REVIEW ARTICLE

Crop response to nitrogen-phosphorus colimitation: theory, experimental evidences, mechanisms, and models. A review

Mounir Seghouani[1,2,3] · Matthieu Nicolas Bravin[2,3] · Alain Mollier[1]

Abstract

Crops need adequate mineral nutrition to ensure optimal growth and yield. Nitrogen (N) and phosphorus (P) are two major elements that are essential for crop growth. However, situations of N-P colimitation are frequent in agroecosystems. Hence, our ability to optimize crop production under these conditions depends on our ability to analyze and predict the response of crops to colimitation. Traditionally, agronomists rely on the law of the minimum (LM) to manage colimitation situations. This law states that crop growth is constrained by the most limiting element. In contrast, the multiple limitation hypothesis (MLH) argues that crops can adapt by balancing their resource allocation with the best compromise to maximize their growth. These two hypotheses result in contrasting growth response patterns. The aim of the present review is to identify the crop response pattern to N-P colimitation through an assessment of experimental results against a conceptual framework and to report the main mechanism involved in this interaction. Finally, an inventory of existing crop models handling N-P colimitation is presented and possible ways of improvement are proposed. This review allowed us to (1) remind of the published theories used to classify colimitation types, (2) highlight the fact that a large range of crops mostly showed MLH-response patterns, (3) report that the variability in crop response patterns is linked to pedoclimatic variation, (4) identify multiple mechanisms that may be involved in plant adaptation to N-P colimitation, (5) suggest that the interplay between the different mechanisms results in complex responses that are difficult to understand experimentally, (6) report that few models handle N-P colimitation and that most of them rely on the law of the minimum, and (7) recommend possible ways to improve model formalization for a better simulation of crop responses under N-P colimitation.

Keywords N and P trade-offs · Nutrient interactions · Liebig's law · Multiple limitation hypothesis · Soil-crop model · Yield response · Crop nutrition · Fertilization experiments

Contents

✉ Alain Mollier
alain.mollier@inrae.fr

1 UMR1391 ISPA, Bordeaux Sciences Agro, INRAE, F-33140 Villenave-d'Ornon, France

2 CIRAD, UPR Recyclage et Risque, F-34398 Montpellier, France

3 Recyclage et Risque, Univ Montpellier, CIRAD, F-34398 Montpellier, France

INRAE ⊘ Springer

1 Introduction

Nitrogen (N) and phosphorus (P) are considered the first and second most important elements in crop nutrition, respectively (Balemi and Negisho 2012). However, both elements have marked differences. N is considered a mobile and available element, especially its nitrate form (Marschner 1995). In contrast, P is viewed as a poorly mobile element (Balemi and Negisho 2012), as it is strongly sorbed to the soil solid phase (Penn and Camberato 2019). Accordingly, the P concentration in soil solution and the overall P availability in soil are usually low (Ziadi et al. 2013). As a consequence of low P availability, the transfer of P in the rhizosphere is mostly driven by the diffusion process (Hinsinger et al. 2011), while that of N is mainly driven by mass flow. At the plant scale, the uptake of N is mainly driven by the root uptake capacity, while the uptake of P is mainly driven by its soil availability (Rengel 1993). Hence, root growth and exploration are important for the uptake of both elements, but are of greater importance for P nutrition. N is often considered to have a preferential status among nutrients. This is because it is the nutrient that the plant needs the most, and the soil N supply is often suboptimal. The essential role of P and the fact that it cannot be substituted by N make us consider N-P colimitation (Rubio et al. 2003).

According to recent ecological studies, N and P colimit production in many ecosystems, including aquatic and terrestrial ones, with ecosystem responses to N and P colimitation tending to be mainly synergistic (Elser et al. 2007; Harpole et al. 2011). Many agrosystems exhibit a lack of N and/or P, which may lead to crop growth limitations (Vitousek et al. 2010; Guignard et al. 2017). To address N and P limitations, agricultural practices rely mainly on fertilizers (Tilman et al. 2002), which may lead to agronomic, economic, and environmental issues. Economic and environmental issues include poor economic profitability due to the low use efficiency of N and P from fertilizers (Hinsinger et al. 2011) and the depletion of nonrenewable P reserves (Vance et al. 2003; Cordell and White 2014), leading to an increase in the price of fertilizers (Lemaire et al. 2008; Srivastava et al. 2021), eutrophication due to both N and P transfer from soil excess to water resources (Edwards and Withers 1998; Di and Cameron 2002), N_2O emissions that contribute to global climate change (Hassan et al. 2022), an overall reduction in biodiversity (Guignard et al. 2017), disturbance of soil biota (Srivastava et al. 2021), and more generally, deterioration of N and P cycles for which variables control of planetary boundaries reaches high-risk levels (Steffen et al. 2015). From an agronomic perspective, an imbalance in the application of N vs P by fertilization practices has emerged (Vitousek et al. 2010). This greatly impacts on the ecosystem balance and especially on species competitiveness (Elser et al. 2010; Peñuelas et al. 2013).

While many studies have approached the objective of reducing N and P inputs to agroecosystems by fertilization, a common shortcoming is that N and P are often studied separately (Sumner and Farina 1986). However, as two strong drivers of crop responses that may interact with each other, N and P should be studied concomitantly. In addition, research on crop responses has traditionally relied on the law of the minimum (Paris 1992). However, the reported strong interactions between N and P cycles challenge the LM theory (Fageria 2001). These N and P interactions should be accounted for to reach optimal yields in both high- and low-input systems (Probert 2004; Aulakh and Malhi 2005).

Addressing the issue of N-P colimitation is complex by design. To be successful, the analysis of N-P colimitation should be based on a clear typology to understand and compare crop responses (Harpole et al. 2011), to understand the interactions of biogeochemical cycles (Marklein and Houlton 2012), and to ensure that the developed models are able to simulate both the crop responses and the involved processes. This is particularly relevant for soil-crop models, which are well-adapted tools to study the effect of agricultural practices and, notably, fertilization on crop nutrition and growth response patterns. Water and N uptake and responses to their shortages were the first processes included in these soil-crop models (Seligman and van Keulen 1980). However, the current development of formalisms able to model the P cycle in agroecosystems (Das et al. 2019; Hinsinger et al. 2011; Mollier et al. 2008) and their integration in models that already include N formalisms (Jones et al. 1984; Daroub et al. 2003; Delve et al. 2009) fuel the quest for concomitantly modeling the N-P colimitation and N×P interactions.

This review aims to summarize the current knowledge on N-P colimitation in agroecosystems and identify possible knowledge gaps. To do so, we will (1) recall the typology that could be used to differentiate and characterize the types of colimitation, (2) identify from N×P fertilization trials the crop response patterns to N-P colimitation (3) identify the main mechanisms that may explain such response patterns, and (4) make an inventory of crop models handling both N and P and the associated formalisms (Fig. 1).

2 Theory on nutrient colimitation and nutrient interactions in crops

It is well known that nutrient deficiency is a major constraint on plant growth and yield production (Lobell et al. 2009). To overcome this issue, agronomists have conducted experiments and studies designed to determine optimal fertilization rates (e.g., Nyiraneza et al. 2021). Field trials mostly tackle only one nutrient at a time. Agronomists vary the rate
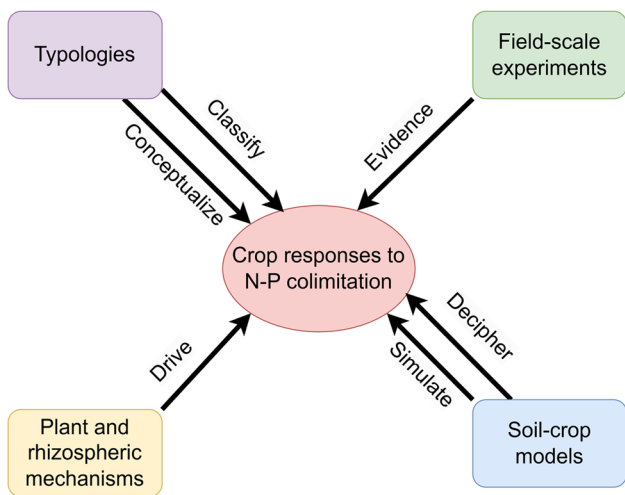
Fig. 1 Different aspects and interactions of the N-P colimitation study and how they help understanding this phenomenon.

of their nutrient of interest while providing the other elements in sufficient quantities so that the latter are not limiting (Fageria 2001). Agronomists conceptually interpret crop responses with one of the two following laws, i.e., the law of the minimum (LM) or the multiple limitation hypothesis (MLH). Hereafter, we present the main theories, concepts, and classifications of crop colimitations. We define a colimitation as a situation where the crop is submitted to at least two nutrient deficiencies at the same time.

2.1 Conceptual background

According to the LM, the crop responds to only one nutrient at a time, the one being the most limiting element. Therefore, other elements do not affect the response of the crop even

if their supply is insufficient as long as there is an element that is even more limiting. This theory remains the simplest way of formalizing crop colimitation (Ågren et al. 2012).

In contrast, the MLH states that being limited by several elements at the same time is the normal state for plants. It is based on a cost−benefit analysis and assumes that plants balance their resources (e.g., light, water, nutrients) in such a way that they become simultaneously limited by several resources at once. Hence, the plant adjusts its physiological and morphological traits in a way that optimizes the acquisition of the most limiting resources. Ultimately, this strategy is aimed at maintaining or maximizing its growth in the context of the plant facing multiple limitations (Vitousek et al. 2010; Chapin et al. 1987; Gleeson and Tilman 1992; Rubio et al. 2003).

The differences in resource allocation strategies between the two theories result in contrasting growth response patterns, as shown in Fig. 2. As per the theory, plant growth responds only to the most limiting nutrient when following the LM. In contrast, plants respond to either of the nutrients when following the MLH. Overall, plant growth is always higher when considering the MLH. However, a high level of input may lead to a negative response and a yield decrease.

MLH has shown applicability in handling colimitation between carbon and most of the nutrients by involving mechanisms such as shoot-to-root ratio balancing (Chapin et al. 1987; Rubio et al. 2003). This is notably the case for nutrients such as P and N, but it is, however, noteworthy that it does not apply to potassium (Hermans et al. 2006). Its use to explain colimitation between nutrients remains uncertain (Ågren et al. 2012). This is mostly because some mechanisms involved in resource acquisition (e.g., enhanced root growth) are the same for all nutrients. This may imply that more complex interactions exist between nutrients and could validate

Fig. 2 Theoretical growth response patterns as a function of nutrient supply in the case of two limiting nutrients (A and B). The curves show growth response predictions for a single limitation (green) and a multiple limitation following either the law of the minimum (blue) or the multiple limitation hypothesis (orange) (adapted from Rubio et al. 2003).
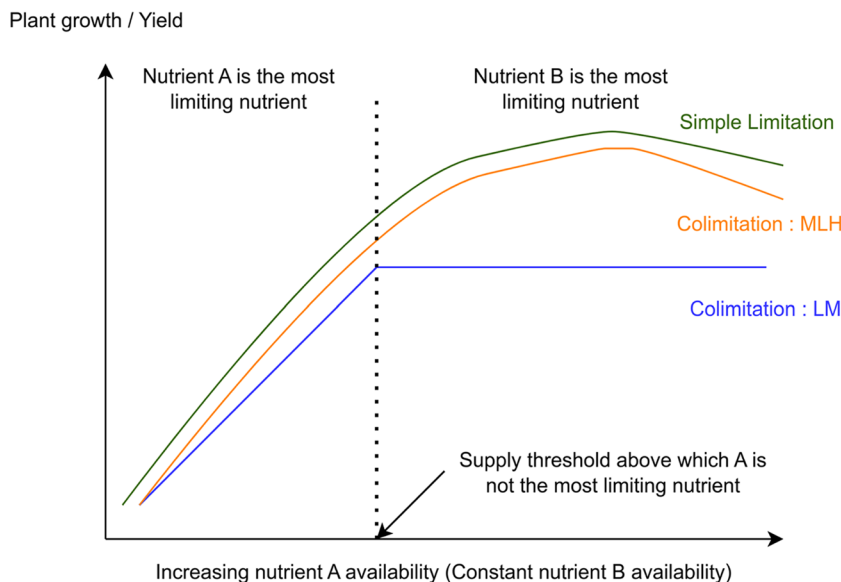
the application of this theory for nutrient colimitation. Evidence of an interplay between nutrients has been reported in the literature (Ågren et al. 2012). These interactions, which may be synergistic or antagonistic (Rietra et al. 2017), would influence the uptake mechanisms and the use efficiency of the related nutrients by the plant (Fageria and Oliveira 2014). This will therefore impact crop responses and ultimately fertilization management. However, due to the small number of field trials involving multiple nutrient limitations, these interactions are often overlooked (Sumner and Farina 1986). The existence of such interactions may support the idea that plant growth response patterns may be more complex than a simple application of the LM, which remains nonetheless a good first approximation (Ågren et al. 2012).

2.2 Typology

Harpole et al. (2011) established a typology to categorize the different types of colimitation. This classification has been developed for a wide spectrum of situations, including natural and marine ecosystems. Its application to agrosystems may be a great opportunity to learn from cross-disciplinary thinking. The typology proposed by Harpole et al. (2011) is presented in Fig. 3 and is compared to simple limitation (a), which is characterized by a response to the limiting nutrient only (A in Fig. 3). The colimitation induced by nutrients A and B can then be subdivided into three categories. The *serial limitation* (b) is characterized by a plant response to only the single supply of the most limiting resource (A in Fig. 3) and by an enhanced response following the supply of both A and B. This category is very similar to what Rietra et al. (2017) define as "Liebig-Synergism." S*imultaneous colimitation* (c) is characterized by a lack of response to a single nutrient supply but by a response to both A and B supply. Simultaneous and serial limitations are synergistic by design. Finally, the *independent colimitation* (d) is characterized by a plant response to each nutrient (A or B) independently and by an additive, synergistic (i.e., super-additive), or antagonistic (sub-additive) response to both A and B supply.

Figure 3 shows that the different categories differ not only in their response to nutrient inputs but also in the interpretation of the origin of the growth response. For the independent colimitation, the effect of A+B supply is clearly subdivided between the effects of A, B, and A×B interaction. In contrast, for the serial and simultaneous limitations, it is unclear whether the additional response to A+B supply is an effect of A×B interaction or an alternative alleviation of A then B limitation, as proposed by Davidson and Howarth (2007).

While several papers use these two typologies (i.e., the LM-MLH and the simple/colimitation), they are mostly used separately, as they address the question from two different points of
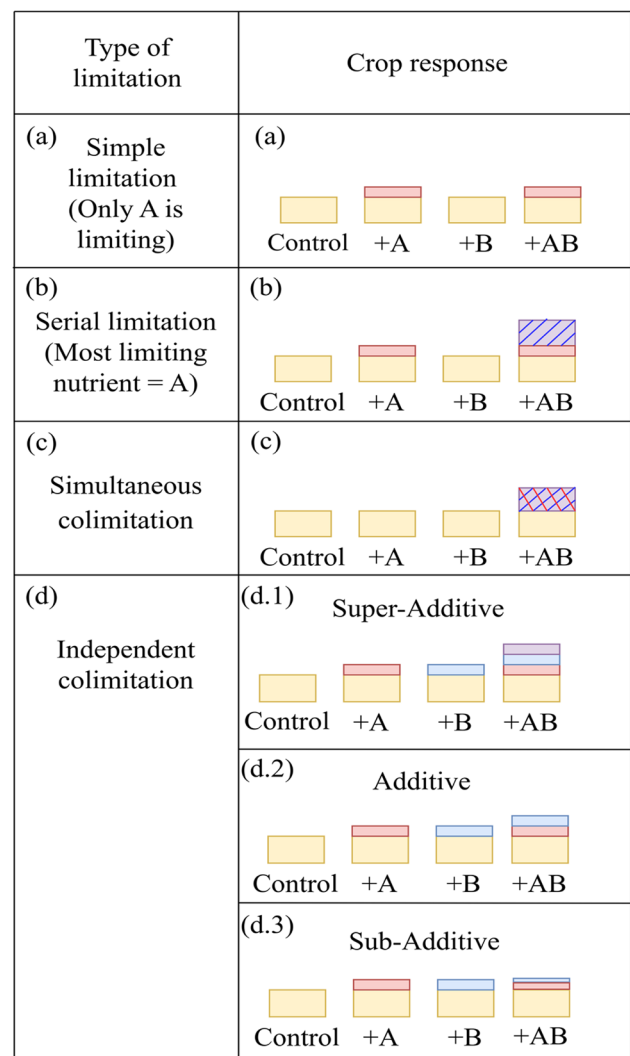
Fig. 3 Typology of crop colimitation compared to single limitation in the case of two limiting nutrients (A and B). Red, blue, and purple colors represent crop responses for A, B, and A×B interactions, respectively (adapted from Harpole et al. 2011).

view. The LM-MLH typology focuses on the response curve to a single nutrient addition, while the typology of Harpole et al. (2011) is based on a comparison of crop response between single and dual nutrient supplies. Some papers have tried to link these two classifications. This includes the resemblance between both definitions of serial limitation and that of the LM (Harpole et al. 2011). Similarly, simultaneous colimitation can be considered an application of LM under a very strict nutrient ratio where the degree of deficiency is equivalent for both nutrients (Ringeval et al. 2021) or if we consider the group of equally limiting resources as a single resource (Harpole et al. 2011). Consequently, the serial and simultaneous colimitations are applications of the LM, while the definition of independent colimitation is more in line with the MLH. This highlights the fact that demonstrating the presence of an independent

colimitation of crop growth by two nutrients invalidates the relevance of LM in this colimitation context. While these typologies may apply in principle to all nutrient interactions, it may be difficult to generalize a given typology and even more so a type of interaction to all possible nutrient interplays. Accordingly, Rubio et al. (2003) show that the crop response depends on the two nutrients involved and consequently propose to study each pair of nutrients specifically. They further suggest that the plant response patterns to colimitation are not symmetrical, i.e., the response may follow the MLH or the LM depending on which of the two nutrients is the most limiting.

Another study conducted by Ågren et al. (2012) compared LM and MLH formalisms to simulate crop responses to colimitation. They found that the transition between limiting elements is smoother than the fixed threshold proposed for the LM and that the growth optimum would be represented by an interval rather than by a single nutrient ratio, as proposed by Güsewell (2004). In the case of more severe deficiencies, crop responses will follow the LM (Ågren et al. 2012). This suggests that the degree of stress influences the crop response pattern to colimitation.

Based on these evidences, we suggest that the study of crop response to colimitation should be performed for each nutrient pair with a gradient of availability of the two nutrients so that the nature of the most limiting nutrient and the degree of stress vary sufficiently. It is also important to identify the mechanisms involved in the crop response to colimitation, particularly when the pattern follows the MLH. This mechanistic understanding allows not only to support the theory but also to understand, quantify, and anticipate the crop response.

3 Experimental evidences of crop responses to nitrogen-phosphorus colimitation

Agronomists have been interested in determining the optimal N and P supply to ensure maximum plant growth. They have found that both elements undergo a dilution effect during biomass accumulation, resulting in a decrease in the element concentration (Lemaire et al. 2019). Hence, a strong correlation exists between plant N and P that could be described by a linear relation (Nyiraneza et al. 2021). This relationship reflects the evolution of the N:P ratio, which decreases during the growth of the crop as the dilution of N is more pronounced (Greenwood et al. 2008). Recent studies show that the crop P dilution curve and P nutrition status may be affected by a deficiency in N (Ziadi et al. 2007; Bélanger and Ziadi 2008). Hence, the nutrient status of N seems to affect that of P, which may greatly influence the diagnosis of deficiencies and the reasoning for fertilization. Therefore, N-P colimitation seems an interesting and agronomically relevant

case to study crop responses to colimitation due to the importance of taking into account the nutrient status of both elements in determining crop needs and responses.

3.1 Analysis of field evidences

Many experiments have been carried out with the intention of verifying the presence or absence of synergy in response to N and P addition. In their review, Aulakh and Malhi (2005) mostly reported synergistic responses in studies conducted on a large set of conditions and crops, including sorghum, sesame, cotton, cucumber, and peas. They showed the high variability of this N×P synergy, which was responsible for 13 to 89% of the yield response of cereals to combined N and P input. Under certain conditions, they even reported that the interaction effect could overshadow the effects of both N and P alone. However, this did not prevent them from finding additive crop responses under certain conditions for crops such as sunflower or linseed.

Few authors have been interested in verifying the validity of the LM and MLH theories by comparing experimental results to theoretical crop response patterns, and most trials do not refer explicitly to the typology of colimitation. The only exception that we found was the work of Paris (1992), who analyzed a fertilization trial under field conditions on maize subjected to different N and P fertilizer doses. They found that the application of the LM allowed us to better explain the response patterns than curves with smoother transitions. As we cannot generalize on the basis of one study, we believe that these results should be confirmed for other crop species and conditions by using factorial N×P experimental protocols. These trials should be run under field conditions, as the results of greenhouse experiments may differ from those of field trials. This is largely explained by the uncontrolled factors that are not found under greenhouse conditions (Sumner and Farina 1986). Furthermore, it is important to highlight the importance of the initial level of the nutrient in the soil which affect heavily the crop responses to fertilizer inputs (Serme et al. 2018; Abdissa et al. 2011). Consequently, a pre-requisite to these trials would be an insufficient soil nutrient supply that would allow a response to nutrient inputs.

We reviewed on January 2023 the results of N-P factorial field trials that share enough data to study the characteristics of N-P colimitation (Table 1).

We searched in Google Scholar and Web of Science for fertilization studies involving both N and P. Keywords included "nitrogen," "phosphorus," "crop responses," "fertilizer rates," "fertilizer crop response," "yield response," "growth response," "fertilizer level," "fertilizer level," and "response curve." We selected only studies that fulfilled certain conditions, including (1) only field trials, (2) factorial

inputs of both N and P fertilizers subjected to the same agricultural practices (irrigation, pesticides, etc.) and other nutrients supplied in sufficient amounts, (3) presence of the response (i) to both N and P separately, or (ii) to one nutrient only but with a significant N×P interaction and that in order to avoid situations of single limitations (Fig. 4), and (4) informations on the effects of N, P, and N×P interaction. Data were treated by considering biomass accumulation first then grain yield to identify the crop response pattern and colimitation type. For the case of multisite and multiyear experiments, we considered that a significant response in only 1 year or one site is sufficient to consider the effect. Overall, 32 fertilization trials were considered, covering a substantial number of crop species and botanical families. Growth response pattern, MLH or LM, and type of colimitation were recorded.

We compared the results of the field trials to both the LM/MLH theories and the classification of colimitation proposed by Harpole et al. (2011). We considered that the LM applies when the crop responds to only one element with a significant interaction. In contrast, if the crop responds to both elements independently, the MLH applies. For MLH cases, we used the significance of the N×P interaction to reveal a synergistic (super-additive) or antagonistic effect (sub-additive). The absence of the N×P effect for the MLH cases was interpreted as a simple additivity. Figure 4 summarizes the way we classified the different situations, while Fig. 5 shows concrete examples from the reviewed studies for each of the reported colimitation types. The results are synthetized in Fig. 6.

While the studied experiments used crops from several botanical families with different photosynthetic pathways and contrasting nutrient requirements (e.g., wheat, maize, tomato, faba bean, kale), nearly all of them responded to both N and P independently (84% of the studied cases), which indicates an MLH growth response pattern (Fig. 6). Additionally, the N×P interaction was in most cases (63%) significant (Fig. 6). In accordance with the growth response pattern, the colimitation type was most often of the independent type (84%), with 41% of super-additive (synergistic) response, and 37% of additive response. In two studies (6%), we found contrasting results depending on the fertilizer levels, where colimitation was super-additive at low levels of input but sub-additive at high levels of input (Fig. 6). The latter coincides with a negative yield response. Notably, simultaneous limitations were not observed.

The diversity of the studied crops (Table 1) shows that these findings are not restricted to a few species only. For example, trials on potato showed that both total and marketable tuber yields responded to N and P and that the N×P interaction was significant (Zewide et al. 2012; Nekinikie and Dechassa 2018). The response of potato yield to N, P, and N×P remained significant despite a significant effect of crop

cultivar (Nekinikie and Dechassa 2018). In parallel, during the last 19 years of a 50-year-field experiment on maize, 20% of the yield increase was attributed to P alone vs a 103% yield increase with N alone, while the addition of both N and P resulted in a 225% yield increase compared to the unfertilized control (Schlegel and Havlin 2017). These results mean that 102% of the increase in maize yield was due to the effect of the N×P interaction. It remains important to study more crops' responses to N and P addition across contrasting pedo-climatic conditions to generalize these findings.

When considering the response of legumes to N and P fertilization, it was found that the effects of N, P, and N×P interaction were all significant on faba and mung bean yield as well as its components, including the number of pods per plant and the 100-kernel weight (Adak and Kibritci 2016; Yin et al. 2018). The effect of the N×P interaction was especially marked at high N fertilizer levels, which fuels the assumption that the N×P interaction is more important at higher yields (Aulakh and Malhi 2005; Yin et al. 2018). In contrast, N×P fertilization trials on common bean showed that the crop responded equally well to N and P, while the N×P interaction was not significant in most cases, except for 1 year and on one site (out of two sites × 2 years) (Chekanai et al. 2018). This example interestingly illustrates that the crop response can follow the MLH without being synergistic or antagonistic.

In addition to the works presented above, we found some works that we could not analyze but that present valuable information. For example, 11 field trials for two brassicas crops, namely, kale and pasja, showed that crops responded mainly to both N and P and with a significant N×P interaction (Wilson et al. 2006). Hence, this result supports the MLH. Zingore et al. (2022) analyzed previous studies of the yield response of maize to nutrient omissions in contrasting soil conditions in Sub-Saharan Africa. They found that the starvation of either N or P resulted in a significant yield reduction in 89 and 78% of cases for N and P, respectively. In most cases, the N supply was responsible on average for a yield response twice as high as the P supply. Zingore et al. (2022) found similar results with rice which responded to N and P starvation regardless of the water management (irrigated lowland, rainfed lowland, and rainfed upland).

Globally, a tendency can be noted, which is that crops respond mostly to both N and P independently, which is consistent with the MLH response pattern. While we found some cases of LM responses, it was most often due to an absence of response to P, implying that N is the most limiting element. We reported only one case of LM-type with an absence of response to N to which the crop seems to be able to respond under nearly any conditions. This seems to be in agreement with the literature, which shows that the effect of P input on N is less marked than that of N on P (Sumner and Farina 1986; Aulakh and Malhi 2005), and this seems

Table 1 Summary of the reviewed fertilization trials including crop name and botanical family, reported responses to N, P and NxP inputs, the type of crop response pattern (LM/MLH) and colimitation type we found for each case, as well as the reference of the associated article. In this table, I-A stands for Independent additive, I-Sup-A and I-Sub-A stand respectively for Independent super-additive and Independent sub-additive, and S-N and S-P stand respectively for Serial N and Serial P

Crop	Scientific name	Botanical family	N response	P response	NxP effect	Growth response pattern	Type of colimitation	Reference
Tomato	*Lycopersicum esculentum* L.	Solanaceae	Yes	Yes	No	MLH	I-A	Abu-Alrub et al. (2019)
Barley	*Hordeum vulgare* L.	Poaceae	Yes	Yes	No	MLH	I-A	Al-Ajlouni et al. (2010)
Kale (site 2)	*Brassica oleracea* var. acephala	Brassicaceae	Yes	Yes	No	MLH	I-A	Chakwizira et al. (2009)
Swede (site 2)	*Brassica napus* subsp. napobrassica	Brassicaceae	Yes	Yes	No	MLH	I-A	Chakwizira et al. (2011)
Common bean	*Phaseolus vulgaris* L.	Fabaceae	Yes	Yes	No	MLH	I-A	Chekanai et al. (2018)
Wheat	*Triticum aestivum* L.	Poaceae	Yes	Yes	No	MLH	I-A	Girma et al. (2007)
Rice	*Oryza sativa* L.	Poaceae	Yes	Yes	No	MLH	I-A	Serme et al. (2018)
Potato	*Solanum tuberosum* L.	Solanaceae	Yes	Yes	No	MLH	I-A	Setu and Mitiku (2020)
Groundnut	*Arachis hypogaea* L.	Fabaceae	Yes	Yes	No	MLH	I-A	Tekulu et al. (2020)
Sorghum	*Sorghum bicolor* L. Moench	Poaceae	Yes	Yes	No	MLH	I-A	Wang et al. (2017)
Potato	*Solanum tuberosum* L.	Solanaceae	Yes	Yes	No	MLH	I-A	Zewide et al. (2012)
Canola	*Brassica napus* L.	Brassicaceae	Yes	Yes	No	MLH	I-A	Nuttall et al. (1992)
Canola	*Brassica napus* L.	Brassicaceae	Yes	Yes	Yes	MLH	I-Sup-A	Brennan and Bolland (2009)
Wheat	*Triticum aestivum* L.	Poaceae	Yes	Yes	Yes	MLH	I-Sup-A	Brennan and Bolland (2009)
Kale (site 1)	*Brassica oleracea* var. acephala	Brassicaceae	Yes	Yes	Yes	MLH	I-Sup-A	Chakwizira et al. (2009)
Alfalfa	*Medicago sativa* L.	Fabaceae	Yes	Yes	Yes	MLH	I-Sup-A	Fan et al. (2016)
Maize	*Zea mays* L.	Poaceae	Yes	Yes	Yes	MLH	I-Sup-A	Getnet and Dugassa (2019)
Safflower	*Carthamus tinctorius* L.	Asteraceae	Yes	Yes	Yes	MLH	I-Sup-A	Golzarfar et al. (2012)
Buckwheat	*Fagopyrum esculentum* Moench	Polygonaceae	Yes	Yes	Yes	MLH	I-Sup-A	Ullah et al. (2012)
Maize	*Zea mays* L.	Poaceae	Yes	Yes	Yes	MLH	I-Sup-A	Kamanga et al. (2014)
Potato	*Solamum tuberosum* L.	Solanaceae	Yes	Yes	Yes	MLH	I-Sup-A	Nekinike and Dechassa (2018)
Egusi melon	*Citrullus lanatus* (thunb.) Mansf	Cucurbitaceae	Yes	Yes	Yes	MLH	I-Sup-A	Olaniyi et al. (2008)
Maize	*Zea mays* L.	Poaceae	Yes	Yes	Yes	MLH	I-Sup-A	Schlegel and Havlin (2017)
Sorghum	*Sorghum bicolor* (L.) Moench	Poaceae	Yes	Yes	Yes	MLH	I-Sup-A	Schlegel and Havlin (2021)
Mung bean	Vigna radiata L.	Fabaceae	Yes	Yes	Yes	MLH	I-Sup-A	Yin et al. (2018)

INRAⱭ ⬚ Springer

Table 1   (continued)

Crop	Scientific name	Botanical family	N response	P response	N×P effect	Growth response pattern	Type of colimitation	Reference
Tef	*Eragrostis* tef (Zuccagni) Trotter	Poaceae	Yes	Yes	Yes	MLH	I-Sup-A (Low Input) / I-Sub-A (High Input)	Dereje et al. (2018)
Faba bean	*Vicia faba* L.	Fabaceae	Yes	Yes	Yes	MLH	I-Sup-A (Low Input) / I-Sub-A (High Input)	Adak and Kibritici (2016)
Kale (site 3)	*Brassica olerace*a var. acephala	Brassicaceae	Yes	No	Yes	LM	S-N	Chakwizira et al. (2009)
Swede (site 1)	*Brassica napu*s subsp. napobrassica	Brassicaceae	Yes	No	Yes	LM	S-N	Chakwizira et al. (2011)
Sesame	*Sesamum indicum* L.	Pedaliaceae	Yes	No	Yes	LM	S-N	El Mahdi (2008)
Globe artichoke	*Cynara cardunculus* L. var. scolymus (L.) Fiori	Asteraceae	Yes	No	Yes	LM	S-N	Ierna et al. (2006)
Wheat	*Triticum aestivum* L.	Poaceae	No	Yes	Yes	LM	S-P	Takahashi and Anwar (2007)

to confirm the assumption of nutrient interactions being nonsymmetrical. However, this tendency does not apply to legumes, which mostly show MLH-type responses regardless of the most limiting nutrient.

3.2 Effect of climatic and soil conditions on between-site variations

Despite the clear tendency evidenced above, the literature review further showed that the crop response to N and P availability varies substantially from one field trial to another. Differences between responses across the different sites may be due to variations in soil nutrient availability (Abdissa et al. 2011; Serme et al. 2018) or the effect of a greater stress effect (e.g., water) which outperform the N and P effect (Chakwizira et al. 2009). The relative importance of climate and soil properties on the crop response to N and P may differ between crops and water management strategies (Zingore et al. 2022).

Many factors varying with time may affect the N×P interaction. These factors may be climatic, such as temperature or global radiation, edaphic, such as soil moisture and aeration, or linked to the genetic and physiological specificity of the plant, such as its age, phenology, growth rate, root plasticity, and shoot-to-root ratio (Fageria 2001; Aulakh and Malhi 2005). In addition to uncontrolled factors, we found that

several technical choices may affect crop nutrition, such as the mode of application, the type of fertilizer, its dose, and the splitting of the dose, which are variable from one trial to another. This variability can affect the results of the trial and our ability to compare the different works between them. This is particularly relevant for N, for which the nutrient status of the plant can be greatly affected by the number and timing of applications. Therefore, to ensure a better ability to compare and interpret the results, we recommend the adoption of homogeneous experimental designs.

Although the majority of the reviewed papers seem to indicate that the response of the crops to an N-P colimitation is of the MLH type, some studies showed that the crop responds to only one element at a time, which supports the application of the LM (Dai et al. 2010). However, some of these results can be interpreted as the soil already providing enough of the nutrients to which the crop is not responding. This hypothesis is supported by the fact that most of these studies consider the amount of N and P added with fertilizers rather than the resulting N and P soil availability. It is, however, well known that crops respond more to the latter (Wilson et al. 2006). Another hypothesis is that the plant is more limited by the plant's capacity to take up nutrients than by their availability in the soil. This hypothesis is more plausible for the lack of response to N than to P, since plant uptake is more limited by plant uptake capacity for N but is
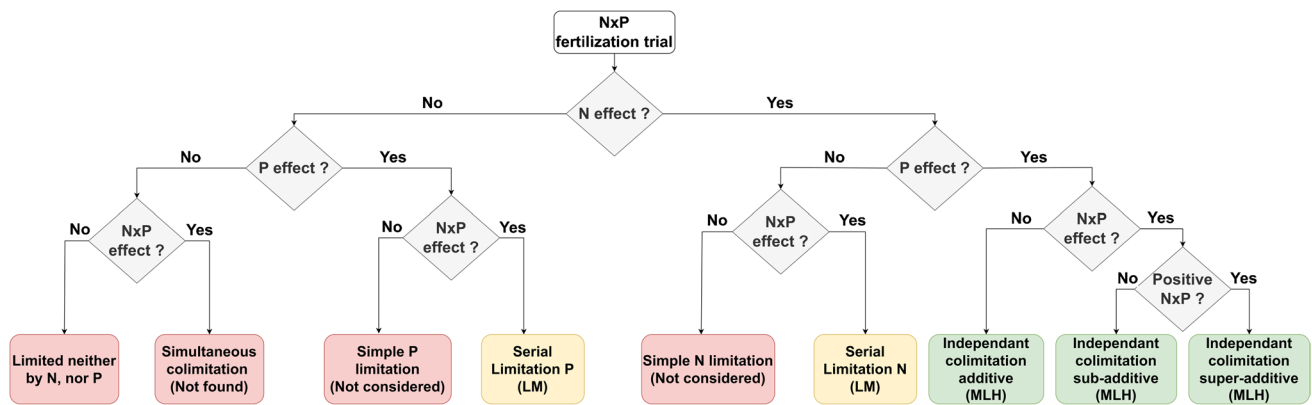
Fig. 4 Flowchart summarizing the successive steps used to classify the fertilization trials and to determine their crop response pattern (MLH/LM) and their type of colimitation. Green boxes stand for the MLH response pattern, yellow boxes for the LM response pattern, and red boxes for cases that are not reported or not considered in this review.

conversely more limited by low soil P availability (Rengel 1993). A third hypothesis is that nutrients other than N and P may constrain the response of crops (Aulakh and Malhi 2005). Accordingly, the few cases where the LM would work better than the MLH could be explained by the specificity of these case studies rather than by the adequation by the design of the crop response to the LM.

3.3 Effect of temporal variations

Setu and Mitiku (2020) and Serme et al. (2018) reported that crops may respond or not to P depending on the year. Nuttall et al. (1992) also found significant N × year and P × year interactions. This interyear variation was already reported by Aulakh and Malhi (2005) for the N×P interaction in a previous review, which found that the response could be highly synergistic or only additive from year to year. This variation may be explained by the weather effect (Nuttall et al. 1992).

Because of the interyear variation, long-term experimentation seems necessary to understand the N×P interaction, except that this may generate other confounding effects, such as long-term soil acidification and soil organic matter mineralization, which will in turn affect the interaction (Sumner and Farina 1986). During a 50-year experiment, Schlegel and Havlin (2017) reported few differences between yield response to N in the last 19 years compared to the first 31 years at 20 kg P ha^{-1}. However, they reported lower yields with 0 kg P ha^{-1}, and hence, the yield response to P addition increased over time, which they explained by the fact that indigenous soil P was depleted over time.

We have reached the same overall conclusions concerning the nature of the N×P interaction as previous reviews (Sumner and Farina 1986; Aulakh and Malhi 2005; Rietra et al. 2017), which is that N×P is mostly synergistic and sometimes additive. Additionally, we presented novel insights into the question of N-P colimitation by confronting experimental

results with a clear typology. We highlighted the fact that crops most often responded to both N and P. This allows us to state that the synergy of the N×P interaction is most often of the independent type and therefore that the crop response pattern to N-P colimitation probably follows the MLH. This does not prevent us from reporting works where the response follows the LM and therefore other types of colimitation, such as serial colimitation. We also reported that the extent of the response to N and P as well as the type of colimitation was affected by climatic and edaphic factors and was subjected to interyear variations. While we found that neither of the two formalisms could explain all of the possible situations, MLH seems to be the formalism that most adequately captures reality in most of them. Additionally, this formalism does not exclude some explanations of LM-like response patterns, as explained above. It remains to be determined which mechanisms can explain this behavior of the plant and to quantify to what extent the LM deviates from reality considering a large set of conditions to know if it is a feasible compromise to trade accuracy for simplicity.

4 Mechanisms of interaction between nitrogen and phosphorus

As mentioned above, crops respond by far to a N-P colimitation by following the MLH rather than the LM (Fig. 6). At the plant level, one of the mechanisms supporting this behavior is the direct substitution of a limited element by another with a similar physiological role (Saito et al. 2008). One example of that is the substitution of potassium by sodium (Battie-Laclau et al. 2013). However, this mechanism is not common between plant nutrients (Rubio et al. 2003). Typically N and P cannot be substituted by each other due to their respective specific role in plant physiology.
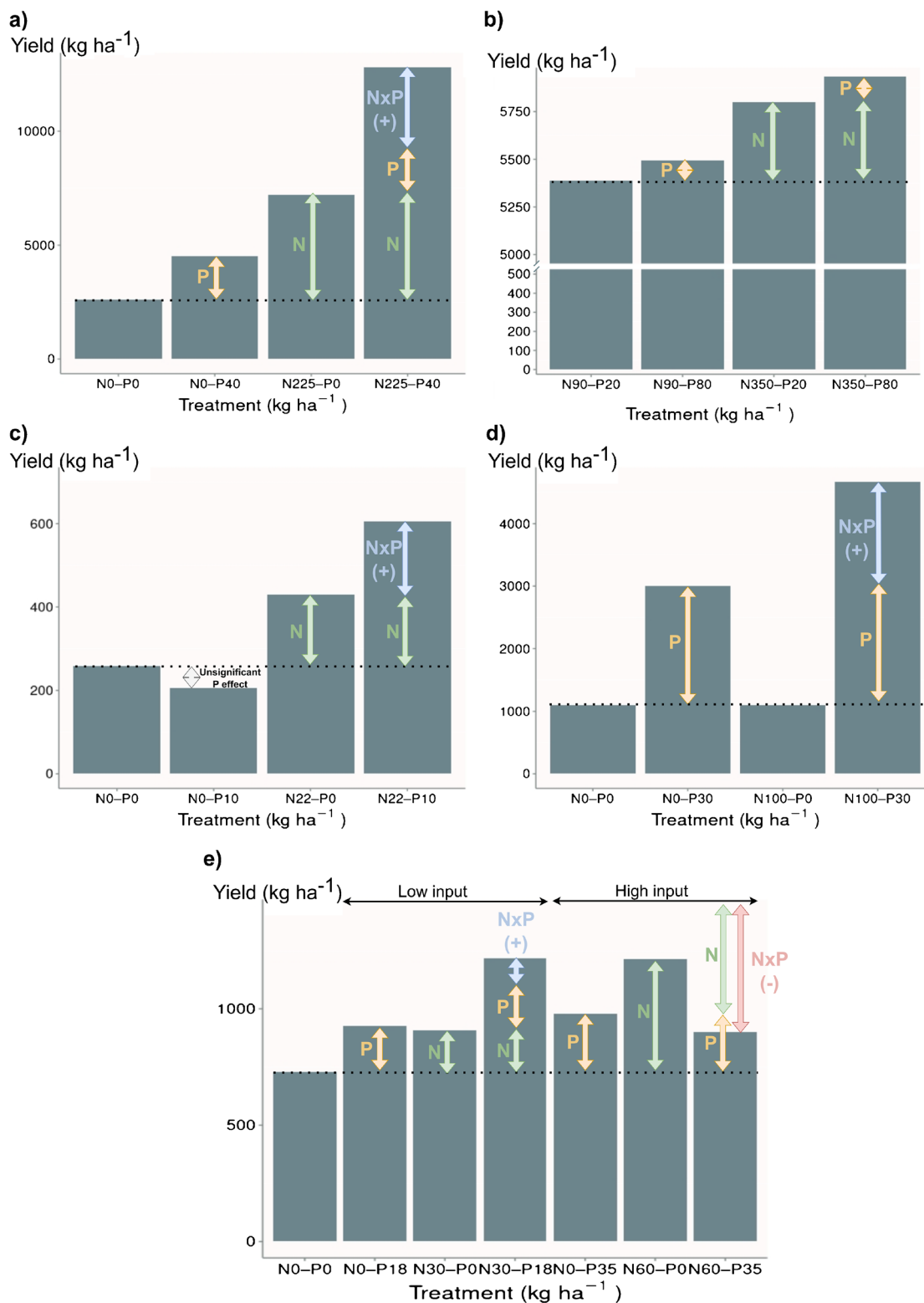
Fig. 5 Examples from the reviewed studies for all the reported cases of colimitation and crop response pattern: (**a**) Independent super-additive (MLH) - Maize (Schlegel and Havlin 2017), (**b**) Independent additive (MLH): Sorghum (Wang et al. 2017), (**c**) Serial N (LM): Sesame (El Mahdi 2006), (**d**) Serial P (LM): Winter wheat (Takahashi and Anwar 2007), (**e**) Independent super-additive (Low Input) - Independent sub-additive (High Input): Faba bean (Adak and Kibritci 2016). The examples show yields for different treatments as compared to control. Each example has treatments corresponding to control, P input, N input, and N×P input. The last example has two treatments for P input, N input, and N×P inputs as the crop behaved differently between low and high inputs. N and P effects are represented respectively by green and orange arrows. N×P effect is represented by either blue (+ positive) or red (− negative).

Agronomists rarely investigate the ecophysiological mechanisms behind the observed N-P colimitation in crops (Sumner and Farina 1986).

Although the mechanisms explaining the MLH-like response to N-P colimitation are still not fully understood, several mechanisms were described (Fageria 2001). These mechanisms have mainly been studied by ecologists in natural ecosystems, we can assume that their findings also apply, at least partly, to agroecosystems. Hereafter, we reviewed briefly the current knowledge on the mechanisms supporting the crop response patterns to N-P colimitation.

These mechanisms were subdivided into two categories. We define direct interactions by which plants invest N compounds directly to acquire P compounds and vice versa. We also consider indirect interactions by which one element influences the availability, uptake, or translocation of the other element through its impact on an intermediate variable, which in turn affects the other element. These direct and indirect mechanisms could occur both within the plant and its rhizosphere All the studied interactions are summarized in Fig. 7.

4.1　Nitrogen fixation and phosphatase secretion

A common example of direct interaction is symbiotic N_2 fixation in which the plant invests ATP (i.e., a P-compound) to acquire N (Schulze et al. 2006). Conversely, several crops can secrete phosphatase enzymes (i.e., N compounds) that hydrolyze organic P in the soil, thus increasing P availability in the soil (Marklein and Houlton 2012). Symbiotic N_2 fixation processes are specific to legume crops only, while a large range of crops appear to secrete phosphatases.

Concerning symbiotic N_2 fixation, plants have to invest 24 mol of P as ATP to fix 1 mol of N as N_2 (Schulze et al. 2006). P deficiency therefore affects symbiotic N_2 fixation (Schulze 2004). The addition of P fertilizer to soils characterized by a low N and P availability results in an enhanced nodulation and a higher nitrogenase activity (Leidi and Rodriguez-Navarro 2000; Kouas et al. 2008; Chekanai et al. 2018). This could explain that the N×P interaction is more complex for legume crops (Aulakh and Malhi 2005) and that legumes always presented a response to P addition contrary to nonlegumes in the reviewed studies (Fig. 6). Accordingly, nonlegume crops would exhibit response patterns to N-P colimitation closer to the LM than legumes when N is the most limiting nutrient.

Concerning acid phosphatase (APase) secretion, a meta-analysis conducted by Marklein and Houlton (2012) on a wide variety of terrestrial ecosystems showed the strong inhibiting effect of P and conversely the stimulating effect of N on APase activity (Fig. 7). Chen and Moorhead (2022) further reported in their meta-analysis that the positive effect of N addition on APase activity was significant only for the first 5 years.

Data about APase activity remain scarce, and hence, the actual P acquired per unit of N invested remains difficult to assess accurately (Marklein and Houlton 2012). Wang et al. (2007) estimated that crops invest approximately 30 mol of N to acquire 1 mol of P through APase secretion.

The literature mentions the existence of an upper threshold of soil N and P availability for both APase secretion and symbiotic N_2 fixation above which the mechanism and the related uptake of P and N are not stimulating anymore (Salvagiotti et al. 2008; Banerjee et al. 2012). At the other hand, if symbiotic N_2 fixation and APase secretion were the only mechanisms to be considered to explain N×P interactions, this would mean that each mechanism could be completely inhibited if the element to invest by the plant (e.g., N for APase secretion) was the most limiting. However, it is a matter of fact that the two mechanisms continue even under conditions of strong limitations on the element to invest (e.g., Pueyo et al. 2021; Marklein and Houlton 2012).

4.2　Impact of the indirect interactions between nitrogen and phosphorus

The literature points out several indirect mechanisms that may affect N-P colimitation. The form of rhizospheric N taken up by plants and its P nutrition statues affect the rhizosphere pH and subsequently P availability in the rhizosphere and P uptake by plants (Zeng et al. 2012; Hinsinger 2001; Rietra et al. 2017; Gérard 2016; Tang et al. 2001). While symbiotic N_2 fixation mainly aims at acquiring N, it tends to acidify the rhizosphere (Fig. 7) and hence to increase indirectly P availability in calcareous soils (Kouas et al. 2008; Alkama et al. 2012).

Additional complexity arises from interactions with other elements then N and P. Carbon (C) is notably involved in numerous mechanisms and the overall plant equilibrium. It is therefore refers to the C-N-P ratio in soil and plants (Achat et al. 2016). Examples of C-N-P balance in the plant are the trade-off in resource allocation between cluster roots and nodules (Thuynsma et al. 2014, Pueyo et al. 2021) and the symbiosis with mycorrhizae (Marschner and Dell 1994; Dotaniya and Meena 2015; Allen et al. 2020). This C-N-P trade-off is more generally illustrated by the fact that the plants adjust their shoot-to-root ratio with consequences on the C/N and C/P ratios (Rubio et al. 2003).

Root growth and plasticity are another explanation for the indirect effect between N and P nutrition. It is however considered that the root architecture is more important for a poorly mobile element in soil such as P than for N (Hill et al. 2006; Rangarajan et al. 2018; Hadir et al. 2020). Qian and Schoenau (2000) proposed that the N effect on root growth
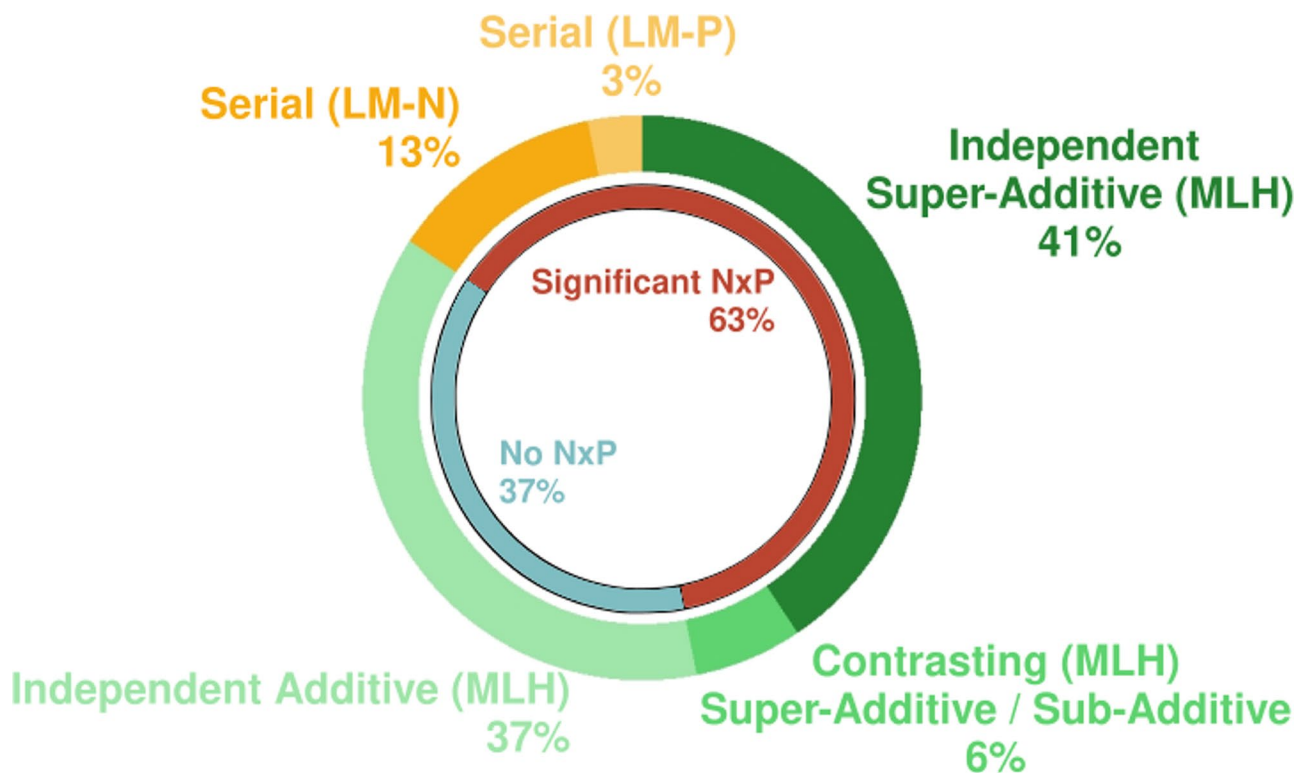
Fig. 6 Characteristics of the growth response pattern of crops in fertilization trials (*n* = 32; see Table 1). LM and MLH stand for the law of the minimum and the multiple limitation hypothesis, respectively. N, P, and N×P represent nitrogen, phosphorus, and nitrogen × phosphorus interactions, respectively. The typology of colimitation is given according to Harpole et al. (2011) (Fig. 3). The independent super- and sub-additive colimitation (contrasting) stands for field trials characterized by a super-additive colimitation at low N and P inputs and a sub-additive colimitation at high N and P inputs.

may improve P absorption through a better exploration of the soil.

In summary, a range of direct and indirect mechanisms are susceptible to be involved in N×P interactions (Fig. 7). Their integration within soil-crop models is however still a numerical challenge and a matter of debate to know whether it may effectively improve the predictive power of model outputs.

5 Nitrogen × phosphorus interactions and colimitation in soil-crop models

Regarding the complexity of the N×P interaction and the mechanism involved, soil-crop models could be a pertinent tool to guide research to fill knowledge gaps (Das et al. 2019). Their utilization is especially relevant to evaluate a greater number of drivers and processes at once compared to what can be done in field experiments. Soil-crop models are also of interest to promptly test a large range of agronomic practices (Hinsinger et al. 2011). The role of modeling approaches in investigating rhizospheric processes linked to P and N nutrition has already been proven (Kuppe et al.

2022). The integration of nutrient deficiencies within crop models started in the 1980s (Jones et al. 2017) and focused mainly on N assuming that other elements are supplied sufficiently, which is not an acceptable hypothesis in most conditions (Probert 2004). Most existing soil-crop models account for either N or P and consequently handle only one nutrient at a time (Zhang et al. 2007). Consequently, the N×P interaction and the question of its formalization have not yet received much attention. This delay in the consideration of the N×P interaction by the soil-crop models may be explained by (1) there is already a delay in the modeling of P uptake compared to N uptake (Das et al. 2019), (2) the integration of the P cycle in crop models is generally done by plugging a P module into an existing model focusing solely on the impact of the element on the crop or through the coupling with a model managing the N effect, leaving aside the possible interaction with other factors (e.g., Zhang et al. 2007), (3) there are few factorial datasets including the variations of two nutrients compared with those focusing on a single nutrient (Sumner and Farina 1986), which implies that it is easier to calibrate and evaluate one nutrient limitation model compared with multiple nutrient limitation
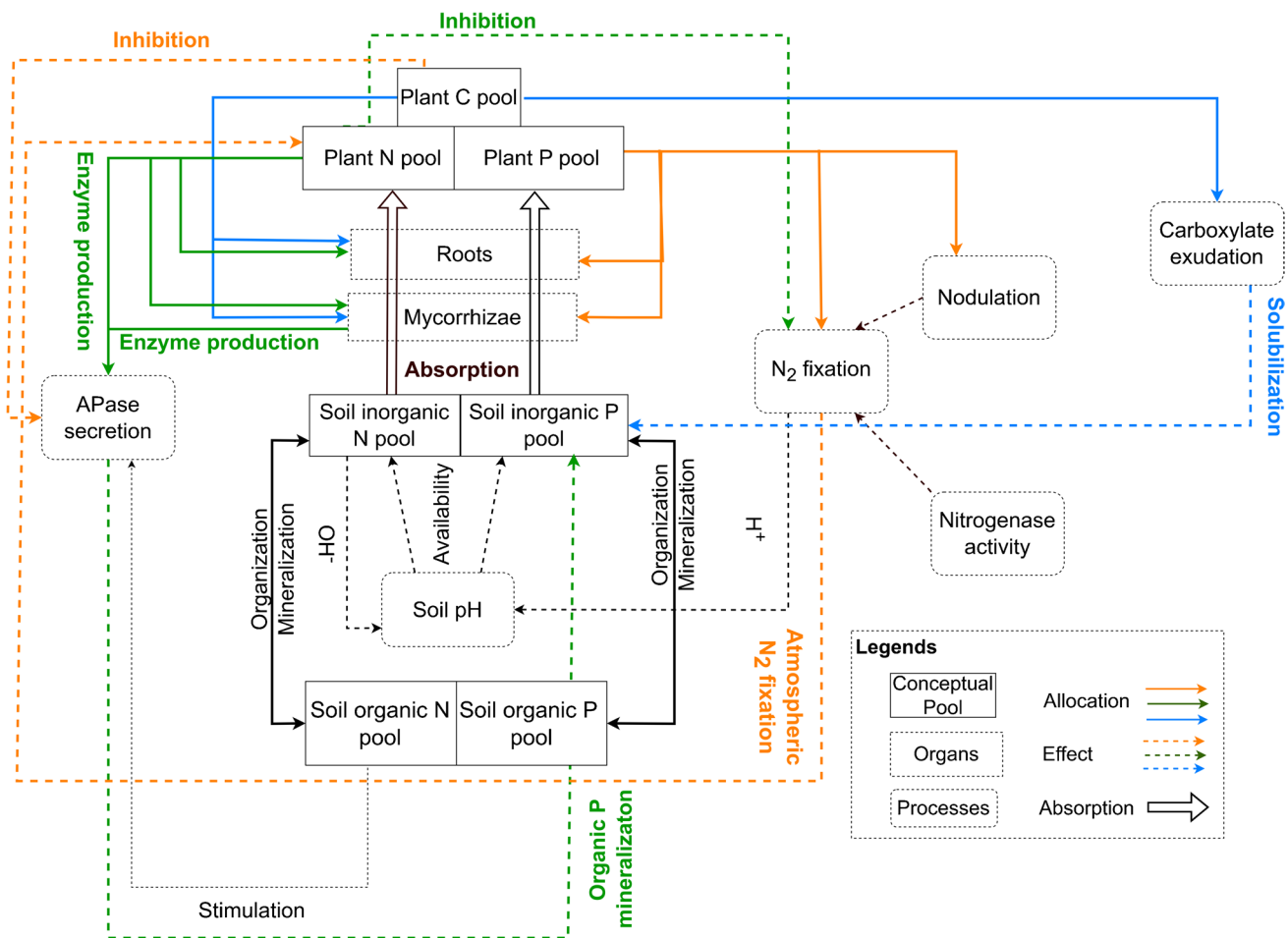
Fig. 7 Schematic representation of mechanisms involved in N and P acquisition and N×P interactions in the soil−plant system of a crop. Nitrogen fixation and all related processes are a specificity of legume crops, while other mechanisms are common to most crops. The representation focuses on the trade-off and effect between nutrients (C, N, P). Blue arrows stand for carbon (C) effect (dashed) and allocation (plain), green for nitrogen (N), and orange for phosphorus (P). Pools of the three nutrients are represented through plain boxes. Processes and organs that are involved in N and P acquisition are also represented respectively with rounded dashed boxes and simple dashed boxes. H^+ and OH^- stand respectively for proton and hydroxyl and APase stands for acid phosphatase.

models, and (4) finally, there are real gaps in our knowledge on the mechanism implied as mentioned before.

5.1 The state of the art

Modern models that manage the N and P cycles concomitantly are scarce currently (Delve et al. 2009). Table 2 summarizes a group of soil-crop models that have marked differences in their formalization in relation to N×P simulation. Among semimechanistic soil-crop models that take into account both the N and P effects on crops, we can mention APSIM (Keating et al. 2003; Delve et al. 2009), DSSAT (Dzotsi et al. 2010), and EPIC (Jones et al. 1984) for daily step crop models (Table 2). We can also mention the monthly time-step crop model SCAN (Rowe et al. 2006) or the biogeochemical model CENTURY (Parton et al. 1992).

Most of these models were not initially developed for P management. They have integrated modules simulating the P cycle only afterward (e.g., Daroub et al. 2003). The functioning of the feedback of a P deficiency on crops in these models is very similar to that of a N deficiency. They rely on a ratio between the current nutrient concentration in tissues and a critical concentration threshold. This concept is very similar (or identical) to that of the dilution curve and nutrition index (Lemaire et al. 2019). If the ratio indicates suboptimal nutrition, the model will use it as a reducing factor for all the affected variables (e.g., Dzotsi et al. 2010; Delve et al. 2009). When the models compute several nutrition indices that are suboptimal, the models handle the situation by applying the LM and conserving the lower ratio, which corresponds to the most marked deficiency. Another approach proposed by Zhang et al. (2007) consists of the joining of

Table 2 Overview of the main soil-crop models handling N and P cycles in (agro-)ecosystems with the related key simulated processes. R and NR stand respectively for "represented" and "not represented."

Crop Model	APSIM	DSSAT	EPIC	QUEFTS	PARNJIB
Model category	Semimechanistic	Semimechanistic	Semimechanistic	Hybrid	Empirical
Spatial scale	Field	Field	Field	Field	Field
General handling of N:P nutrient statues					
Stoichiometric factors N/P	No	Limit P uptake	NR	NR	NR
N-P colimitation management	Law of the minimum	Law of the minimum	Law of the minimum	Mean of the potential yields	Reduction factor accounting for all stresses
Soil and root representation					
Soil representation	1D profile	1D profile	1D profile	No spatialization	No spatialization
Root representation	Root depth, density, and Biomass per layer	Root depth, density per layer, Root radius	Rooting depth and weight per layer	NR	NR
Root response to N deficiency	NR	Reduce shoot-to-root	NR	NR	NR
Root response to P deficiency	NR	Partitioning coef	NR	NR	NR
pH simulation	Computed/proton balance	Input	Computed	Input	Input
Rhizospheric processes					
Symbiotic N_2 fixation	R	R	R	NR	NR
Nodules representation	Implicit	R	NR	NR	NR
N effect on N_2 fixation	Triggered by N deficiency/no direct effect on the rate	Triggered by N deficiency/no direct effect on the rate	Inhibition	NR	NR
P effect on N_2 fixation	NR	NR	NR	NR	NR
N effect on APase secretion	NR	NR	NR	NR	NR
P effect on APase secretion	NR	NR	NR	NR	NR
Organic acid secretion	Citrate only	NR	NR	NR	NR
Mycorrhizae	NR	NR	NR	NR	NR
References	Delve et al. (2009); Keating et al. (2003); Robertson et al. (2002)	Dzotsi et al. (2010); Jones et al. (2003); Boote et al. (2008)	Sharpley and Williams (1990) Jones et al. (1984)	Sattari et al. (2014)	Reid (2002)

three different models, namely, N_ABLE, PHOSMOD, and POTAS, which, respectively, handle N, P, and K. At each time step, each component will compute the biomass growth increment allowed by each of the three resources. Then, the model will perform a strict application of the LM keeping only the lower of the three computed growth increments. The evaluation of this model showed satisfactory prediction for biomass, yield, and N concentration. However, discrepancies were reported for the simulation of P concentration as well as the biomass and yield under certain fertility conditions. According to the authors, this may be due to the lack

of a formalization of the N×P interaction and suggests the need for substantial improvements in this aspect.

As reported earlier, one of the flaws of the LM is that it does not allow for a representation of the synergistic effect of the N×P interaction in most situations. Therefore, we may hypothesize that models that are based solely on this formalism will mostly fail to reproduce responses to N and P, as N-P colimitation responses are mostly of the MLH type (Fig. 6). Consequently, the use of these models as decision-making tools would lead to an overestimation of the fertilizer need.

There are only a few studies involving these models in N-P colimited situations. We can notably mention the

evaluations of the DSSAT model on maize and sorghum submitted to contrasting N and P fertility conditions for which the model was able to find the most limiting factor and to produce good quality simulation for N and P nutrient uptake with variations depending on irrigation and fertilization. The model was able to simulate both aerial dry biomass (with a normalized root mean square error (nRMSE) of 10–22% for maize and 13–29% for sorghum) and yield (nRMSE = 16% and 19% for maize and sorghum, respectively) well (Amouzou et al. 2018). Similar observations were found for the evaluation of the APSIM model. Such models can then be used to identify the most limiting nutrients. The yield predictions of the model in the context of dual stresses were also found to be satisfactory (Kinyangi et al. 2004; Delve et al. 2009). The recent work of Das et al. (2022) evaluated the APSIM model against a 35-year-long dataset with a broad range of N and P fertilization rates. They reported that the model was able to account for 88% of the grain yield variations. However, they found that the model tends to overpredict lower yields, and they judged the model performance just below satisfactory for yield simulation. The EPIC model was used by Worou et al. (2015) to simulate rice grown in multiple sites with contrasting N and P inputs. The model simulations showed satisfactory results in predicting the leaf area index (LAI) with a model efficiency (EF) of 0.98. The prediction of the aerial biomass and yield was decent but less precise, with EFs of 0.61 and 0.67, respectively. Furthermore, they reported unsatisfactory results in the validation of the model with over 100% rRMSE (relative root mean square error) for grain yields. However, the authors attributed this error to an inability of the model to reproduce severe environmental conditions such as flooding and drought rather than the model handling of nutrient limitations. The fact that these models had good results by relying solely on the LM may imply that although it does not reflect the biological reality, the LM remains a good approximation. However, the small number of evaluations of these models prevents us from drawing more general conclusions.

The QUEFTS crop model proposes an approach quite different from those previously mentioned. This model has been specially designed to manage the interaction between N, P, and K. It is considered a hybrid model because it combines at the same time relations that are rather mechanistic and others that are purely empirical (Janssen et al. 1990). While the prediction of nutrient availability in soil is computed independently for each nutrient, the actual uptake of each nutrient depends both on its own availability in soil and on the soil availability of the two other elements. Based on the actual uptake of the elements, the model computes two possible yields for each nutrient based on the uptake of each of the two other nutrients. The final yield is the mean of all the potential yields. This formalism encompasses multiple interactions between nutrients during both nutrient uptake and yield formation. These formalisms suggest that the yield simulated by the model varies with the availability of any of the elements. The predicted yield response would then follow the MLH. The QUEFTS model has been widely used and has shown satisfactory results (Sattari et al. 2014), with nRMSE ranging between 13.5 and 24.4% for crop N uptake and between 13.6 and 42% for crop P uptake across the reviewed studies (Xu et al. 2013; Xu et al. 2019; Wei et al. 2022; Yibati et al. 2022). A similar approach is proposed by the LINTUL-Cassava-NPK model, which uses a combined nutrient nutrition index that is more strongly impacted when the crop suffers from multiple limitations. This model showed a decent simulation of storage root dry matter (root mean squared error of 308 g m^{-2}) yield and nutrient uptake (root mean squared error of 0.8 g m^{-2} for P and 5.1 g m^{-2} for N) under contrasting nutrient supply conditions (Adiele et al. 2022).

Some purely empirical models also include formalisms that are consistent with MLH-like response patterns. This is notably the case for the PARNJIB model, which computes a potential yield from weather and nutrient soil availability (Reid 2002). The reductions are then scaled to the potential yield. The applied reduction factor is equal to the square root of the sum of the squares of the reduction factors of each nutrient (Reid 1999). Such formalization implies a strong interaction between nutrients, and we may hypothesize that such a model is likely to follow the MLH. However, as the nutrients in sufficient supply do not impact the final yield (Reid 2002), we assume that the model is able to have MLH behavior in the domain where the two nutrients are in suboptimal conditions. According to the model formalisms, the model would be able to reproduce cases of independent colimitation but not those of serial and simultaneous colimitation (Fig. 3). However, it is noteworthy that the model is formalized in such a way that during a severe shortage of one nutrient, the final yield is more strongly affected by this nutrient supply. This behavior is closer to the LM.

Ågren et al. (2012) proposed another empirical model that offers the possibility of representing an MLH-like response through its flexible allocation parameters. Although this study and model are innovative in comparing the MLH to the LM from a modeling perspective, the fact that the simulations are not compared to real datasets prevents the two possible ways of formalizing the colimitation from being evaluated.

Both the QUEFTS and PARNJIB models seem to be able to represent an MLH-type response pattern, with few parameters and a straightforward formalization. In addition, both seem to perform well and have been evaluated under contrasting conditions and with different crops. Notably, most empirical models are more likely to reproduce the MLH-type response patterns than most mechanistic models. We hypothesize that this situation may be due to the lack of

knowledge and related formalisms on the implied mechanisms. Although most empirical models have the advantages of being easy and parsimonious, they also have some disadvantages. For instance, the empirical relations used in these models are only valid within a restricted domain of validity (Reid 2002), which hampers their robustness and genericity. These models are also not fitted to be interpreted from a mechanistic perspective (Reid 2002). As a consequence, they do not represent the most adapted tools to combine the adequate prediction of agronomic parameters related to N-P colimitation with the mechanistic understanding of the processes involved in N×P interactions.

The lack of representation of rhizospheric processes within field-scale soil-crop models is clear (Table 2). In particular, for those linked to P, such as APase secretion or organic acid exudation, there are only a few exceptions, such as citrate inclusion within the APSIM crop model (Wang et al. 2013). N_2 fixation is a more commonly represented mechanism, especially in semimechanistic models (Table 2), although its formalization may be too simplistic. Indeed, none of the reviewed models explicitly represents the nodules with the exception of the DSSAT crop model. Additionally, we can clearly see that most of the semimechanistic models represent N_2 fixation and its inhibition by N input in the soil. In contrast, the P effect on N_2 fixation is globally missing (Table 2). This may imply that even though these models simulate N_2 fixation, they cannot be used to simulate MLH-like response patterns related to P supply. Finally, few models seem to handle the feedback of N and P shortages on the shoot-to-root ratio (Table 2).

While this review focuses mainly on crop responses, it is important to mention that N and P cycles may interact with soil processes such as the decomposition of SOM through the C:N:P ratio of the soil. This formalism was previously addressed in the literature (e.g., Lewis and McGechan 2002), although the extent of its impact on crop responses is yet to be determined.

It is commonly accepted that the degree of complexity of models is inversely proportional to their spatiotemporal scale. It seems that the modeling of the response to an N-P colimitation does not follow this rule. Indeed, while all semimechanistic soil-crop models reviewed in this paper follow strictly the LM, some global models have a more complex formalization. This is the case for the global ecosystem model CASA-CNP (Wang et al. 2007; 2010), which balances C, P, and N allocation following a "cost−benefit analysis." This method allocates nutrient in the most efficient way to optimize growth. They rely on rhizospheric processes such as APase secretion (investment of N to acquire P) and symbiotic N_2 fixation (investment of P to acquire N). Another example would be that of the land surface model ORCHIDEE, which represents N and P effects on N_2 fixation, APase secretion, and shoot-to-root ratio (Goll et al. 2017). The adaptation of the N14CP ecosystem model to agricultural settings shows that when the model simulation was evaluated against multiple long-term experiments with different management strategies, the model simulated reasonably well yield in most situations (15% of yield underestimation), but when P was the most limiting, the model significantly underestimated yield by 77% (Janes-Bassett et al. 2020). We hypothesize that this may be due to the lack of formalisms representing N investment in acquiring P.

Similarly, terrestrial ecosystem models seem to be well advanced in the handling of colimitation, and while they use LM as a general approach, they include formalisms such as flexible C:P ratios, APase secretion, and N and P effects on N_2 fixation, as reviewed by Achat et al. (2016). The FUN model also allocates C, N, and P in an optimal way to ensure the highest net production. It relies not only on both plant APase secretion and N_2 fixation but also on mycorrhizal uptake and APase exudation. A key feature of this model is that it simulates different types of mycorrhizae to favor N or P acquisition (Allen et al. 2020).

The development of N-P colimitation modeling in ecosystems and global models proves that the integration of similar formalisms within soil-crop models is a realistic goal. Soil-crop models should be inspired by these other models and implement new formalisms based on current knowledge on N-P.

5.2 Future improvements

The prevalence of the LM within soil-crop models confirms the general statement of Yin et al. (2021) that crop models seem to grow in number but are not necessarily improved. They argue that crop models should rely on physiological knowledge, which will improve both the fitness and allow the mechanistic understanding of the model outputs.

To ensure this physiological meaning in the N×P interaction, rhizosphere mechanisms should be represented, as they seem at the core of this interaction (Fig. 7). It is noteworthy that some global models and terrestrial ecosystems models have already integrated such rhizosphere mechanisms with simple formalisms (e.g., Wang et al. 2007; Achat et al. 2016). Analytical solution for the one- or two-dimensional convection-diffusion is a way for simplifying and upscaling rhizosphere mechanisms to practical fields (Darrah et al. 2006; de Willigen and van Noordwijk 1994; Roose et al. 2001; Lin et al. 2023). Hence, our mechanistic understanding and data availability are crucial to parametrize and evaluate the analytical solution for representing rhizosphere mechanisms in soil-crop models (Hinsinger et al. 2011). Considering the rhizosphere mechanisms reviewed in Section 3, APase secretion and the effect of P on symbiotic N_2 fixation are good candidates to be incorporated in soil-crop models to enable them to reproduce MLH response patterns.

Models that do not explicitly simulate root traits will have difficulty reproducing more complex effects of N-P

colimitation. Accordingly, this would be the case for most soil-crop models that have a 1D representation of the root profile (Table 2). Although this 1D may be sufficient to handle shoot-to-root variations through stress factors (e.g., Dzotsi et al. 2010; Göll et al. 2017), Naab et al. (2015) have already reported the limits of their model in simulating several common practices linked to P management, such as deep or banded fertilization. They pointed out the need for a 2D representation of the root system for a better simulation of P uptake. Although it simulated only a part of the crop cycle, models with a more spatially resolved root system have proven to be able to simulate the effect of N×P interaction (Rangarajan et al. 2018).

Another limitation is related to the fact that most models consider pH as a fixed input parameter rather than a computed variable (Table 2). Some models, such as EPIC, compute it annually (Table 2). which may improve the simulation quality of the model over the long-term, but it will not be able per se to integrate the effect of pH changes on N×P interactions within an annual crop cycle. From the reviewed models, only an earlier version of APSIM seems to compute pH based on a comprehensive proton balance and at a daily time step (Hochman et al. 1998).

Finally, interactions within the plants such as the interplay between nutritional status and nutrient allocation mechanisms also deserve to be accounted for. While models have not developed yet such a formalism to our knowledge, agronomists have reported evidence of a N×P interaction (Bélanger and Ziadi 2008).

Considering the large number of processes involved, the quest for implementing all of them seems unrealistic. As illustrated by Wang et al. (2013), exhaustivity is not necessarily a pre-requisite for a good simulation. They showed that the integration of citrate exudation did not heavily impact the quality of the P simulation in the APSIM model. Hence, the key steps prior to implement new processes within soil-crop models are the preliminary selection, evaluation, and ranking of the processes to implement is a key step prior to their formalization and integration within crop models. The priority should be given to the processes that are well known, that affect the most crop responses, and that can be formalized as simply as possible. The evaluation of the simulations obtained by including the abovementioned mechanisms as well as those obtained by using the LM against real datasets would allow us to quantitatively compare between LM and MLH formalisms with clear quantification and to determine which is better to represent N-P colimitation in the soil-crop model.

In view of the important number of mechanisms potentially involved in the N×P interaction as well as different ways to implement them in crop models, from very mechanistic approaches to rather empiric ones, we assume that the development of such aspects would result in a greater diversification of soil-crop models.

6 Conclusion

The study of N-P colimitation needs a clear theoretical framework. Previous works proposed two theories of growth, namely, the law of minimum (LM) and the multiple limitation hypothesis (MLH). According to the LM, the plants respond only to the most limiting nutrient, while the MLH is based on a cost−benefit analysis and accounts for growth responses to all the involved nutrients. Several categories of colimitation do exist, and they are based on the growth response due to each nutrient input as well as the presence or absence of a synergistic or antagonistic effect. The fact that these typologies were used mainly for ecological studies on natural ecosystems does not prevent their utilization in analyzing crop responses in agro-ecosystems.

By confronting the results of field experimentation against these typologies, we found that when the crop response is exposed to a N-P colimitation, it follows the MLH in the vast majority of cases and that the N×P interaction is mostly synergistic. This is especially true for legume crops. However, this tendency may vary according to both climatic and edaphic factors. Temporal differences were also reported due to both interyear variations and long-term cultivation effects.

We subsequently identified several direct (e.g., N_2 fixation and APase secretion) and indirect (e.g., root plasticity and pH modification) mechanisms that could explain these crop response patterns. However, we reported many knowledge gaps in these mechanisms, such as the relative weight of each of these mechanisms, the exact conversion ratio between N and P investment, and its variations according to the studied species as well as the climatic and edaphic conditions. However, these gaps are complex to investigate because of the interplay between the different processes.

Soil-crop models are appropriate tools to capture and decipher the complexity of N-P colimitation and N×P interactions. However, currently, few models handle both nutrients at the same time. Additionally, those that handle both nutrients manage the crop responses with an application of LM. This consideration is not aligned with experimental evidences. Moreover, no studies have evaluated whether this simplification is worth the reduced biological relevance compared with the MLH. Nevertheless, while all mechanisms cannot be integrated into crop models, implementing those that are the most important with a simple but (semi)mechanistic formalism would actively contribute to enhancing the quality of the simulation of crop responses to N-P colimitation and thus allow us to optimize and benefit from this interaction.

All this knowledge concerning N and P nutrition should be better accounted for to support the achievement of higher yields and more sustainable agroecosystems. Unraveling knowledge on N×P interactions would allow us to make better use of the involved mechanisms and leverage them

to optimize our management practices, including a better balance in fertilizer inputs as well as an overall reduction in the use of synthetic fertilizer and hence enhance the sustainability of the systems while ensuring higher yields.

Data availability All data analyzed are included in the present paper.

Code availability Not applicable

Declarations

Ethics approval Not applicable

Consent to participate Not applicable

Consent for publication Not applicable

Conflict of interest The authors have no commercial conflicts of interest to declare. The research done by the Recyclage et Risque group, to which M. SEGHOUANI and M. BRAVIN belong, aims at suggesting methods and models to recycle agricultural, agro-industrial, and urban organic residues in agriculture by minimizing agro-environmental issues and managing recycling at the territory scale.

References

Abdissa Y, Tekalign T, Pant LM (2011) Growth, bulb yield and quality of onion (Allium cepa L.) as influenced by nitrogen and phosphorus fertilization on vertisol I. growth attributes, biomass production and bulb yield. Afr J Agric Res 6:3252–3258

Abu-Alrub I, Saleh S, Awaga AA (2019) Effect of different rates of nitrogen and phosphorus fertilizers on yield and quality of greenhouse tomato under the UAE condition. EC Agric 5:139–146

Achat DL, Augusto L, Gallet-Budynek A, Loustau D (2016) Future challenges in coupled C-N–P cycle models for terrestrial ecosystems under global change: a review. Biogeochemistry 131:173–202. https://doi.org/10.1007/s10533-016-0274-9

Adak M, Kibritci M (2016) Effect of nitrogen and phosphorus levels on nodulation and yield components in faba bean Vicia faba L. Legum Res 39:991–994. https://doi.org/10.18805/lr.v0iOF.3773

Adiele JG, Schut AGT, Ezui KS, Giller K (2022) LINTUL-cassava-NPK: a simulation model for nutrient-limited cassava growth. Field Crop Res 281:108488. https://doi.org/10.1016/j.fcr.2022.108488

Ågren GI, Wetterstedt JÅM, Billberger MFK (2012) Nutrient limitation on terrestrial plant growth–modeling the interaction between nitrogen and phosphorus. New Phytol 194:953–960. https://doi.org/10.1111/j.1469-8137.2012.04116.x

Al-Ajlouni MM, Al-Ghzawi ALA, Al-Tawaha AR (2010) Crop rotation and fertilization effect on barley yield grown in arid conditions. J Food Agric Environ 8:869–872

Alkama N, Ounane G, Drevon JJ (2012) Is genotypic variation of H+ efflux under P deficiency linked with nodulated-root respiration of N2–fixing common-bean (*Phaseolus vulgaris* L.). J Plant Physiol 169:1084–1089. https://doi.org/10.1016/j.jplph.2012.03.013

Allen K, Fisher JB, Phillips RP, Js P, Brzostek ER (2020) Modeling the carbon cost of plant nitrogen and phosphorus uptake across temperate and tropical forests. Front for Glob Chang 3:43. https://doi.org/10.3389/ffgc.2020.00043

Amouzou KA, Naab JB, Lamers JPA, Becker M (2018) CERES-Maize and CERES-Sorghum for modeling growth, nitrogen and phosphorus uptake, and soil moisture dynamics in the dry savanna of West Africa. Field Crop Res 217:134–149. https://doi.org/10.1016/j.fcr.2017.12.017

Aulakh M, Malhi S (2005) Interactions of nitrogen with other nutrients and water: effect on crop yield and quality, nutrient use efficiency, carbon sequestration, and environmental pollution. Adv Agron 86:341–409. https://doi.org/10.1016/S0065-2113(05)86007-9

Balemi T, Negisho K (2012) Management of soil phosphorus and plant adaptation mechanisms to phosphorus stress for sustainable crop production: a review. J Soil Sci Plant Nutr 12:547–561. https://doi.org/10.4067/S0718-95162012005000015

Banerjee A, Sanyal S, Sen S (2012) Soil phosphatase activity of agricultural land: a possible index of soil fertility. Agric Sci Res J 2:412–419

Battie-Laclau P, Laclau JP, Piccolo MC, Arenque BC, Beri C, Mietton L, Muniz MRA, Jordan-Meille L, Buckeridge MS, Nouvellon Y, Ranger J, Bouillet JP (2013) Influence of potassium and sodium nutrition on leaf area components in Eucalyptus grandis trees. Plant Soil 371:19–35. https://doi.org/10.1007/s11104-013-1663-7

Bélanger G, Ziadi N (2008) Phosphorus and nitrogen relationships during spring growth of an aging Timothy Sward. Agron J 100:1757–1762. https://doi.org/10.2134/agronj2008.0132

Boote KJ, Hoogenboom G, Jones JW, Ingram KT (2008) Modeling nitrogen fixation and its relationship to nitrogen uptake in the CROPGRO model, in: Ma L, Ahuja LR, Bruulsema TW (Eds.), Quantifying and understanding plant nitrogen uptake for systems modeling. CRC Press, Florence, USA, pp. 13–46. ISBN: 9780429140532

Brennan R, Bolland M (2009) Comparing the nitrogen and phosphorus requirements of canola and wheat for grain yield and quality. Crop Pasture Sci 60:566–577. https://doi.org/10.1071/CP08401

Chakwizira E, Fletcher AL, de Ruiter JM, Meenken E, Maley S, Wilson DR (2009) Kale dry matter yield responses to nitrogen and phosphorus application. Agron N Z 39:59–70

Chakwizira E, Fletcher AL, Meenken ED, Johnstone P, Maley S, Arnold N, Armstrong S, George M, Sim R, Minchin R, Morton J, Stafford A (2011) Dry matter response of swede crops to nitrogen and phosphorus application in Southland and central North Island regions of New Zealand. Agron N Z 41:23–37

Chapin FS, Bloom AJ, Field CB, Waring RH (1987) Plant responses to multiple environmental factors. BioScience 37:49–57. https://doi.org/10.2307/1310177

Chekanai V, Chikowo R, Vanlauwe B (2018) Response of common bean (Phaseolus vulgaris L.) to nitrogen, phosphorus and rhizobia inoculation across variable soils in Zimbabwe. Agric Ecosyst

Environ 266:167–173. https://doi.org/10.1016/j.agee.2018.08.010

Chen J, Moorhead DL (2022) Progressively decreased nitrogen-stimulation of soil phosphatase activity with long-term nitrogen addition. Appl Soil Ecol 169:104213. https://doi.org/10.1016/j.apsoil.2021.104213

Cordell D, White S (2014) Life's bottleneck: sustaining the world's phosphorus for a food secure future. Annu Rev Environ Resour 39:161–188. https://doi.org/10.1146/annurev-environ-010213-113300

Dai XQ, Zhang HY, Spiertz JHJ, Yu J, Xie GH, Bouman BAM (2010) Crop response of aerobic rice and winter wheat to nitrogen, phosphorus and potassium in a double cropping system. Nutr Cycl Agroecosyst 86:301–315. https://doi.org/10.1007/s10705-009-9293-4

Daroub SH, Gerakis A, Ritchie JT, Friesen DK, Ryan J (2003) Development of a soil-plant phosphorus simulation model for calcareous and weathered tropical soils. Agric Syst 76:1157–1181. https://doi.org/10.1016/S0308-521X(02)00082-3

Darrah PR, Jones DL, Kirk GJD, Roose T (2006) Modelling the rhizosphere: a review of methods for 'upscaling' to the whole-plant scale. Eur J Soil Sci 57:13–25. https://doi.org/10.1111/j.1365-2389.2006.00786.x

Das B, Huth N, Probert M, Condron L, Schmidt S (2019) Soil phosphorus modeling for modern agriculture requires balance of science and practicality: a perspective. J Environ Qual 48:1281–1294. https://doi.org/10.2134/jeq2019.05.0201

Das BT, Schmidt S, Biggs J, Lester DW, Bourne N, Huth NI (2022) Simulating long-term phosphorus, nitrogen, and carbon dynamics to advance nutrient assessment in dryland cropping. Field Crop Res 85:108590. https://doi.org/10.1016/j.fcr.2022.108590

Davidson EA, Howarth RW (2007) Nutrients in Synergy. Nature 449:1000–1001. https://doi.org/10.1038/4491000a

de Willigen P, van Noordwijk M (1994) Mass flow and diffusion of nutrients to a root with constant or zero-sink uptake I Constant Uptake. Soil Sci 157:16

Delve RJ, Probert ME, Cobo JG, Ricaurte J, Rivera M, Barrios E, Rao IM (2009) Simulating phosphorus responses in annual crops using APSIM: model evaluation on contrasting soil types. Nutr Cycl Agroecosyst 84:293–306. https://doi.org/10.1007/s10705-008-9243-6

Dereje G, Alemu D, Adisu T, Anbessa B (2018) Response of yield and yield components of Tef [Eragrostis tef (Zucc.)Trotter] to optimum rates of nitrogen and phosphorus fertilizer rate application in Assosa Zone, Benishangul Gumuz Region. Ethiop J Agric Sci 28:81–94

Di HJ, Cameron KC (2002) Nitrate leaching in temperate agroecosystems: sources, factors and mitigating strategies. Nutr Cycl Agroecosyst 64:237–256. https://doi.org/10.1023/A:1021471531188

Dotaniya ML, Meena VD (2015) Rhizosphere effect on nutrient availability in soil and its uptake by plants: a review. Proc Natl Acad Sci India Sect B Biol Sci 85:1–12. https://doi.org/10.1007/s40011-013-0297-0

Dzotsi KA, Jones JW, Adiku SGK, Naab JB, Singh U, Porter CH, Gijsman AJ (2010) Modeling soil and plant phosphorus within DSSAT. Ecol Model 221:2839–2849. https://doi.org/10.1016/j.ecolmodel.2010.08.023

Edwards AC, Withers PJA (1998) Soil phosphorus management and water quality: a UK perspective. Soil Use Manag 14:124–130. https://doi.org/10.1111/j.1475-2743.1998.tb00630.x

El Mahdi ARA (2008) Response of sesame to nitrogen and phosphorus fertilization in Norther Sudan. J Appl Biosci 8:304–308

Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x

Elser JJ, Fagan WF, Kerkhoff AJ, Swenson NG, Enquist BJ (2010) Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. New Phytol 186:593–608. https://doi.org/10.1111/j.1469-8137.2010.03214.x

Fageria VD (2001) Nutrient interactions in crop plants. J Plant Nutr 24:1269–1290. https://doi.org/10.1081/PLN-100106981

Fageria NK, Oliveira JP (2014) Nitrogen, phosphorus and potassium interactions in upland rice. J Plant Nutr 37:1586–1600. https://doi.org/10.1080/01904167.2014.920362

Fan J-W, Du Y-L, Wang B-R, Turner NC, Wang T, Abbott LK, Stefanova K, Siddique KHM, Li FM (2016) Forage yield, soil water depletion, shoot nitrogen and phosphorus uptake and concentration, of young and old stands of alfalfa in response to nitrogen and phosphorus fertilisation in a semiarid environment. Field Crop Res 198:247–257. https://doi.org/10.1016/j.fcr.2016.08.014

Gérard F (2016) Clay minerals, iron/aluminum oxides, and their contribution to phosphate sorption in soils—a myth revisited. Geoderma 262:213–226. https://doi.org/10.1016/j.geoderma.2015.08.036

Getnet BE, Dugasa T (2019) Response of maize yield and yield related components to different levels of nitrogen and phosphorus fertilizers. Acta Sci Agric 3:3–8

Girma K, Freeman KW, Teal R, Arnall DB, Tubana B, Holtz S, Raun WR (2007) Analysis of yield variability in winter wheat due to temporal variability, and nitrogen and phosphorus fertilization. Arch Agron Soil Sci 53:435–442. https://doi.org/10.1080/03650340701466754

Gleeson S, Tilman D (1992) Plant allocation and the multiple limitation hypothesis. Am Nat 139:1322–1343. https://doi.org/10.1086/285389

Goll DS, Vuichard N, Maignan F, Jornet-Puig A, Sardans J, Violette A, Peng S, Sun Y, Kvakic M, Guimberteau M, Guenet B, Zaehle S, Penuelas J, Janssens I, Ciais P (2017) A representation of the phosphorus cycle for ORCHIDEE (revision 4520). Geosci Model Dev 10:3745–3770. https://doi.org/10.5194/gmd-10-3745-2017

Golzarfar M, Rad AHS, Delkhosh B, Bitarafan Z (2012) Safflower (Carthamus tinctorius L) response to different nitrogen and phosphorus fertilizer rates in two planting seasons. Žemdirbystė=Agric 99:159–166

Greenwood D, Karpinets T, Zhang K, Bosh-Serra A, Boldrini A, Karawulova L (2008) A unifying concept for the dependence of whole-crop N : P ratio on biomass: theory and experiment. Ann Bot 102:967–977. https://doi.org/10.1093/aob/mcn188

Guignard M, Leitch A, Acquisti C, Eizaguirre C, Elser JJ, Hessen DO, Jeyasingh PD, Neiman M, Richardson AE, Soltis PS, Soltis DE, Stevens CJ, Trimmer M, Weider LJ, Woodward G, Leitch IJ (2017) Impacts of nitrogen and phosphorus: from genomes to natural ecosystems and agriculture. Front Ecol Evol 5:70. https://doi.org/10.3389/fevo.2017.00070

Güsewell S (2004) N : P ratios in terrestrial plants: variation and functional significance. New Phytol 164:243–266. https://doi.org/10.1111/j.1469-8137.2004.01192.x

Hadir S, Gaiser T, Hüging H, Athmann M, Pfarr D, Kemper R, Ewert F, Seidel S (2020) Sugar beet shoot and root phenotypic plasticity to nitrogen, phosphorus, potassium and lime omission. Agriculture 11:21. https://doi.org/10.3390/agriculture11010021

Harpole WS, Ngai JT, Cleland EE, Seabloom EW, Borer ET, Bracken MES, Elser JJ, Gruner DS, Hillebrand H, Shurin JB, Smith JE (2011) Nutrient co-limitation of primary producer communities. Ecol Lett 14:852–862. https://doi.org/10.1111/j.1461-0248.2011.01651.x

Hassan MU, Aamer M, Mahmood A, Awan MI, Barbanti L, Seleiman MF, Bakhsh G, Alkhabsheh HM, Babur E, Shao J, Rasheed A, Huang G (2022) Management strategies to mitigate N2O

emissions in agriculture. Life 12:439. https://doi.org/10.3390/life12030439

Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation? Trends Plant Sci 11:610–617. https://doi.org/10.1016/j.tplants.2006.10.00

Hill JO, Simpson RJ, Moore AD, Chapman DF (2006) Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. Plant Soil 286:7–19. https://doi.org/10.1007/s11104-006-0014-3

Hinsinger P (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant Soil 237:173–195. https://doi.org/10.1023/A:1013351617532

Hinsinger P, Brauman A, Devau N, Gérard F, Jourdan C, Laclau JP, Le Cadre E, Jaillard B, Plassard C (2011) Acquisition of phosphorus and other poorly mobile nutrients by roots. where do plant nutrition models fail? Plant Soil 348:29–61. https://doi.org/10.1007/s11104-011-0903-y

Hochman Z, Braithwaite S, Probert ME, Verburg K, Helyar KR (1998) SOILpH—a new APSIM module for management of soil acidification. In Agronomy*/Growing a Greener Future. Proceedings Ninth Australian Agronomy Conference, Wagga Wagga, pp 709–712.

Ierna A, Mauromicale G, Licandro P (2006) Yield and harvest time of globe artichoke in relation to nitrogen and phosphorus fertilization. Acta Hortic 700:115–120. https://doi.org/10.17660/ActaHortic.2006.700.16

Janes-Bassett V, Davies J, Rowe E, Tipping E (2020) Simulating long-term carbon nitrogen and phosphorus biogeochemical cycling in agricultural environments. Sci Total Environ 714:136599. https://doi.org/10.1016/j.scitotenv.2020.136599

Janssen B, Guiking FCT, Eijk D, Smaling EMA, Wolf J, van Reuler H (1990) A system for quantitative evaluation of the fertility of tropical soils (QUEFTS). Geoderma 46:299–318. https://doi.org/10.1016/0016-7061(90)90021-Z

Jones CA, Cole CV, Sharpley AN, Williams JR (1984) A simplified soil and plant phosphorus model: I. documentation. Soil Sci Soc Am J 48:800–805. https://doi.org/10.2136/sssaj1984.03615995004800040020x

Jones JW, Hoogenboom G, Porter CH, Boote KJ, Batchelor WD, Hunt LA, Wilkens PW, Singh U, Gijsman AJ, Ritchie JT (2003) The DSSAT cropping system model. Eur J Agron 18:235–265. https://doi.org/10.1016/S1161-0301(02)00107-7

Jones JW, Antle JM, Basso B, Boote KJ, Conant RT, Foster I, Godfray HCJ, Herrero M, Howitt RE, Janssen S, Keating BA, Munoz-Carpena R, Porter CH, Rosenzweig C, Wheeler TR (2017) Brief history of agricultural systems modeling. Agric Syst 155:240–254. https://doi.org/10.1016/j.agsy.2016.05.014

Kamanga BCG, Waddington SR, Whitbread AM, Almekinders CJM, Giller CJM (2014) Improving the efficiency of use of small amounts of nitrogen and phosphorus fertiliser on smallholder maize in central Malawi. Exp Agric 50:229–249. https://doi.org/10.1017/S0014479713000513

Keating BA, Carberry PS, Hammer GL, Probert ME, Robertson MJ, Holzworth D, Huth NI, Hargreaves JNG, Meinke H, Hochman Z, McLean G, Verburg K, Snow V, Dimes JP, Silburn M, Wang E, Brown S, Bristow KL, Asseng S, Chapman S, McCown RL, Freebairn DM, Smith CJ (2003) An overview of APSIM, a model designed for farming systems simulation. Eur J Agron 18:267–288. https://doi.org/10.1016/S1161-0301(02)00108-9

Kinyangi J, Delve RJ, Probert ME (2004) Testing the APSIM model with data from a phosphorus and nitrogen replenishment experiment on an Oxisol in Western Kenya. In: Delve RJ, Probert ME (eds) Modelling nutrient management in tropical cropping

systems. ACIAR Proceedings No. 114, pp 101–109. ISBN: 186320 414 8

Kouas S, Alkama N, Abdelly C, Drevon J-J (2008) Proton release by nodulated roots varies among common bean genotypes (*Phaseolus vulgaris*) under phosphorus deficiency. J Plant Nutr Soil Sci 171:242–248. https://doi.org/10.1002/jpln.200700114

Kuppe CW, Schnepf A, von Lieres E, Watt M, Postma JA (2022) Rhizosphere models: their concepts and application to plant-soil ecosystems. Plant Soil 474:17–55. https://doi.org/10.1007/s11104-021-05201-7

Leidi EO, Rodríguez-Navarro DN (2000) Nitrogen and phosphorus availability limit N2 fixation in bean. New Phytol 147:337–346. https://doi.org/10.1046/j.1469-8137.2000.00703.x

Lemaire G, Jeuffroy M-H, Gastal F (2008) Diagnosis tool for plant and crop N status in vegetative stage. Eur J Agron 28:614–624. https://doi.org/10.1016/j.eja.2008.01.005

Lemaire G, Sinclair T, Sadras V, Bélanger G (2019) Allometric approach to crop nutrition and implications for crop diagnosis and phenotyping. A Review. Agron Sustain Dev 39:27. https://doi.org/10.1007/s13593-019-0570-6

Lewis DR, McGechan MB (2002) A Review of field scale phosphorus dynamics models. Biosyst Eng 82:359–380. https://doi.org/10.1006/bioe.2002.0102

Lin W, Ning X, Ou Z (2023) Analytical solutions of the nitrogen uptake model with Michaelis-Menten flux. Appl Math Comput 438:127570. https://doi.org/10.1016/j.amc.2022.127570

Lobell DB, Cassman KG, Field CB (2009) Crop yield gaps: their importance, magnitudes, and causes. Ann Rev Environ Resour 34:179–204. https://doi.org/10.1146/annurev.environ.041008.093740

Marklein AR, Houlton BZ (2012) Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. New Phytol 193:696–704. https://doi.org/10.1111/j.1469-8137.2011.03967.x

Marschner H (1995) Mineral nutrition of higher plant (second ed.) Academic Press, New York 889 pp. ISBN: 9780080571874

Marschner H, Dell B (1994) Nutrient uptake in mycorrhizal symbiosis. Plant Soil 159:89–102. https://doi.org/10.1007/BF00000098

Mollier A, De Willigen P, Heinen M, Morel C, Schneider A, Pellerin S (2008) A two-dimensional simulation model of phosphorus uptake including crop growth and P-response. Ecol Model 210:453–464. https://doi.org/10.1016/j.ecolmodel.2007.08.008

Naab JB, Boote KJ, Jones JW, Porter CH (2015) Adapting and evaluating the CROPGRO-peanut model for response to phosphorus on a sandy-loam soil under semi-arid tropical conditions. Field Crop Res 176:71–86. https://doi.org/10.1016/j.fcr.2015.02.016

Nekinikie M, Dechassa N (2018) Effect of nitrogen and phosphors application on yield and yield components of improved potato (*Solanum tuberosum* L.) cultivars at Holetta, Central Highlands of Ethiopia. J Nat Sci Res 8(23):19–25

Nuttall WF, Moulin AP, Townley-Smith LJ (1992) Yield response of canola to nitrogen, phosphorus, precipitation, and temperature. Agron J 84:765–768. https://doi.org/10.2134/agronj1992.00021962008400050001x

Nyiraneza J, Bélanger G, Benjannet R, Ziadi N, Cambouris A, Fuller K, Hann S (2021) Critical phosphorus dilution curve and the phosphorus-nitrogen relationship in potato. Eur J Agron 123:126205. https://doi.org/10.1016/j.eja.2020.126205

Olaniyi JO (2008) Growth and seed yield response of egusi melon to nitrogen and phosphorus fertilizers application. Am-Eurasian J Sustain Agric 2:255–260

Paris Q (1992) The return of von Liebig's "Law of the Minimum." Agron J 84:1040–1046. https://doi.org/10.2134/agronj1992.00021962008400060025x

Parton WJ, Ojima DS, Schimel DS, Kittel TGF (1992) Development of simplified ecosystem models for applications in earth system

studies: the century experience. In: Ojima DS (ed) Modeling the earth system. Proceedings from the 1990 Global Change Institute on Earth System Modeling, 16–27 July 1990. Aspen Global Change Institute, Aspen pp 281-302.

Penn C, Camberato J (2019) A critical review on soil chemical processes that control how soil pH affects phosphorus availability to plants. Agriculture 9:120. https://doi.org/10.3390/agriculture9060120

Peñuelas J, Poulter B, Sardans J, Ciais P, van der Velde M, Bopp L, Boucher O, Godderis Y, Hinsinger P, Llusia J, Nardin E, Vicca S, Obersteiner M, Janssens IA (2013) Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. Nat Commun 4:2934. https://doi.org/10.1038/ncomms3934

Probert ME (2004) A capability in APSIM to model P responses in crops. In: Delve RJ, Probert ME (eds) Modelling nutrient management in tropical cropping systems. ACIAR Proceedings No. 114, pp 92–100

Pueyo JJ, Quinones MA, Coba de la Pena T, Fedorova EE, Lucas MM (2021) Nitrogen and phosphorus interplay in lupin root nodules and cluster roots. Front Plant Sci 12:644218. https://doi.org/10.3389/fpls.2021.644218

Qian P, Schoenau JJ (2000) Effect of swine manure and urea on soil phosphorus supply to canola. J Plant Nutr 23:381–390. https://doi.org/10.1080/01904160009382024

Rangarajan H, Postma JA, Lynch JP (2018) Co-optimization of axial root phenotypes for nitrogen and phosphorus acquisition in common bean. Ann Bot 122:485–499. https://doi.org/10.1093/aob/mcy092

Reid JB (1999) Forecasting nutrient responses in annual crops. Agron N Z 29:69–72

Reid JB (2002) Yield response to nutrient supply across a wide range of conditions 1. model derivation. Field Crop Res 77:161–171. https://doi.org/10.1016/S0378-4290(02)00088-6

Rengel Z (1993) Mechanistic simulation models of nutrient uptake: a review. Plant Soil 152:161–173. https://doi.org/10.1007/BF00029086

Rietra R, Heinen M, Dimkpa C, Bindraban PS (2017) Effects of nutrient antagonism and synergism on yield and fertilizer use efficiency. Commun Soil Sci Plant Anal 48:1895–1920. https://doi.org/10.1080/00103624.2017.1407429

Ringeval B, Kvakić M, Augusto L, Ciais P, Goll DS, Mueller ND, Müller C, Nesme T, Vuichard N, Wang X, Pellerin S (2021) Insights on nitrogen and phosphorus co-limitation in global croplands from theoretical and modeling fertilization experiments. Glob Biogeochem Cycles 35(6). https://doi.org/10.1029/2020GB006915

Robertson M, Carberry P, Huth N, Turpin JE, Probert ME, Poulton PL, Bell M, Wright GC, Yeates SJ, Brinsmead RB (2002) Simulation of growth and development of diverse legume species in APSIM. Crop Pasture Sci 53:429–446. https://doi.org/10.1071/AR01106

Roose T, Fowler AC, Darrah PR (2001) A mathematical model of plant nutrient uptake. J Math Biol 42:347–360. https://doi.org/10.1007/s002850000007

Rowe E, Vanwijk M, Deridder N, Giller K (2006) Nutrient allocation strategies across a simplified heterogeneous African smallholder farm. Agric Ecosyst Environ 116:60–71. https://doi.org/10.1016/j.agee.2006.03.019

Rubio G, Zhu J, Lynch JP (2003) A critical test of the two prevailing theories of plant response to nutrient availability. Am J Bot 90:143–152. https://doi.org/10.3732/ajb.90.1.143

Saito MA, Goepfert TJ, Ritt JT (2008) Some thoughts on the concept of colimitation: three definitions and the importance of bioavailability. Limnol Oceanogr 53:276–290. https://doi.org/10.4319/lo.2008.53.1.0276

Salo TJ, Palosuo T, Kersebaum KC, Nendel C, Angulo C, Ewert F, Bindi M, Calanca P, Klein T, Moriondo M, Ferrise R, Olesen JE, Patil RH, Ruget F, Takac J, Hlavinka P, Trnka M, Rötter RP (2016) Comparing the performance of 11 crop simulation models in predicting yield response to nitrogen fertilization. J Agric Sci 154:1218–1240. https://doi.org/10.1017/S0021859615001124

Salvagiotti F, Cassman KG, Specht JE, Walters DT, Weiss A, Dovbermann A (2008) Nitrogen uptake, fixation and response to fertilizer N in soybeans: a review. Field Crop Res 108:1–13. https://doi.org/10.1016/j.fcr.2008.03.001

Sattari SZ, van Ittersum MK, Bouwman AF, Smit AL, Janssen BH (2014) Crop yield response to soil fertility and N, P, K inputs in different environments: testing and improving the QUEFTS model. Field Crop Res 157:35–46. https://doi.org/10.1016/j.fcr.2013.12.005

Schlegel AJ, Havlin JL (2017) Corn yield and grain nutrient uptake from 50 years of nitrogen and phosphorus fertilization. Agron J 109:335–342. https://doi.org/10.2134/agronj2016.05.0294

Schlegel AJ, Havlin JL (2021) Irrigated grain sorghum response to 55 years of nitrogen, phosphorus, and potassium fertilization. Agron J 113:464–477. https://doi.org/10.1002/agj2.20453

Schulze J (2004) How are nitrogen fixation rates regulated in legumes? J Plant Nutr Soil Sci 167:125–137. https://doi.org/10.1002/jpln.200320358

Schulze J, Temple G, Temple S, Beschow H, Vance CP (2006) Nitrogen fixation by white lupin under phosphorus deficiency. Ann Bot 98:731–740. https://doi.org/10.1093/aob/mcl154

Seligman N, van Keulen H (1980) PAPRAN: A simulation model of annual pasture production limited by rainfall and nitrogen. In: Frissel MJ, Van Veen JA (eds) Simulation of N behaviour of soil-plant systems. Pudoc, Wageningen, pp 60–97. https://doi.org/10.1002/jpln.19811440414

Serme I, Dicko M, Ouattara K, Sidibe B, Wortmann C (2018) Rainfed rice response to fertilizer in the Sudan Savanna of West Africa. Afr J Agric Res 1033–1041. https://doi.org/10.5897/AJAR2018.13160

Setu H, Mitiku T (2020) Response of potato to nitrogen and phosphorus fertilizers at Assosa, western Ethiopia. Agron J 112:1227–1237. https://doi.org/10.1002/agj2.20027

Sharpley AN, Williams JR (1990) EPIC—Erosion/productivity impact calculator: 1. model documentation. USDA-technical bulletin, No 1768. US Government Printing Office, Washington, DC

Srivastava R, Basu S, Kumar R (2021) Phosphorus starvation response dynamics and management in plants for sustainable agriculture. J Plant Biochem Biotechnol 30:829–847. https://doi.org/10.1007/s13562-021-00715-8

Steffen W, Richardson K, Rockström J, Cornell SE, Fetzer I, Bennett EM, Biggs R, Carpenter SR, de Vries W, de Wit CA, Folke C, Gerten D, Heinke J, Mace GM, Persson LM, Ramanathan V, Reyers B, Sörlin S (2015) Planetary boundaries: guiding human development on a changing planet. Science 347:1259855. https://doi.org/10.1126/science.1259855

Sumner M, Farina M (1986) Phosphorus interactions with other nutrients and lime in field cropping systems. Adv Soil Sci 5:201–236. https://doi.org/10.1007/978-1-4613-8660-5_5

Takahashi S, Anwar MR (2007) Wheat grain yield, phosphorus uptake and soil phosphorus fraction after 23 years of annual fertilizer application to an Andosol. Field Crops Res 101:160–171. https://doi.org/10.1016/j.fcr.2006.11.003

Tang C, Hinsinger P, Jaillard B, Rengel Z, Drevon JJ (2001) Effect of phosphorus deficiency on the growth, symbiotic N2 fixation and proton release by two bean (*Phaseolus vulgaris*) genotypes. Agronomie 21:683–689. https://doi.org/10.1051/agro:2001161

Tekulu K, Taye G, Assefa D (2020) Effect of starter nitrogen and phosphorus fertilizer rates on yield and yield components, grain protein content of groundnut (Arachis Hypogaea L.) and residual

INRAE ② Springer

soil nitrogen content in a semiarid north Ethiopia. Heliyon 6:e05101. https://doi.org/10.1016/j.heliyon.2020.e05101

Thuynsma R, Valentine A, Kleinert A (2014) Phosphorus deficiency affects the allocation of below-ground resources to combined cluster roots and nodules in Lupinus albus. J Plant Physiol 171:285–291. https://doi.org/10.1016/j.jplph.2013.09.001

Tilman D, Cassman K, Matson P, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. Nature 418:671–677. https://doi.org/10.1038/nature01014

Ullah I, Ghullamullah S, Ayub M, Khan AA, Anwar S, Khan SA (2012) Response of common wheat to nitrogen and phosphorus fertilization. Sarhad J Agric 28:171–178

Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol 157:423–447. https://doi.org/10.1046/j.1469-8137.2003.00695.x

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol Appl 20:5–15. https://doi.org/10.1890/08-0127.1

Wang YP, Law RM, Pak B (2010) A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. Biogeosciences 7:2261–2282. https://doi.org/10.5194/bg-7-2261-2010

Wang E, Ridoutt BG, Luo Z, Probert ME (2013) Using systems modelling to explore the potential for root exudates to increase phosphorus use efficiency in cereal crops. Environ Model Softw 46:50–60. https://doi.org/10.1016/j.envsoft.2013.02.009

Wang C, Zhou L, Zhang G, Xu Y, Zhang L, Gao X, Gao J, Jian N, Shao M (2017) Optimal fertilization for high yield and good quality of waxy sorghum (Sorghum bicolor L. Moench). Field Crop Res 203:1–7. https://doi.org/10.1016/j.fcr.2016.12.009

Wang Y-P, Houlton BZ, Field CB (2007) A model of biogeochemical cycles of carbon, nitrogen, and phosphorus including symbiotic nitrogen fixation and phosphatase production. Glob Biogeochem Cycles 21(1). https://doi.org/10.1029/2006GB002797

Wei J, Li S, He P, Xu X, Tan D, Li Y, Li G, Guo Y, Cui R (2022) QUEFTS model-based estimation of the nutrient requirements and fertilizer recommendation for Chinese onion. HortScience 57:297–303. https://doi.org/10.21273/HORTSCI16225-21

Wilson DR, Reid JB, Zyskowski RF, Maley S, Pearson AJ, Armstrong SD, Catto WD, Stafford AD (2006) Forecasting fertiliser requirements of forage brassica crops. Proc N Z Grassl Assoc 68:205–210. https://doi.org/10.33584/jnzg.2006.68.2646

Worou ON, Gaiser T, Oikeh S (2015) Sensitive parameters for EPIC model evaluation and validity under soil water and nutrients limited conditions with NERICA cropping in West Africa. Afr J Agric Res 10:2286–2299. https://doi.org/10.5897/AJAR2014.9423

Xu X, He P, Pampolino MF, Chuan L, Johnston AM, Qiu S, Zhao S, Zhou W (2013) Nutrient requirements for maize in China based on QUEFTS analysis. Field Crop Res 150:115–125. https://doi.org/10.1016/j.fcr.2013.06.006

Xu Y, He P, Xu X, Qiu S, Ullah S, Gao Q, Zhou W (2019) Estimating nutrient uptake requirements for potatoes based on QUEFTS analysis in China. Agron J 111:2387–2394. https://doi.org/10.2134/agronj2018.09.0572

Yibati H, Zhang Y, Li Q, Yu X, Ping H (2022) Estimation of cotton nutrient uptake based on the QUEFTS Model in Xinjiang. Agronomy 12:1427. https://doi.org/10.3390/agronomy12061427

Yin Z, Guo W, Xiao H, Liang J, Hao X, Dong N, Leng T, Wang Y, Wang Q, Yin F (2018) Nitrogen, phosphorus, and potassium fertilization to achieve expected yield and improve yield components of mung bean. PLoS ONE 13:e0206285. https://doi.org/10.1371/journal.pone.0206285

Yin X, Struik PC, Goudriaan J (2021) On the needs for combining physiological principles and mathematics to improve crop models. Field Crop Res 271:108254. https://doi.org/10.1016/j.fcr.2021.108254

Zeng H, Liu G, Kinoshita T, Zhang R, Zhu Y, Shen Q, Xu G (2012) Stimulation of phosphorus uptake by ammonium nutrition involves plasma membrane H+ ATPase in rice roots. Plant Soil 357:205–214. https://doi.org/10.1007/s11104-012-1136-4

Zewide I, Ibrahim AM, Tadesse S (2012) Effect of different rates of nitrogen and phosphorus on yield and yield components of potato (Solanum tuberosum L.) at Masha district Southwestern Ethiopia. Int J Soil Sci 7:146–156. https://doi.org/10.3923/ijss.2012.146.156

Zhang K, Greenwood D, White P, Burns I (2007) A dynamic model for the combined effects of N, P and K fertilizers on yield and mineral composition; description and experimental test. Plant Soil 298:81–98. https://doi.org/10.1007/s11104-007-9342-1

Ziadi N, Bélanger G, Cambouris AN, Tremblay N, Nolin MC, Claessens A (2007) Relationship between P and N concentrations in corn. Agron J 99:833–841. https://doi.org/10.2134/agronj2006.0199

Ziadi N, Whalen JK, Messiga AJ, Morel C (2013) Assessment and modeling of soil available phosphorus in sustainable cropping systems. Adv Agron 122:85–126. https://doi.org/10.1016/B978-0-12-417187-9.00002-4

Zingore S, Adolwa IS, Njoroge S, Johnson JM, Saito K, Phillips S, Kihara J, Mutegi J, Murell S, Dutta S, Chivenge P, Amouzou KA, Oberthur T, Chakraborty S, Sileshi GW (2022) Novel insights into factors associated with yield response and nutrient use efficiency of maize and rice in Sub-Saharan Africa A. Review. Agron Sustain Dev 42:82. https://doi.org/10.1007/s13593-022-00821-4