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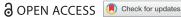
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Effects of Nutrient Antagonism and Synergism on Yield and Fertilizer Use Efficiency

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ABSTRACT

Interaction among plant nutrients can yield antagonistic or synergistic outcomes that influence nutrient use efficiency. To provide insight on this phenomenon, peer-reviewed articles were selected that quantified the interaction effects of nutrients on crop yield levels. In total 94 articles were selected that described 117 interactions between all macro- and micronutrients for different agricultural crops. In 43 cases the interaction was synergistic, in 17 cases the interaction was antagonistic, and in 35 cases the interaction was zero-interaction; the other 23 cases were non-significant (16) or showed a negative response (7). Generally: (a) when the availability of two nutrients is characterized as deficient, a large increase in yield can be expected by diminishing these deficiencies: (b) for most macronutrients the mutual interactions on yield levels are synergistic; and (c) antagonistic effects on yield are often found for divalent cations. Knowledge of nutrient interactions can guide fertilizer design and optimization of fertilization strategies for high yields and high nutrient use efficiencies.

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Antagonism; fertilizer; macronutrients; micronutrients; synergism

Introduction

The increase in global food demand will require an increased use of natural resources such as water, land, and nutrients to produce crops (Tilman et al. 2011). Three major pathways have been identified to meet this growth: decreasing the loss of agro-ecological production capacity, decreasing the demand of food per capita, and increasing the production of food (Dogliotti, Giller, and Van Ittersum 2014). The growth of the global food production is projected to require increased use of chemical fertilizers, but since the current environmental impact of agriculture and fertilizer use has reached its planetary boundaries (Steffen et al. 2015), the nutrient use efficiency of fertilizers should be increased dramatically. The current yield trends are insufficient to meet forecasted food demands (Ray et al. 2013), which implies a daunting challenge to limiting the use of fertilizers and increasing yields. This problem reveals the great potential to increase the nutrient use efficiency, and consequently, yield levels by considering all essential plant nutrients (macronutrients N, P, K, Ca, Mg, and S and micronutrients Cl, Fe, B, Mn, Zn, Cu, Mo, and Ni) in fertilizer products and fertilization strategies (Bindraban et al. 2015; Dimkpa and Bindraban 2016).

One of the causes of the current stagnating yield levels is the deficiency or imbalance of nutrients (Lobell, Cassman, and Field 2009). This problem suggests the need for a great potential to increase the nutrient use efficiency, and consequently, yield levels by considering all essential plant nutrients (macronutrients N, P, K, Ca, Mg, and S and micronutrients Cl, Fe, B, Mn, Zn, Cu, Mo, and Ni) in fertilizer products and fertilization strategies. To achieve these benefits, it will be imperative to apply balanced amounts of the most limiting nutrients to obtain the highest yield while minimizing nutrient losses, that is, when fertilization is fine-tuned to local soil chemical conditions and crop requirements (Roy et al. 2006).

In designing fertilizers with the right nutrient composition, antagonistic (negative) nutrient interactions should be minimized, whereas synergistic (positive) nutrient interactions should be maximized for optimal nutrient use efficiency. These actions require proper knowledge of possible positive and negative interactions between nutrients. The objective of this review is to provide an overview of the effects of these interactions on fertilizer use efficiencies and crop yields. To this end, the occurrence of antagonism and synergism in crops was assessed by posing a number of questions: (1) what is the quantitative nature of nutrient antagonism and synergism, (2) is there a relationship between the uptake of micro- and macronutrients, (3) which mechanisms are responsible for the interactions, and (4) what is the influence of nutrient transporters, reductase enzymes, and phytosiderophore production.

Material and methods

We reviewed the scientific literature on the effects of nutrients and their interactions on the yield of crops. The keywords were obtained from well-known references on mineral nutrition of plants: specifically 'fertilizer technology' (Chien, Prochnow, and Cantarella 2009; Mortvedt, Cox, and Shuman 1991), "fertilization," "interactions between plant nutrients" (Tisdale, Nelson, and Beaton 1985), "micronutrients" (Alloway 2008; Welch 1995), "principles of ion uptake by plants" (Epstein and Bloom 2005; Mengel et al. 2001; White 2012), and "specific fertilization of various important crop types" (Fageria, Baligar, and Jones 2011).

To compile a dataset of quantitative effects of interactions, we searched for peer-reviewed literature investigating the effects of interactions between nutrients on yield using Scopus (Elsevier). The search-query was: ((TITLE-ABS-KEY ((nitrogen AND magnesium) OR (potassium AND iron) OR (calcium AND iron) OR (magnesium AND calcium) OR (zinc AND calcium) OR (iron AND phosphorus) OR (manganese AND potassium) OR (copper AND phosphorus) OR (nitrogen AND potassium) AND TITLE-ABS-KEY ((potassium AND phosphorus) OR (calcium AND potassium) OR (magnesium AND phosphorus) OR (zinc AND phosphorus) OR (nitrogen AND borate) OR (potassium AND borate) OR (calcium AND manganese)))) AND (TITLE-ABS-KEY (nutrient OR fertilizer)) AND (TITLE-ABS-KEY (antagonism OR interaction OR synergism)) AND (TITLE-ABS-KEY (plant OR crop OR root OR leaves)) AND NOT (TITLE-ABS-KEY (trees OR cadmium OR toxic OR lead OR moss OR forest)) AND (LIMIT-TO (DOCTYPE, "ar")). This search produced a total of 349 publications (accessed Nov 6, 2014). The papers found using this method were selected. The references in the papers and references to the selected papers were used for additional publications.

The papers were screened on interaction between nutrients as reflected in the yield. To address the research questions as listed above, several exclusion criteria were used. The experimental papers that did not include original data or a statistical evaluation of the interaction were excluded. Because the main focus for this review was on the positive effects of fertilization, a large number of studies about the toxic effects of copper, zinc, and boron were excluded. Papers describing the variation of nutrient supply by different soils and possible effects on nutrient interactions were also not considered. In total 94 papers were selected to compile the dataset on synergistic and antagonistic effects.

Approach

Interactions between nutrients occur when the supply of one nutrient affects the uptake, distribution, or function of another nutrient. Depending on the nutrient supply, the interaction can modify plant growth and yield. Interactions can be assessed by examining the relationship between nutrient supply and nutrient concentrations in plants and by examining the relationship between nutrient supply and plant growth (Robson and Pitman 1983). It has resulted in many possible relations between the supply of a nutrient and the effects on plants (Landon 1991; Robson and Pitman 1983) that have been discussed in detail in various reviews and textbooks (Alloway 2008; Fageria et al. 2013; Pan 2012; Tisdale, Nelson, and Beaton 1985; White 2012; Wilkinson, Grunes, and Sumner 2000; Zhang, Shen, and Zhu 2006). Knowledge about these interactions is important to understand nutrient uptake processes. In many publications, the effects on



concentrations, or accumulation in plants, is used as the main parameter to assess nutrient interactions (Gunes, Alpaslan, and Inal 1998).

Nutrient interaction in crops is probably one of the most important factors affecting yields of annual crops (Fageria 2014). On the one hand, nutrient interaction at the root uptake level may be studied deterministically based on well-conditioned experiments, and on the other hand, it can be determined agronomically by studying nutrient availability and fertilizer effects on crop yield. The deterministic approach eliminates external influences such as other limiting nutrients, water limitation or water excess, temperature and pH, but these results may often not be transferred to field conditions. In contrast, agronomic studies have the disadvantage that external influences are uncontrolled and that the results can be valid only for the prevailing conditions because of a host of confounding variables. According to Fageria (2014): "Interactions occur when the supply of one nutrient affects the absorption and utilization of another nutrient. [...] Nutrient interactions affect plant growth and development only when the supply of a determined nutrient is too low compared to the applied ones. In other words, yield decrease occurs only when the supply of some nutrients falls below the critical level. If the soil or growth medium has sufficient supply of other essential nutrients compared to the added one, plant growth will not be affected adversely, even though the uptake of some nutrients may decrease. Hence, plant growth or yield is considered a better criterion for evaluating nutrient interactions in crop plants." The rationale for performing this review is to improve fertilization toward balanced fertilizer application and enhanced fertilizer use efficiency. Therefore, we have selected the crop yield approach in this review while not further considering nutrient uptake.

The effect of interactions between nutrients on yield of crops has been reviewed before for specific nutrients: for N (Aulakh and Malhi 2005; Fageria 2014), for K (Daliparthy, Barker, and Mondal 1994; Dibb and Thompson 1985), for P (Sumner and Farina 1986), and specific for N-K interactions (Zhang et al. 2010), but not for the entire array of all essential nutrients.

Synergism, zero-interaction, and antagonism

Pan (2012) described theoretical studies (Rubio, Zhu, and Lynch 2003; Wallace 1990; Zinn, Witholt, and Egli 2004) to classify nutrient interactions on the basis of quantitative descriptions of data and models. We adopted their methodology that is most common in the literature studying this phenomenon. Yield will be used as the main parameter to assess nutrient interactions, which can either be synergism, antagonism, or zero-interaction. Synergism refers to the response that is greater than expected from the individual responses (Aulakh and Malhi 2005; Fageria 2014, 2001; Roy et al. 2006; Tisdale, Nelson, and Beaton 1985; Wallace 1990; Wilkinson, Grunes, and Sumner 2000). The yield expected (y_{ab}) on the basis of the individual responses (y_a and y_b) for the situation of zero-interaction follows from

$$\frac{y_{ab}}{y_0} = \frac{y_a}{y_0} \times \frac{y_b}{y_0} \tag{1}$$

where y_0 is the yield in the reference or control treatment (Table 1). The calculation of the expected yield (y_{ab}) as a product of the individual responses according to Eq. (1) is based on Wallace (1990) and, to our knowledge, is an operational definition and is not based upon a plant physiological process. By using relative yields, it is possible to compare between different experiments, crops, fertilizers, and to account for variations in the control treatments. Wallace (1990) has suggested that many interactions can be described according to Eq. (1). Therefore, we also used this criterion for zero-interaction. Antagonism refers to the yield in response of two nutrients in which the combined effect is less than expected from the individual responses (expected from individual responses: zero interaction, according to Eq. (1)) (Aulakh and Malhi 2005; Fageria 2001; Sumner and Farina 1986), or in other words, that the actual relative yield is less than the product of the individual yield effects. Thus, even if the yield in a plot treated with nutrient a and b is higher than the plots treated with a or b, the effect is synergistic only when the yield response exceeds the expected yield on the basis of

Table 1. Definition of synergistic, antagonistic, zero-interaction, and Liebig-synergism.

Interaction	Description	Evaluation
Synergism	Nutrient interaction is synergistic where the yield due to the combined application of two nutrients is more than the yield expected on the basis of the effects from the individual applications of the nutrients.	$\frac{y_{ab}}{y_0} > \frac{y_a}{y_0} \times \frac{y_b}{y_0}$
Antagonism	Nutrient interaction is antagonistic where the yield due to the combined application of two nutrients is less than the yield expected on the basis of the effects from the individual applications of the nutrients.	$\frac{y_{ab}}{y_0} < \frac{y_a}{y_0} \times \frac{y_b}{y_0}$
Zero-interaction	Where the yield obtained from a combination of two nutrients is equal to the yield expected on the basis of the individual application of the nutrients, the interaction is said to be zero-interaction.	$\frac{y_{ab}}{y_0} \approx \frac{y_a}{y_0} \times \frac{y_b}{y_0}$
Liebig-synergism	Typically in situations where the availability of one nutrient is limiting crop production, the addition of another nutrient shows no effect on yield, whereas addition of both nutrients shows an increased (synergistic) effect. Wallace (1990) introduced the term Liebig-synergism to describe this effect, referring to the Liebig limitation of the first nutrient.	$\frac{y_{ab}}{y_0} > \frac{y_a}{y_0} imes \frac{y_b}{y_0}$

the individual responses, that is, the actual relative yield is greater than the product of the individual yield effects (Aulakh and Malhi 2005).

Results and discussion

In total 116 interactions between nutrients on crop yield have been identified in the 94 publications. Details are presented in Appendix 1, and the major findings regarding nutrient interactions are discussed below. It is expected that the use of the categories synergism and antagonism is useful to describe the interaction between a pair of nutrients because it gives an indication of the yield response that might be expected from the use of fertilizers containing these nutrients.

An example of synergism is given in Table 2_see below: Fageria and Oliveira (2014) found large increase in rice grain yield by using K and P. The observed effect (relative yield) of the combination of both nutrients is compared to the calculated effect obtained as the product of the individual effects (i.e., 1.1×1.2), and appears greater (1.6) than the product of the individual effects according to Eq. (1), indicating synergism.

Synergism was identified in 23 cases, especially between macronutrients (Figure 1a). The Liebigsynergism, in which a deficiency is so severe that it first has to be resolved to obtain synergism with other nutrients, was coincidently identified also in 20 cases. Table 3 presents an example of the Liebig-synergism. This interaction appears to be antagonistic at zero Cu application, as the addition of N did not raise yield, but rather suppressed it, suggesting Cu deficiency to be the prime factor limiting yield. When both nutrients were supplied simultaneously, the yield increase was much higher than the yield due to the individual effects.

The distinction between synergism and the Liebig-synergism is essential for a fertilization strategy. In the 23 studies that show a synergistic interaction, the quotient of the actual and the predicted yield increase varies between 1 and 3 (Appendix 1). When severely limiting factors occur, and are corrected, resulting in Liebig-synergism, the response in yield is difficult to predict (Wallace 1990). In the 20 studies that show a Liebig-synergistic interaction, the quotient of the actual and the predicted yield increase varied between 1.5 and 35, demonstrating the variation involved in Liebig-synergism, as a result of the negligible response by a second nutrient that cannot overcome the severely limiting prime nutrient.

Synergistic interactions are well known for N x K and N x P interactions (Aulakh and Malhi 2005). They are not only important for the yield but also help to explain their combined effect on root growth, and the relevance for synchronized applications of, for example, N and K, during the growing season (Aulakh and Malhi 2005), ultimately resulting in improved nutrient use efficiency (NUE) (kg product per kg applied N, corrected for control in which no fertilizer is used) (Table 5). Some micronutrients reveal synergism with macronutrients (Figure 1a). The addition of Zn resulted in a higher yield of wheat on a calcareous soil, and the increase due to Zn was largest at the highest addition of macronutrients (Table 6) (Sakal, Singh, and Sinha 1988).

Table 2. Example of synergism. The yield^a is given as function of the application of nutrients.

Rice grain yield (g plan	nt ^{–1}) at 150 kg ha ^{–1} N (Fageria a	nd Oliveira 2014)	actual	expected
	100 mg kg ⁻¹ P	200 mg kg ⁻¹ P		
100 mg kg^{-1} K	10.7 (1.0)	12.3 (1.1)		
$200 \text{ mg kg}^{-1} \text{ K}$	12.6 (1.2)	16.6 (1.6)	1.6>	$1.1 \times 1.2 = 1.4$

^arelative yield between parentheses.

Table 3. Example of a specific type of synergism: Liebig-synergism. The yielda is given as a function of the application of nutrients.

Wheat yield (g plant ⁻¹)) (Wapakala 1973)		actual	expected
_	$0~{ m kg~ha^{-1}~N}$	$44 \text{ kg ha}^{-1} \text{ N}$		
0 kg ha ⁻¹ Cu	1.30 (1.0)	1.08 (0.8)		
14 kg ha ⁻¹ Cu	1.50 (1.2)	1.96 (1.5)	1.5 >	$0.8 \times 1.2 = 1$

^arelative yield between parentheses.

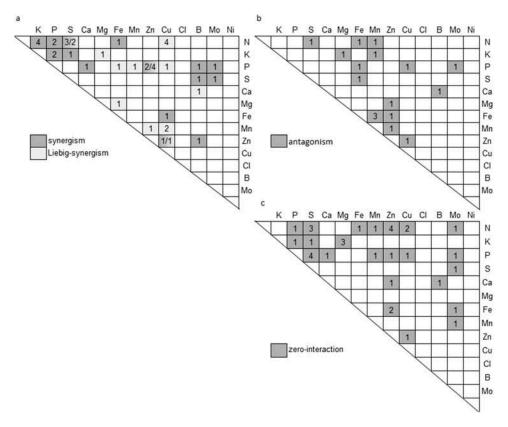


Figure 1. Interactions between nutrients. Number in squares refer to the number of studies of each type of interaction a. synergistic or Liebig-synergistic (totaling 43 cases). b. zero-interaction (totaling 35 cases). c. antagonistic (totaling 17 cases).

Some synergistic responses to nutrients may result from soil reactions such as the acidifying or reducing effects of the fertilizer nutrient. NH_4 fertilizers increase yield of barley and oats under Mn deficiency (Petrie and Jackson 1984) due to the reduction of the unavailable Mn(IV) to available Mn (II) in soil (Husted et al. 2005). Also, thiosulfate can reduce Mn(IV) in soil and increase the Mn uptake by Mn-deficient plants (Husted et al. 2005).

Table 5. Improved nitrogen use efficiency due to interaction with other nutrients (partly based on Aulakh and Malhi 2005).

Crop and N fertilization	NUE kg grain per kg applied N	Additional fertilizer	NUE kg grain per kg applied N	reference
Canola 120 kg N/ha	0.7	+60 kg S/ha	5.8	(Brennan and Bolland 2009)
Wheat 80 kg N/ha	2-14.6	+20 kg S/ha	5.7-17.3*	(Salvagiotti et al. 2009)
Wheat 120 kg N/ha	20.3	+90 kg P/ha	25.9	(Dwivedi et al. 2003)
Rice 120 kg N/ha	21.6	+60 kg P/ha	24.6	(Dwivedi et al. 2003)
Corn 100 kg N/ha	8.8	+60 kg P/ha	13.6	(Singh 1991)
Sorghum 120 kg N/ha	11.7	+60 kg P/ha	17.1	(Roy and Wright 1973)
Sunflower 60 kg N/ha	8.8	+30 kg P/ha	12.6	(Aulakh and Malhi 2005)
Field Pea 40 kg N/ha	10.3	+30 kg P/ha	15.2	(Aulakh and Malhi 2005)
Soybean 80 kg N/ha	0	+0.4 kg Fe/ha	9	(Caliskan et al. 2008)
Tobacco 224 kg N/ha	0.9	+0.22 kg Mo/ha	3.1	(Sims, Atkinson, and
3		•		Smitobol 1975)
Wheat 118–214 kg N/ha	25	+0.2 kg Zn/ha foliar	36	(Seadh et al. 2009)
Cauliflower 120 kg N/ha	68**	+4.2 kg Zn/ha	122**	(Balyan and Dhankar 1978)

^{*} variation between locations, ** fresh weight.

Table 6. Grain yield of wheat (t ha⁻¹) as influenced by NPK and Zn applications (Sakal, Singh, and Sinha 1988).

NPKa	0 kg Zn ha ⁻¹	5 kg Zn ha ^{–1}	10 kg Zn ha ^{–1}
$N_0P_0K_0$	1.45	1.58	1.64
$N_{50}P_{30}K_{25}$	2.73	2.88	3.03
$N_{100}P_{60}K_{50}$	3.53	3.84	4.04

adose of N, P, and K in terms of N, P_2O_5 , K_2O in kg ha⁻¹. LSD (5%) = 0.220.

Zero-interaction was identified in 35 cases (Figure 1c). An example for zero-interaction is given in Table 7. Either K or P individually improve the yield of soybean. The interaction effect in this case is predictable, as it follows from the individual effects: the relative yield increase is (about) equal to the product of the relative yield increase for the individual effects $(1.5 \approx 1.16 \times 1.30)$ (Aulakh and Malhi 2005; Fageria 2001; Sumner and Farina 1986). It is noteworthy that zero-interaction does not imply no effect of fertilizer on yield, but rather the lack of an additive effect.

Antagonism was identified in 17 cases. An example of antagonism is given in Table 8. Either Zn or Mg has strong positive effects on the growth of wheat, while the combined effect is less than the product of the individual effects. The quotient of the predicted and the actual yield varies between 0.3 and 0.9. Such interactions appear also, for example, between N and minerals that improve the symbiotic N fixation in plants (e.g., Mo, Ca, or Cu) (Robson and Pitman 1983): they both improve the N deficiency. Antagonisms are detected mainly between cations: K, Cu, Fe, Mn, and Zn (Figure 1b), as will be discussed later in the section about preferential transport of nutrients. Two exceptions that do not involve these cations are the antagonisms for Mo x P and N x S. The interaction between Mo x P, as determined by Vistoso, Alfaro, and Mora (2012) showed that both the addition of P or Mo increased the Mo accumulation by white clover. The antagonism for N x S was specific for the third grass cut, whereas the N x S interaction in the first grass cut was synergistic (Kowalenko 2004). According to Aulakh and Malhi (2005), such seasonal variations have also been observed for the N x P interaction in pumpkin and N x K in rice, and they have suggested synergic interactions in high yielding seasons and antagonisms at lower yielding seasons. Knowledge of these antagonisms is relevant to estimate the amount of fertilizers to be used. Therefore, it is relevant to note that most of the antagonisms involve interactions between micronutrients and rarely between macronutrients (Figure 1b).

For some combinations of nutrients, various types of interactions were found, such as for Zn x P (synergism, Liebig-synergism, zero-interaction) (Table 9). Table 9 also shows that for a large number of nutrient combinations, no interactions have been reported. Remarkably, interactions of nutrients with Ca, Mg, and S are rare, as was previously noted by Aulakh and Malhi (2005). No studies were



Table 7. Example of a zero-interaction. The yield^a is given as function of the application of nutrients.

soybean seed yield	(t ha-1) (Abbasi et al. 2012)		actual	expected
0.111.0	28 kg ha ⁻¹ K	112 kg ha ⁻¹ K		
$0 \text{ kg ha}^{-1} \text{ P}$	1.77 (1.00)	2.05 (1.16)		
60 kg ha ⁻¹ P	2.30 (1.30)	2.59 (1.46)	1.46 ≈	$1.16 \times 1.30 = 1.51$

^arelative yield between parentheses.

Table 8. Example of a negative interaction: Antagonism. The yield* is given as function of the application of nutrients.

Wheat shoot biomass (g pot ⁻¹) (Kumar, Bhatia, and S	hukla 1981)	actual	expected
	$0 \text{ mg kg}^{-1} \text{ Mg}$	60 mg kg ⁻¹ Mg		
0 mg kg ⁻¹ Zn	12 (1)	19 (1.6)		
20 mg kg ⁻¹ Zn	21 (1.7)	22 (1.9)	1.9 <	$1.6 \times 1.7 = 2.7$

^{*}relative yield between parentheses.

Table 9. Number of interactions assessed in this review.

Category	Number of studies
Synergism	23
Liebig-synergism	20
Zero-interaction	35
antagonism	17
Negative effect of nutrients on yield	7
no interaction could be detecteda	15
Total number	117

^aif there was no significant effect on yield, the interactions could not be categorized.

found that show interactions for the cations: K x Zn, K x Cu, Fe x Ca, Mg x Ca, Mg x Cu, Ca x Cu, and Mg x Mn (Figure 1). Also no interactions were found for the micronutrients Cl and Ni.

Besides interactions between nutrients that affect yield, nutrients also can have an effect on the content or uptake of other nutrients. For example, the effect of K x Mg interaction often has been studied because nutrient content is relevant for animal feed. Optimal growth of ryegrass is reached at a Mg content of 1 g kg⁻¹ dw (dry weight) in ryegrass (Smith, Cornforth, and Henderson 1985), but lactating cows require animal feed with a Mg content of 1.6–2.4 g kg⁻¹ dw (Suttle and Underwood 2010). Supply of K had a negative effect on the Mg content of crops, but the K content of crops was not affected (Bedi and Sekhon 1977; Bolton and Penny 1968; Ohno and Grunes 1985; Ologunde and Sorensen 1982), or even increased (Narwal, Kumar, and Singh 1985). High ryegrass yields, in combination with high Mg content in grass (2.5 g Mg kg⁻¹ dw), are obtained in practice by balancing limited levels of K with increased levels of Mg (Reijneveld et al. 2014).

Summarizing, our systematic assessment shows that with the exception of a limited number of studies for N x S and Mg x K, interactions between macronutrients are synergistic or zero-interaction. On the other hand, rather unpredictable large yield responses result from resolving nutrient deficiencies, Liebig-type synergisms, which in most cases involve Fe, Cu, Mn, and Zn. For these cations, synergisms among each other is rare. In most cases, antagonism does involve one of the cations Ca, Mg, Fe, Mn, Zn, or Cu. Figure 1 shows that only a limited number of studies have reported interactions for each combination of nutrients. Such a small number of studies does not allow disentangling the variations due to crop species, and other variables such as soil conditions. Additionally, in some studies, a negative effect of the application of nutrients on yield was found (Table 9). As this cannot be the intention of the use of fertilizers, these studies were assigned to a separate category (see Appendix 1). However, they can provide information about specific nutrient interactions and are, therefore, discussed after the following section. Finally, in some studies, no significant effect of nutrients on yield was obtained, and therefore, no interaction effects can be derived (Table 9).



Relationship between uptake of micronutrients and application of macronutrients

Various authors have investigated if an increase in yield, especially via N fertilization, will lead to a dilution of nutrients in crops (Rengel, Batten, and Crowley 1999), and a possible decrease of nutrient content in food and crops has been discussed in various publications (Fan et al. 2008). However, in field experiments (Table 10), the increased yield via N fertilizer does not lead to a significant change of the nutrient content in the grain of corn, wheat, and rice, likely due to the adequate soil supply of these nutrients (Mg, Zn, Cu, Fe and Mn in Table 10). The Zn content in the grain decreased in three studies, whereas it increased in two. The use of N fertilizer increased the S content in sorghum (by 9%) (Kaufman et al. 2013), wheat (McGrath 1985), and rice (Marr, Batten, and Lewin 1999), increasing the total accumulation by crops per unit area. Similarly, an increase in yield via various fertilizers does not lead to large increases or decreases in nutrient concentrations in potato (White et al. 2009) or corn (Heckman et al. 2003). The content of nutrients in brown rice was not affected by S treatment for S-deficient soils (Juliano et al. 1987). A decrease in Zn content of wheat grain was found, however, in a field without Zn deficiency, as a function of P fertilizer input (Zhang et al. 2012), whereas an increase in the Zn content of corn occurred if Zn was deficient (Friesen, Juo, and Miller 1980), revealing the complexity of the edaphic and biological system (Alloway 2008).

Assuming a rather constant micronutrient content, it is possible to estimate the crop nutrient accumulation from the yield. The nutrient contents in Table 10, however, are for the grain and not for the whole crop. Other references, as given in Table 11, provided the nutrient accumulation by crops, which, when no crop residues are left behind, is similar to the nutrient removal from the field. In Table 12, the fertilization rates used in various studies are presented, together with the recommended fertilization rates under deficiency. Comparison of Table 11 with Table 12 shows that the fertilization rates of micronutrients are rather high compared to the annual nutrient removal, as these fertilization rates are part of a strategy in which fertilization is performed only when there are indications for deficiency, based on low concentrations in soil or crop, or visual symptoms. Such a high dose is assumed to suffice for several years. Only boron is used annually, or more frequently, as it is easily leached in areas of high rainfall (Alloway 2008). The strategy to create a large stock in the soil, which in case of Cu, Mn, and Zn, is likely to be effective, as the nutrients are hardly lost by leaching and are applied only if they favorably affect yield. An annual-application approach is also applied, for example, in Australia with single superphosphate that contains about 600 mg Zn kg⁻¹ fertilizer from rock phosphate and suffices to sustain wheat grain production (Brennan 2001). The use of compound NPK fertilizers containing 1% Zn is promoted in Turkey (Cakmak 2008), and many fertilizer blends are sold that contain micronutrients.

Studies about the effects of an annual fertilization with micronutrients to compensate for the removal by crop are rare. In a study in which the effects of P x Zn interactions on corn have been investigated over a period of 25 years in a calcareous soil (Mallarino and Webb 1995), there was no induction of Zn deficiency by long-term high P fertilization, with zero-interaction between P and Zn. Brennan (2001) studied the effectiveness of Zn applications on the yield of wheat in sandy acidic soils. Zinc applications performed in 1983 were still effective in 1996, although the Zn application was 50% less effective in terms of yield response after 13 years as compared to Zn applied in 1996 (Brennan 2001). The total Zn removal from the field by wheat grain in 13 years was 7% of the applied 3 kg Zn ha $^{-1}$.

Summarizing, fertilizer application recommendations that considered a balanced application of nutrients have been reported, but without consideration of antagonism and synergism. The micronutrients content in plants remain relatively constant with increasing yield and increased application of macronutrients if sufficient micronutrients are available to the crop.

Specific mechanisms for antagonistic or synergistic responses to nutrients

In most cases, the authors of the studies listed in Appendix 1 did not assign specific mechanisms for the nutrient interactions. According to Pan (2012), non-specific interactions are typical for interactions

Table 10. Effects of macronutrient fertilizer on yield and content of micronutrients in the grain^a. In case of a significant effect of the fertilizer on the nutrient concentration, the nutrient concentration at the lowest and highest fertilizer input is given; otherwise the average content is given.

	Fertilizer input low-high							
	(kg/ha/yr)	Yield t/ha	Mg g/kg	Zn mg/kg	Cu mg/kg	Fe mg/kg	Mn mg/kg	Reference
ه .	0 – 275N	6.8 – 11.6	1.5	33	3.6	26	29	(Marr, Batten, and Lewin 1999)
	0 – 130 N	34 – 42 ^d	4.6				46 – 63	(Riedell 2010)
	0 – 240 N	6.1 – 8.9		15 – 17	1.2 – 1.6	13 – 16	3.0 - 3.4	(Xue et al. 2014)
	0 – 240 N	9.5 – 11	1.9	18	3.6	89	45 – 77	(Izsáki 2009)
	0 – 72 P	7.4 – 7.9	0.34	23 - 17	6.8 - 6.1	224 – 198	95	(Izsáki 2014)
	0 – 160 N	4.3 - 6.2	1.1	26 – 24	2.2		6.4	(Feil et al. 2005)
_	0 – 224 N	4 – 17	1.4 – 1.6	28	2.3 – 2.6	20 – 24	2 – 9	(Ciampitti and Vyn 2013)
(pot)	25 – 200 mg/kg P	1.7 – 7.6 ^d	1.8	27 - 24	5.2		17	(Fageria, Moreira, and Coelho 2012)
	0 - 100 N	5.1 – 8.0	1.5	17	2.8	06	14	(Kaufman et al. 2013)
neat	0 - 300 N	5.7 – 9.2	1.0	27	2	35	19	(McGrath 1985)
Winter wheat	40 – 160 N	4.2 - 5.1	1.3	24		47 – 56	20	(Zebarth, Warren, and Sheard 1992)
	67 – 194 N	6.6 - 8.2		38 – 42	3.4 - 3.8	39	46 – 55	(Svecnjak et al. 2013)
	0 – 400 P	3.5 - 6.5		29 – 13	5.3 - 4.5	31 – 37	26 – 31	(Zhang et al. 2012)

aln case of bean, corn, rice, and wheat, the concentrations are for the grain (dry matter) and not the whole plant. In case of brown rice, the grain without the hull.

^bdata from the years 1992–1993

'data from the year 2001. dyield in grams per plant. concentration in leaves.

Table 11. Annual nutrient uptake (kg/ha/year) for some crops.

Crop		Yield (t/ha)	N	Р	K	Ca	Mg	Zn	Cu	Mn	Fe	В	ref.
Lowland rice	straw	9.4	65	15	156	26	15	0.55	0.08	4.72	2.55	0.07	a
	grain	6.4	86	15	20	5	7	0.22	0.10	0.37	0.51	0.03	a
Upland rice	straw	6.3	56	3	150	23	13	0.16	0.04	1.32	0.65	0.05	a
	grain	4.6	70	10	56	4	5	0.14	0.06	0.28	0.12	0.03	a
Dry bean	straw	1.9	13	2	35	17	7	0.05	0.01	0.03	0.90		a
	grain	0.004	119	12	61	8	6	0.12	0.04	0.05	0.40		a
Corn	straw	11.9	72	5	153	33	21	0.18	0.05	0.45	2.05	0.10	a
	grain	8.5	127	17	34	8	9	0.19	0.01	0.08	0.21	0.04	a
Sweet corn	grain		57	10	38	2	4	0.08	0.02	0.05	0.10	0.03	b
	residue		141	15	194	23	15	0.15	0.06	0.34	0.41	0.06	b
Corn	silage	15	183	28	189	25	19	0.03	0.03	0.41	2.0		c
Grass		10	318	42	353	52	23	0.17	0.06	1.05	4.9		c

^aBrazil (Fageria, Baligar, and Jones 2011).

Table 12. Fertilization rates of micronutrients (kg/ha) for deficient situations for different countries.

Micronutrient		Fertilization rate in kg/ha					
	Range in various studies ¹	Netherlands ²	Germany ³	USA⁴	Austria ⁵		
В	0 – 17	0.2 - 1.5	2, 0.5*	1 – 3	0.4 - 2.5, 0.4*		
Cu	1.1 - 13.4	2.5 – 6	4, 0.5*	15	1 -10, 0.5*		
Fe		not recommende	ed		0.5 - 1.5*		
Mn	3 – 40	15*	1.0*	3 – 6	10 - 20, 1.5 - 3*		
Мо	0.01 - 0.5	1, 0.05*			1, 0.3*		
Zn	0.6 - 17		7, 0.5*	2 – 9	5 - 10, 0.3*		

^aamount for a single foliar application.

with N (e.g., N x P, N x S), as they influence all stages of plant growth, and too many associated processes. Specific nutrient interactions have been classified as soil, rhizosphere, and plant processes (Zhang, Shen, and Zhu 2006), with the rhizosphere processes classified as cation-cation, cation-anion, or anion-anion interactions (Pan 2012). The antagonisms (Figure 1b) between the cations, Cu, Fe, Mg, Mn, and Zn suggest that with cation-cation interactions, similar uptake mechanisms and competition between the cations might explain these effects. There are also some cation-anion interactions that might be specific, notably P x Zn interaction. One mechanism is that the control of P uptake by a plant is lost under Zn deficiency, as the expression of high-affinity P transporter proteins is linked to the Zn status of plants, suggesting in turn that complex plant-specific genetic and membrane transport processes are relevant for the P x Zn interaction (Bouain et al. 2014; Huang et al. 2000). Below we attempt to relate the important nutrient interactions in Figure 1 to specific mechanisms.

Preferential transport of nutrients

Nutrient uptake occurs by proteins embedded in root membranes that catalyze the transport of nutrients across the membrane. Similar cations and similar anions compete for binding to specific carrier proteins, whereas the uptake of cations versus anions occurs through different transport proteins (Table 13). Some of the identified plasma membrane transporters seem to be specific for nutrients, and others are less specific. The molecular mechanism of Mg uptake is understood poorly, and, therefore, no plasma membrane transporters for Mg are listed in Table 13.

^baverage for eight corn varieties (Heckman 2007).

caverage from large number of analyses (>1000) in the Netherlands (Evers et al. 2000).

^b compilation of studies (Martens and Westermann 1991).

^cadvice in the Netherlands, application is sufficient for a period of 4 years (Hoeks et al. 2012).

^dadvice in Germany, application is sufficient for a period of 4 years (Landwirtschaftskammer Niedersachsen 2008).

eadvice in Wisconsin (Laboski and Peters 2012).

^fadvice in Austria (BMLFUW 2006).



Table 13. Plasma membrane transporters for nutrients.

Plasma membrane transporter families	Role for nutrient	Reference
Ammonium transporters (AMT)	NH ₄ ⁺	1
Nitrate transporters (NRT)	NO ₃ -	1
Anion channels	CI ⁻	1
K channels	K ⁺	1
Ca channels	Ca ²⁺	1
Phosphate-transporters (PhT)	H ₂ PO ₄ ²⁻	1
SulP	SO_4^{2-4}	1
P3A-type H-ATPases	Na ⁺ , K ⁺ , Ca ²⁺ , Zn ²⁺	1
P1B-Zn-ATPases	Zn ²⁺ , Co ²⁺ , Cu ²⁺	1
P2B-(Ca)-ATPases	Ca ²⁺	1
yellow-stripe1-like (YSL)	Fe ²⁺	1
natural resistant-associated macrophage (NRAMP)	Mn ²⁺ , Fe ²⁺ , Co ²⁺	1
Zinc (ZIP)	Zn ²⁺ , Cu ²⁺ , Fe ²⁺	1
Copper transporter (COPT)	Cu ²⁺	1
Borate-transporter (BOR)	H ₂ BO ₃ ⁻	2
Molybdate-transporter (MOT)	MoO ₄ ²⁻	2

^a(Schulz 2010), ²(White 2012).

The transport proteins are unable to differentiate effectively between similar ions such as: potassium (K+) and rubidium (Rb+) (White 2012), sulfate (SO₄2-) and selenate (SeO₄2-) (White et al. 2007, 2004), sulfate (SO₄²⁻) and molybdate (MoO₄²⁻) (Fitzpatrick, Tyerman, and Kaiser 2008; Shinmachi et al. 2010), phosphate (PO₄³⁻) and arsenate (AsO₄³⁻) (White 2012), suggesting that the selectivity of some transport proteins in the plasma membrane of root cells is based partly on the physicochemical similarities between ions (White 2012). Indeed, some of the plasma membrane transporters families in Table 13 are able to transport various nutrients, an action that might specifically explain the antagonism on yield (Figure 1c) between nutrients.

Chaudhry et al. (1973) reported an antagonistic response on rice yield of the Cu x Zn interaction, and a negative effect of Zn on Cu uptake by rice plants occurred if Cu in the plant was deficient. As Cu and Zn have two plasma membrane transporters in common (P1B-Zn-ATPases and/or ZIP), these findings suggest that competition at the common plasma membrane transporters might be relevant in case of an antagonism. In contrast, additive (Agarwala et al. 1995) and synergistic responses (Chaudhry and Loneragan 1970; Khurana and Chatterjee 2000) were reported for Cu x Zn in combination with a positive effect of Zn on Cu uptake and vice versa, in case of deficient and adequate Cu and Zn levels in the growing medium. The zero-interaction and synergistic crop responses show that competition of Cu and Zn at the common plasma membrane transporter is outweighed by other processes if Cu and Zn levels in the growing medium are deficient or adequate.

The crop yields suggest that competition on plasma membrane is not likely to affect a major interaction between Mo x S (Figure 1), for which we found one study showing synergism (Sims, Leggett, and Pal 1979), one zero-interaction (Olsen and Watanabe 1979), and another no effect (Dhankar et al. 1996). None of the studies showed antagonism for Mo x S, probably because the nutrients contents were not deficient.

Ammonium has a negative effect on K uptake via K-channels (Hoopen et al. 2010), but K does not have the same effect on ammonium uptake via ammonium transporters (White 2012). While a positive N x K interaction is reported in many experiments, the interaction is found to be very complex, depending on the form of N and with contradictory findings (Zhang et al. 2010), and therefore cannot simply be explained by competition at the plasma membrane level.

The antagonism between Mn x Fe was noticed in three studies (Bansal, Chahal, and Nayyar 1999; Ghasemi-Fasaei and Ronaghi 2008; Kobraee and Shamsi 2011), and these two nutrients have one plasma membrane transporter in common (NRAMP). In two of these studies, there is a negative effect of Fe on Mn uptake (Bansal, Chahal, and Nayyar 1999; Ghasemi-Fasaei and Ronaghi 2008), and in only one study (Kobraee and Shamsi 2011), there is a negative effect of Mn on Fe uptake. In a hydroponic study, a strong effect of solution Fe concentration on Mn accumulation by soybean occurred, but no effect of solution Mn concentration on Fe uptake occurred (Heenan and Campbell 1983). Besides affecting Mn uptake at the common plasma membrane transporter, Fe has several other plasma membrane transporters, but other mechanisms also play a role in the antagonism between Mn and Fe.

Effect of nutrients on root reductase activity and phytosiderophore production

The activity of the reductase enzymes and phytosiderophore ("plant iron carrier": class of chelating compounds, common in grasses, that sequester iron) might be the mechanism that explains the synergistic interactions between Fe x N, Fe x P, P x Zn, Cu x Fe; Cu x P; and B x Zn (Figure 1). The positive influence of macronutrients on root reductase activity and phytosiderophore production might help to explain the positive responses of crops to macronutrients even under Fe or Zn deficiencies.

Iron deficiency by plants is caused by its low availability in soils, especially alkaline and calcareous soils, where the availability of other metallic micronutrients, specifically Zn, is also low. To mobilize Fe in the soil for uptake, grasses produce phytosiderophores (plant iron carriers) (strategy II), and other plants (dicots and non-grass monocots) produce reductases capable of reduction of Fe(III) to Fe(II) that can then be taken up by plants (strategy I). The release of phytosiderophores also can be induced by Zn deficiency (Aciksoz et al. 2011), and they also can mobilize other metals (Zn, Cu) (Römheld 1991). Various Fe-reducing substances, phenolics and carboxylates, can be produced by plants to increase the Fe availability (White 2012). Root ferric chelate reductase for instance is determined by Fe-deficiency but also can be regulated by Cu status in strawberry plants (Mukherjee et al. 2006; Pestana et al. 2013). Iron(III)-phytosiderophores are taken up by roots via yellow stripe1 (YS1) transporters (Schulz 2010), and plants such as peanut that cannot produce phytosiderophores can take up iron(III)-phytosiderophores. Corn in combination with peanut induces the production of phytosiderophores by corn and explains the positive effect of intercropping corn with peanut (Xiong et al. 2013). Nitrogen and S fertilization also may catalyze higher production of phytosiderophores and have been reported in soil and field experiments to increase Zn and Fe content in wheat (Kutman, Yildiz, and Cakmak 2011; Shi et al. 2010), Fe content in a Fe-deficient wheat plant in hydroponic experiments (Aciksoz et al. 2011) (Zuchi, Cesco, and Astolfi 2012), and Fe content in a pot experiment using brown rice in soil (Wu, Lu, and Hu 2014).

Antagonisms between Fe x Mn and Fe x Zn were found (Figure 1b), which also might be related to ferric-chelate reductase activity, as it has been shown that the ferric-chelate reductase activity of various plants, for example, alfalfa (Barton et al. 2000), sugar beet (Chang et al. 2003), cucumber (Lucena et al. 2003), and cowpea and bean (Dimkpa et al. 2015, 2008), can be inhibited by the high availability of metals.

Summarizing, although it has been a subject for research only recently (Keuskamp et al. 2015), the effects of nutrients on the reductase enzymes or phytosiderophore production might be a mechanism for interactions between macronutrients and Fe, Zn, and Cu.

Management strategies

Identifying synergisms is the most obvious management strategy to improve the response to fertilizers. Liebig-type synergisms are stimulated by solving nutrient deficiencies. The example in Table 3 shows that nutrient deficiencies are not always better identified by looking only at the response to a deficient nutrient, but by including a combination of nutrients. Synergisms only can be identified using different fertilizers, combinations, and reference treatments. It is also expected that the improvement of various agronomic factors (e.g., water, weed, tillage, cultivar) will improve the responses to fertilizers (Ghosh et al. 2002).

Crop and plant ecophysiological processes inherit various opportunities to overcome nutrient antagonisms while stimulating synergisms due to 1) different nutrient requirements during the season, 2) different uptake routes for nutrients (leaf, roots), and 3) effects of different plants (intercropping). According to Aulakh and Malhi (2005), the synergism between N x K can be exploited by a combined application throughout the season. This combined application corresponds with the enhancement of the N x S synergism for teff by a split application of combined N and S



(Habtegebrial and Singh 2006), and with high yields in tomato using split application of NK fertilizers within the growing season on sandy soils (Locascio et al. 1997).

While many synergisms have been identified between nutrients applied via the soil, only a few synergistic responses have been reported using other application methods. Synergism between a nutrient application via soil N fertilization and foliar Fe fertilization was reported for soybean (Caliskan et al. 2008), and synergism between foliar fertilizers Mn x Mo was found on canola (Brennan and Bolland 2011). Besides soil (possible for all nutrients) and foliar fertilization (possible for B, Ca, Cu, Fe, Mn, Mo, N, Ni, S, Zn (Fageria et al. 2009)), nutrients can be supplied with the seed (e.g., Mo) (Draycott and Christenson 2003; Fageria et al. 2009) or by irrigation (which is mainly though the soil). A combination of seed, soil, or foliar applications of fertilizers might initiate an effective strategy to obtain a more efficient use of fertilizers and overcome antagonisms while enhancing synergism.

Nutrient combinations that show an antagonistic response when applied together might be delivered via different routes, whereas a synergistic response can be exploited best when nutrients are added together. An example of synergism is the combination of Fe foliar fertilizer with urea, which stimulates the uptake of Fe via wheat leaf penetration (Aciksoz et al. 2014) similar to the synergism between urea and Zn or Mn in foliar fertilization (Yassen, Abou El-Nour, and Shedeed 2010). Foliar fertilization of S alone did not increase soybean grain yield, whereas soybean responded positively if S was applied in a mixture with NPK (Garcia and Hanway 1976) suggesting a synergism in which nutrients have to be applied together. However, either soil or foliar applications of Mn were not effective to correct Feinduced Mn deficiency in bean (Moosavi and Ronaghi 2010), and soil application of Mn was not effective to correct Mn deficiency due to soil or foliar application of Fe in chickpea (Ghasemi-Fasaei et al. 2005) or wheat (Ghasemi-Fasaei and Ronaghi 2008). These complex responses reveal that preventing antagonism and creating synergism is not straightforward and calls for an in-depth understanding of plant physiological processes (Fageria et al. 2009; Pandey, Krishnapriya, and Bindraban 2014).

Synergisms may be stimulated using intercropping. The synergism between N x P on corn was increased by intercropping with Gliricidia sepium, a leguminous tree (Akinnifesi et al. 2007). As mentioned earlier, the increased production of phytosiderophores as a response to fertilization of one crop and the improved Fe nutrition by a second crop, might be a mechanism for synergistic responses due to intercropping (Xiong et al. 2013). Manganese deficiency of berseem clover in alkaline soils in NW India could be remedied by mixed cropping with other fodder crops including oat, ryegrass, or mustard, resulting in a higher yield of berseem clover (Arneja and Sadana 2012); and mixed cropping with barley, oat, and wheat increased the Fe content in peanut plants under peanut Fe-deficiency (Zuo and Zhang 2008). These studies show that deficiencies can be alleviated by intercropping, and by doing so, these crops may show a higher response to fertilizers, although this possibility still has to be verified.

Conclusions

There is a need to increase the fertilizer use efficiency, that is, to obtain more yield per unit of fertilizer applied, to contribute to sustainable agriculture. Interactions among nutrients on nutrient uptake and accumulation and crop yield, including zero-interaction, synergism, or antagonism, reinforce balancing the composition, amount, timing, and mode of delivery of fertilizers to plants and soil, thereby aiming to overcome antagonism and stimulate synergism.

This review provides an overview on synergistic and antagonistic nutrient interactions on crop yield and sets the stage for delineating fertilizer strategies in terms of fertilizer design and delivery. A total of 117 interactions between nutrients on crop yield have been identified in 94 publications: 43 synergistic (of which 21 were of special type Liebig- synergistic), 17 antagonistic, and 35 resulted in zero-interaction. In some studies, no significant yield responses were found to assess interaction (16), and seven negative results were reported that were difficult to explain.

Because nutrient interactions could be studied for a limited number of crops, nutrients, soil types, and climates, only general, rather than conclusive, findings can be reported, and these results do not allow for extrapolation to other production conditions:



- In cases where the availability of two nutrients can be characterized as deficient, increasing the availability of both nutrients often results in a large increase in yield. Identification of deficiencies and the use of optimal ratios between nutrients are therefore important in developing efficient fertilizer application schemes.
- Most macronutrients have synergistic interactions. Synergistic interactions between nutrients result in actual relative yields that are a factor 1-3 greater than yield predicted on the basis of individual nutrients. As macronutrients form the basis for fertilizer applications, it is worthwhile to take these synergistic interactions into account.
- Antagonisms and negative effects of nutrients often are related to the divalent cations that probably share similar uptake mechanisms. Strategies to overcome these problems might be to differentiate the fertilization of these nutrients between soil and foliar applications. In some instances, this combined avenue has appeared effective, such as foliar fertilization of micronutrients in combination with urea. This differentiation however has rarely been studied for interacting nutrients.

Knowledge of nutrient interactions can guide fertilization trials and optimization of fertilization strategies for high yields and high nutrient use efficiencies. Stimulating reductase activity or phytosiderophore production, intercropping, and the use of micronutrients can be strategies to decrease deficiencies and increase responses to macronutrients, whereas a balanced fertilization of macronutrients can exploit the synergisms. Although the available data do not allow to disentangle the impact of confounding variables on reported yield responses to nutrient applications systematically, the information reveals several generic principles that can be accounted for as initial steps toward more balanced application of nutrients, and to explore the option of delivery of the nutrients to the plant through roots and leaves.

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Appendix 1. Interactions between nutrients

Literature has been examined for studies about interactions between nutrients. Studies that determined the yield as a function of the supply of two nutrients combined or supplied separately have been included in Table 14. The yield (y) is given for the zero treatment (y_0) , for the treatment with nutrient $a(y_a)$, nutrient $b(y_b)$, and the combined treatment (y_{ab}) . An interaction between two nutrients is synergistic when the combined effect of two nutrients on yield (y_{ab}/y_0) is greater than the product of their individual effects $(y_a/y_0 \times y_b/y_0)$. When the combined effect is less, the interaction is antagonistic. The expected yield for the combined treatment (Eq. (1)) is calculated as proposed by Wallace (1990) as the product of the relative yields from the single effects (y_a and y_b). Zero-interaction indicates the absence of interaction $(y_{ab}/y_0 = y_a/y_0 \times y_b/y_0)$. A specific case of synergism has been defined by Wallace (1990) as Liebig-synergism. In this case, the yield in the combined treatment (y_{ab}) is higher than any of the individual treatments $(y_0, y_a \text{ or } y_b)$, and the yield at the starting point (y_0) is limited dominantly by one nutrient. In the end point (y_{ab}) , there is synergism.

In some studies, a variety of concentrations has been studied. Only one combination of two nutrients is given in Table 14. In most cases, the highest supply of nutrients was chosen, except in the case of toxic effects (if there is a yield decrease due to the addition of a single nutrient that is known to be toxic at high concentrations). In those cases, the concentrations with the highest yield have been chosen.

Some studies have given an ANOVA table about the interaction and the effect of individual treatments. The type of interaction has been estimated from the ANOVA table and figures presented in these studies.

Note: ideally in nutrient interaction studies all other factors should be at an optimum level, except the nutrients under investigation (Fageria, Baligar, and Jones 2011). This is rather difficult to comply with when studying interactions between nutrients such as iron, manganese, and zinc where the availability is often determined by the soil conditions.

Table 14. Dataset of 117 interactions between nutrients on crop yield (for explanation of table see text in Appendix 1) on the basis of 94 references, for 74 combinations^a of nutrients.

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$y_a^{\ \ h}$	8.0	1.5	16		22		8.9				12.6					13.7	2.9		23.6			1.8	1.5	10.3	2.4	5.9	3.3	88	9.0					21	5.9	3.1		
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	yield ^d	shoot (g/pot) shoot (g/pot)	shoot (g/pot)	shoot (g/pot)	shoot (g/pot) dm (t/ha)	seed (kg/ha)	gram (vna) dm (g/pot)	dm (g/pot)	dm (g/pot)	grain (t/ha) shoot (g)	dm (g/pot) dm (g/pot)	(e4/+) diezo	grain (t/ha)	dm (g/plant)	dm. (g/pot)	shoot (g/pot)	dm. (g/pot) dm (g/pot)	dm (g/pot)	dm (g/pot)	dm (g/pot)	grain (t/ha)	
	nutrients ^c	K/Mg mg/l K/Mg mmol/l	K/Mg mg/ ka	K/Mg mg/	K/Mg mg/l K/Mg kg/ha	N/Fe kg/ha	N/Fe kg/na N/Fe mg/kg	N/Fe mg/kg	P/Fe mg/kg	P/Zn+Fe P/Fe mmol/	S mg/kg /Fe mg/	kg N/Mn kg/ha	N/Mn kg/ha	K/Mn umol/ I	P/Mn umol/ dm. (g/pot)	P/Mn umol/	Ca/Mn mg/l Fe/Mn mg/	Fe/Mn mg/ ka	Fe/Mn mg/ ka	Fe/Mn	Fe/Mn mg/ kg	
	crop ^b	sorghum Iucerne	corn	corn	Cowpea ryegrass	soybean	wneat soybean T-203	soybean Hawkeye	white lupine	maize soybean	sorghum radish	harlov gats	wheat	soybean	barley oats	potato	cotton maize	chickpea	wheat	soybean	soybean	
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y _{ab} 1	3.4	3.1	26 21	23	10.4	74	17	2.3	6.4		1.87	17	4.5	48		1	22.1	4.3	3.6	3.8	3.7	3.8	9.3 2 465
T _{ab} ^k	8/30	2/1	150/20	120/4.2	214/0.24	128/54	300/10	250/5	40/5		53/10		75/10	80/20			60/20	56/4	15/16	50/40	220/65	40/40	214/0.24 44/12 2400/21
y _b j	3.6	3.4	4 4	14	8.4	10	5 2	1.6	3.1		1.86	13	1.2	49		9.00	20.6	3.0	3.0	3.32	0.63	3.00	6.9 1.50 61
T _b i	0/30	1/0	0/20	0/4.2	118/0.24	32/54	0/10	9/2	9/2		0/10		0/10	0/20			0/20	0/4	0/16	0/40	5.5/65	0/40	118/0.24 0/14 0/21
y _a h	3.4	3.1	16 28	17	9.1	8.0	9	1.7	5.6		1.58	1	2.4	35		9.93	18.5	3.4	3.2	3.12	2.40	3.19	9.1 1.08 20
Та 9	0/8	2/0	150/0	120/0	214/0	128/0.1	300/0	250/0	40/0		53/0		75/0	0/08		1.2/0	0/09	26/0	15/0	20/0	550/6.5	40/0	214/0 44/0 2400/0
yo f	3.3	3.3	9.8	8.8	6.8	6.8	7 7	1.7	3.1		1.56	13	1.5	49		8.97	11.9	2.7	2.1	2.73	1.29	2.09	6.8 1.30 31
T ₀ e	0/0	0/0	0/0	0/0	118/0	32/0.1	0/0	0/0	0/0		0/0	0/0	0/0	0/0		0/0	0/0	0/0	0/0	0/0	5.5/6.5	0/0	118/0 0/0 0/0
yield ^d	shoot (g/pot)	shoot (g/pot)	grain (g/pot) shoot (g/pot)	product (t/ha)	grain (t/ha)	shoot (g/pot)	shoot (g/pot)		seed (g/pot)	biomass (g/	seed (ka/ha)	seed (g/plant)	shoot (g/ plant)	shoot (mg/	grain (t/ha)	grass (g/pot)	Shoot (g/pot)	grain (t/ha)	grain (t/ha)	grain (t/ha)	grain (g wt/	grain (t/ha)	grain (t/ha) grain (t/ha) grain (mg/ plant)
nutrients ^c	Fe/Mn mg/	Fe/Mn mg/	N/Zn mg/kg N/Zn mg/kg	N/Zn kg/ha	N/Zn kg/ha	P/Zn umol/ا 19/3 مرکرا	P/Zn mg/kg	P/Zn mg/kg	P/Zn mg/kg	P/Zn uM	P/Zn kg/ha	P/Zn kg/ha	P/Zn mg/kg	P/Zn mg/l	P/Zn kg/ha	Ca*/Zn g/kg	Mg/Zn mg/	Fe/Zn kg/ha	Fe/Zn kg/ha	Fe/Zn mg/ kg	Mn/Zn ug/l	Mn/Zn mg/	N/Cu kg/ha N/Cu kg/ha N/Cu mg/kg
crop ^b	dry bean	dry bean	wheat pearl millet	cauliflower	wheat	potato	maize	wheat	bean	maize	sovbean	dwarf bean	maize	maize	wheat	ryegrass	Wheat	rice	rice	soybean	wheat	soybean	wheat wheat oats
n. a	78	28	29	29	29	<u>~</u> ~	3 5	31	31	31	31	31	31	31	31	33	34	35	35	35	36	36	37 37 37

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Table	

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reference	(Antil et al. 1988) (Kumar, Yadav, and Yadav 1990)	(Dias and Oliveira 1996)	(Awan and Abbasi 2000)	(Shukla and Singh 1979) (Dekock, Cheshire, and Hall 1971)	(Cheshire, Dekock, and Inkson 1967)	(Nautiyal and Chatterjee 2002)	(Khurana and Chatterjee 2000)	(Agarwala et al. 1995) (Khurana and Chatterjee 2000)	(Chaudhry et al. 1973)	(Chaudhry and Loneragan 1970)	(Sinha, Dube, and Chatterjee 2003)	(Khurana and Chatterjee 2002)	(Keeratikasikorn, Bell, and Loneragan 1991)	(Singh et al. 2010)	(Redondo-Nieto et al. 2003)	(Sinha, Jain, and Chatterjee 2000) (Sims, Atkinson, and Smitobol 1975)	(Mandal, Pal, and Mandal 1998)	(Vistoso, Alfaro, and Mora 2012)	(Continued)
, T	ט ט	I	_o	ט ט	ŋ	I	I	エエ	Ū	_O	I	I	ட	I	I	Τщ	G	ט	
ratio ⁿ	1.3	-	0.0	1.0	15	3	4.8	1.1		10.9	1.4	3.1	7.2	1.0	0.4	35.1	0.9	0.3	
type ^m	L-S L-S	add	⋖	add L-S	S	r-S	F-S	add S	⋖	L-S	S	S	r-S	add	⋖	S add	add	∢	
y _{ab} 1	12 2.52	4	59	15.8 71	692	16	3.7	14.6	7.6	1.7	7.8	56	4.50	46	1.1	3.9	3.0	13.4	
T _{ab} ^k	80/5 120/5	3/0.0002	20/2	100/5 1200/21	1200/21	10/1	550/550	65/65 55/65	64/16	16/7	3/0.3	2/0.3	100/2	3/0.005	1.36/ 0.0465	330/65 224/0.22	50/1	200/9	
$y_b^{\ \ j}$	0.7	2.5	35	12.5 61	49	6.5	0.63	11.30	6.83	1.40	0.79	3.91	0.25	32.4	1.01	0.03	2.3	7.7	
T _b i	0/5 0/5	0.6/	0/5	0/5 0/21	0/21	0/1	5.5/550	65/0.65 5.5/65	16/16	2/0	0.15/0.3	0.02/0.3	0/2	0/0.005	0.68/	3.3/65 0/0.22	0/20	9/0	
y _a h	11	4	27	13.5 25	45	8.6	1.32	7.40	3.58	0.10	3.54	6.13	0.63	35.9	0.80	3.3	1.7	11	
T _a 9	80/0 120/0	3/0	20/0	50/0 1200/0	1200/0	10/0	550/5.5	0.65/65 55/6.5	64/8	16/0	3/0.0003	2/0.0003	100/0	3/0	1.36/ 0.0093		20/0	200/0	
yo f	0.8	2.1	28	10.5	4	10.2	1.09	6.10	7.18	0.90	0.51	2.85	0.25	25.6	0.29	0.09	1.22	1.9	
T ₀ e	0/0	0/9:0	0/0	0/0	0/0	0.01/0.01	5.5/6.5	0.65/0.65 5.5/6.5	16/8	0/0	0.15/	0.02/	0/0	0/0	0.68/	3.3/0.65 0/0	0/0	0/0	
yield ^d	dm (g/pot) Shoot g/pot)	shoot (g/ plant)	shoot (g/ plant)		grain (mg/ plant)	shoot (g/ plant)	grain (g wt/ pot)	plant (g/plant) grain (g wt/ pot)	grain (g/pot)	grain (g/plant)	shoot (g/ plant)	shoot (g/ plant)	seed (g/plant)	product (fw g)	shoot (g/ plant)	seed (g/plant) grain (t/ha)	shoot (g/ plant)	shoot (g/ plant)	
nutrients ^c	N/Cu mg/kg N/Cu mg/kg	N/Cu mmol/l	P/Cu mg/kg	P/Cu mg/kg P/Cu mg/kg	Fe/Cu mg/ ka	Mn/Cu umol/l	Mn/Cu ug/l	Zn/Cu ug/l Zn/Cu ug/l	Zn/Cu mg/ kg	Zn/Cu mg/ kg	P/B mmol/l	S/B mmol/l	Ca/B mg/kg	Ca/B mmol/	Ca/B mmol/	B/Zn mg/l N/Mo mg/ ka	P/Mo mg/ ka	P/Mo mg/ kg	
crop ^b	raya wheat	rice	maize	wheat oats	oats	cauliflower	wheat	maize wheat	rice	wheat	mustard	mustard	peanut	carrot	pea, bean	mustard tobacco	lentil	White clover	
nr	37	37	39	39	43	4	4	45 45	45	46	28	29	09	09	09	64	69	69	

Table 14. (Continued).

a n	crop ^b	nutrients ^c	nutrients ^c yield ^d	T_0^{e}	yo f	Б _Е Т	y _a h	T _o ° y _o f T _a g y _a h T _b i y _b i T _{ab} k y _{ab} ' type ^m ratio ⁿ °	y _b j	T _{ab} ^k	yab 1	type ^m	ratio ⁿ	۲°	reference
69	brassica napus	P/Mo mg/	grain (g/plant)	0/0	6.9	6.9 160/0	9.0	9.0 0/0.3	7.2	160/03	13	S	4.	G	7.2 160/0.3 13 S 1.4 G (Liu et al. 2010)
70	70 sorghum	S/Mo mg/	dm (g/pot)	0/0	6.3	30/0	10	0/0.062	9	30/0.062	10	add	1.0	g	1.0 G (Olsen and Watanabe 1979)
70	70 raya crop S/Mo mg/ dm (g/pot)	kg S/Mo mg/	dm (g/pot)									n.e.		G	G (Dhankar et al. 1996)
70	tobacco	S/Mo mg/	leaf (t/ha)	0/0	2.7	2.7 224/0	2.7	2.7 0/2.2	5.6	224/2.2	3.0 S	S	::	щ	1.1 F (Sims, Leggett, and Pal 1979)
73	sorghum	kg Fe/Mo mg/	dm (g/pot)	0/0	6.3	6.3 5/0	11	0/0.062	9	5/0.062	12	add	1.0	G	1.0 G (Olsen and Watanabe 1979)
74	canola	Mo/Mn kg/ g	grain (t/ha)	0/0	1.84	1.84 0.04/0	2.06	2.06 0/1	2.15	2.15 0.04/1	2.3	2.3 add	6.0	ш	0.9 F (Brennan and Bolland 2011)
		5													

combination of two nutrients

rutrients: treatment with nutrient a and b, given as a/b. Unit depends on the type of study. In water hydroponic studies (mg/l, mmol/l solution), pot studies (mg/kg soil) or field studies (kg/ha). Underlined is foliar application.

type of yield: mass of the shoot, grains, etc. ${}^{\rm e}_{\rm T_0}$

control treatment, given is the amount of nutrient a and b in the control treatment (example: 10/0 is 10 and 0 kg/ha of resp. nutrient a and b)(units: °).

yield in control treatment ${}^{9}\Gamma_{a}$

treatment with nutrient a

 $^{
m h}\!y_a$ yield in treatment a'T $_{
m b}$

treatment with nutrient b

yield in treatment b

treatment with nutrient a + b

 y_{ab} yield in treatment in which nutrient a and b have been combined.

type of interaction: synergism (S), Liebig-synergism (L-S), antagonism (A), approximately zero-interaction (add.), no effect (n.e.). A negative effect, $y_0 > y_{ab}$ (neg.), is difficult to categorize. Pratio

 $(y_{ab}/y_o) (y_{a}/y_o \times y_b/y_o)^{-1}$. In case there is a positive effect on yield of treatment a+b then synergism if the ratio >1, antagonism if ratio <1. $^{\circ}$ Ty

type of study: field study (F), hydroponic study (H), and greenhouse study with soils, or purified sand, in pots (G).