed (and expected) yield ( $\text{Mg ha}^{-1}$ ), and TND (see equation (7) below), and the explanatory variables are the presence of maize in species combinations (categorical; two levels: with and without), the spatial arrangement (categorical; three levels: strip, row and mixed), the origin of the data (categorical; two levels: from China and outside China), TND, and the rate of N (and P) fertilizer input in the intercrops ( $\text{kg ha}^{-1}$ ).

**NE.** The NE is defined as the difference between the observed yield and the expected yield<sup>24</sup>.

$$\text{NE} = (Y_1 + Y_2) - (\text{EY}_1 + \text{EY}_2) \quad (1)$$

where  $Y_1$  and  $Y_2$  are the observed yields of species 1 and 2 in the intercrop, and  $\text{EY}_1$  and  $\text{EY}_2$  are the expected yields of the two species, which were calculated as the product of the monoculture yield and the land share<sup>35</sup>.

$$\text{EY}_1 = M_1 \times \text{LS}_1 \quad (2)$$

$$\text{EY}_2 = M_2 \times \text{LS}_2 \quad (3)$$

where  $M_1$  and  $M_2$  are the yields (per unit area of the respective sole crop) of species 1 and 2 in monoculture, and  $\text{LS}_1$  and  $\text{LS}_2$  are the land shares of species 1 and 2 in intercropping. The land share was calculated on the basis of the densities of a species in the intercrop and in the sole crop or on the basis of the row or plant arrangement<sup>35</sup>.

**LER.** The LER is defined as the sum of partial LERs (relative yields) per species ( $\text{pLER}_1$  and  $\text{pLER}_2$ ):

$$\text{LER} = \text{pLER}_1 + \text{pLER}_2 = \frac{Y_1}{M_1} + \frac{Y_2}{M_2} \quad (4)$$

where  $Y_1$  and  $Y_2$  are the yields (per unit of total area of the intercrop) of species 1 and 2 in intercropping, and  $M_1$  and  $M_2$  are the yields of species 1 and 2 in monoculture (same as above).

**NFER and PFER.** Because no N was applied to many of the legumes in some of the selected studies, we could not compare the N use efficiency of sole crops and intercrops. As an alternative, we used relative indicators. In analogy with the LER and water equivalent ratio<sup>13</sup>, we defined the NFER and PFER as the amount of N and P fertilizer used in sole crops to produce the same yields as obtained in intercropping.

$$\text{NFER} = \frac{\text{Nfert}_1 \times \frac{Y_1}{M_1} + \text{Nfert}_2 \times \frac{Y_2}{M_2}}{\text{Nfert}_{\text{IC}}} \quad (5)$$

$$= \text{pLER}_1 \times \frac{\text{Nfert}_1}{\text{Nfert}_{\text{IC}}} + \text{pLER}_2 \times \frac{\text{Nfert}_2}{\text{Nfert}_{\text{IC}}}$$

$$\text{PFER} = \frac{\text{Pferti}_1 \times \frac{Y_1}{M_1} + \text{Pferti}_2 \times \frac{Y_2}{M_2}}{\text{Pferti}_{\text{IC}}} \quad (6)$$

$$= \text{pLER}_1 \times \frac{\text{Pferti}_1}{\text{Pferti}_{\text{IC}}} + \text{pLER}_2 \times \frac{\text{Pferti}_2}{\text{Pferti}_{\text{IC}}}$$

where  $\text{Nfert}_{\text{IC}}$  and  $\text{Pferti}_{\text{IC}}$  are the N and P fertilizer input per unit area (in  $\text{kg ha}^{-1}$ ) of the intercrop<sup>35</sup>;  $\text{Nfert}_1$  and  $\text{Pferti}_1$  are the N and P fertilizer input per unit area of species 1 in monoculture; and  $\text{Nfert}_2$  and  $\text{Pferti}_2$  are the N and P fertilizer input of species 2 in monoculture. The NFER and PFER express the relative amount of N and P fertilizer that would be required if sole crops were used to achieve the same yields as a unit area of intercrop. Values of the NFER and PFER larger than 1 indicate fertilizer savings in intercropping. An NFER and PFER equal to the LER indicate that the nutrient use efficiency gains of intercropping are primarily due to concentrating production on less land<sup>39</sup>. If the fertilizer input in the intercrop is intermediate between those in the sole crops, the NFER and PFER will tend to be larger than the LER. If the fertilizer amount in the intercrop is higher than those in the sole crops, the NFER and PFER will tend to be smaller than the LER.

**TND.** An index for TND was used to express the proportion of the total growing period of an intercropping system in which species are growing alone. TND was calculated using the sowing and harvest dates of each species in the intercrop<sup>23</sup>:

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

$$= 1 - \frac{P_{\text{overlap}}}{P_{\text{system}}}$$

where  $P_{\text{overlap}}$  represents the period of overlap between the growing periods of the intercropped species, and  $P_{\text{system}}$  represents the duration of the whole intercrop from

the sowing of the first crop till the harvest of the last crop. A TND of 0 means full overlap of the two species (the species are sown and harvested at the same time). A TND of 1 means no overlap, which refers to double cropping (the second species is sown after the first is harvested). Double cropping was not included in our analysis.

**Statistical analysis.** Linear regression with mixed-effects models (function `lme` in R package `nlme`<sup>64,65</sup>) was used to estimate the average values of NE, observed and expected yields, N and P fertilizer input, TND, LER, NFER, and PFER and to compare differences in these parameters between intercrops with and without maize, differences in NE between intercrops with different spatial arrangements, and the relationship between NE and TND or fertilizer input. We used the publication and the experiment within publications as random effects to account for differences among the studies (publications) and the experiments (sites  $\times$  years) within studies. A variance model (function `varIdent` in R package `nlme`) was used to account for the heterogeneity of variance<sup>66</sup> between intercrops with and without maize. The associations between the NEs of intercrops and the variables (such as N input, P input, TND, observed and expected yields, species combinations with and without maize, spatial arrangement and the origin of intercrops) were further visualized with principal component analysis, using the `vegan` package in R (ref. <sup>67</sup>).

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

## Code availability

The R code used for the analysis is available from the corresponding author on reasonable request.

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## Author contributions

C.L., E.H., T.W.K., C.Z., H.L., F.Z. and W.v.d.W. designed the study. C.L. and Y.Y. collected the data. C.L. and W.v.d.W. performed the statistical analyses and led the writing of the manuscript. All authors reviewed the manuscript and contributed to the interpretation and manuscript revisions.

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41477-020-0680-9>.

**Correspondence** and requests for materials should be addressed to F.Z. or W.v.d.W.

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### Software and code

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- |                 |   |
|-----------------|---|
| Data collection | Data was collected from the Chinese knowledge infrastructure and Web of Science. The search and selection process is presented in detail. |
| Data analysis   | R version 3.3.3 was used for data analysis.   |

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# Ecological, evolutionary & environmental sciences study design

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Study description	We did a global meta-analysis on comparing the difference in absolute yield gain of different intercropping strategies and we analysed how a coherent of management factors such as species choice, intercropping patterns, temporal niche differentiation and fertilizer input impact the yield gain of intercropping. We found that there are two syndromes of production in intercropping: high-input and high-yield system and low-input and low-yield system. And we discussed the reasons for the syndromes in the context of ecology, socio-economic forces, and we discussed the implication of our study for future intercropping design and challenges of mechanisation in intercropping.
Research sample	The dataset was built by collecting literature data from Web of Science and from the Chinese National Knowledge Infrastructure. The dataset includes sufficient information for our analysis, such as the yields of sole crops and intercrops in each study, the sowing dates and harvesting dates of each crop, the species combinations in intercropping, the intercropping patterns and the nutrient input rates, etc (Li et al. (2020) and Yu et al. (2015)). Yu, Y., Stomph, T.-J., Makowski, D., Van der Werf, W., 2015. Temporal niche differentiation increases the land equivalent ratio of annual intercrops: A meta-analysis. Field Crops Research 184, 133-144. Li, C. J. et al. 2020. Yield gain, complementarity and competitive dominance in intercropping in China: A meta-analysis of drivers of yield gain using additive partitioning. European Journal of Agronomy 113:125987 doi:https://doi.org/10.1016/j.eja.2019.125987
Sampling strategy	The search and selection strategy for the dataset about Chinese intercropping is fully described in Li et al. (2020). Another dataset is a subset of Yu et al. (2015), and the search and selection process is clearly included in the paper and our selection of the subset is included in the manuscript.
Data collection	One data set (about Chinese intercropping) was built by collecting data in literature from the Chinese National Knowledge Infrastructure. Chunjie Li collected the data, and the data collection criteria are included in Li et al. (2020). The other data set (about non-Chinese intercropping) was a subset of a database compiled by Yu et al. (2015). The selection procedure is included in the paper and supplementary information. Yang Yu collected the original data set, and Chunjie Li did the selection of subset. The selection criteria are included in Materials and Methods of the manuscript.
Timing and spatial scale	We built the data set about Chinese intercropping in January 2015. The subset of Yu et al. (2015) about non-Chinese intercropping was built in 2012.
Data exclusions	No data was excluded from the analysis.
Reproducibility	The study is fully reproducible using the data and methods detailed in the manuscript.
Randomization	The dataset about Chinese intercropping is a sample by searching literature before January 2015 from the available online literature sources (Web of Science and Chinese National Knowledge Infrastructure). The other dataset about non-Chinese intercropping is a sample from literature, and the sampling strategy is described in Yu et al. (2015).
Blinding	Blinding is not relevant to our study.
Did the study involve field work?	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No

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Materials & experimental systems	Methods
n/a	n/a
Involvement in the study	Involvement in the study
<input checked="" type="checkbox"/> <input type="checkbox"/> Antibodies	<input checked="" type="checkbox"/> <input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/> <input type="checkbox"/> Eukaryotic cell lines	<input checked="" type="checkbox"/> <input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/> <input type="checkbox"/> Palaeontology	<input checked="" type="checkbox"/> <input type="checkbox"/> MRI-based neuroimaging
<input checked="" type="checkbox"/> <input type="checkbox"/> Animals and other organisms	
<input checked="" type="checkbox"/> <input type="checkbox"/> Human research participants	
<input checked="" type="checkbox"/> <input type="checkbox"/> Clinical data	