



# Critical dilution curves for phosphorus, potassium, and sulfur along with relationships to nitrogen for major crops

Mario Fontana · Gilles Bélanger · Ignacio Ciampitti · Noura Ziadi · Thomas Guillaume · Samuel Steiner · Luca Bragazza

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## Abstract

**Background and Aims** The concept of crop nutrient dilution with increasing shoot biomass as plant ages, initially developed for nitrogen (N), has been extended to other major nutrients such as phosphorus (P), potassium (K), and sulfur (S). Published critical dilution curves for P, K, and S are presented in this review paper along with a discussion on i) their stability across combinations of genotype, environment, and management ( $G \times E \times M$ ); ii) the influence of N on P, K, and S critical dilution curves along with the implications for the relationships between nutrients; and iii) practical implications and future research perspectives.

**Results** The study of P dilution is more advanced than that of K and S and the published critical P dilution curves suggest more stability across  $G \times E \times M$  situations for maize than for potatoes. Data, however,

are lacking to refine the critical dilution curves for P, K, and S along with determining their universality or domain of applicability. The crop N status has been shown to affect the critical curves of P, K, and S. Conversely, N status appears to be similarly affected by K status, poorly by P status and unaffected by S status, though more data are necessary to confirm this.

**Conclusion** Overall, the strong interaction between nutrients and the need to consider them when developing critical dilution curves is highlighted. Critical dilution curves of P, K, and S offer new opportunities for the efficient analysis of co-limitations and diagnosis of multi-element crop nutrition. The universality or domain of applicability of those critical dilution curves, their theoretical framework, and their practical field applications remain to be clarified.

**Keywords** Nutrient status · Fertilization · Crop productivity · Nutrient interactions · Co-limitation · Multi-limitation

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M. Fontana (✉) · T. Guillaume · S. Steiner · L. Bragazza  
Field-Crop Systems and Plant Nutrition, Route de Duillier  
60, CH-1260 Nyon, Switzerland  
e-mail: mario.fontana@agroscope.admin.ch

G. Bélanger · N. Ziadi  
Agriculture and Agri-Food Canada, Quebec Research  
and Development Centre, Québec G1V 2J3, Canada

I. Ciampitti  
Department of Agronomy, Purdue University,  
West Lafayette, IN, USA

## Introduction

The concept of crop nutrient dilution with increasing shoot biomass has been widely developed and studied, primarily for nitrogen (N). This research has led to the development of critical N dilution curves and the development of a theoretical framework that elucidates this dilution process (Lemaire et al. 2019). Nutrient concentrations of phosphorus (P), potassium

(K), and sulfur (S) have also been shown to decrease with increasing shoot biomass during crop vegetative developmental stages. As for N, the dilution of P, K, and S can be modeled according to a power function and critical dilution curves can be established to estimate the nutrient status of crops based on their nutrient concentration for a given shoot biomass (Lemaire et al. 2019, 2021). Developing crop nutrient critical dilution curves requires data from field trials with fertilization gradients, as well as repeated biomass sampling during vegetative developmental stages to estimate shoot biomass and nutrient concentration (Lemaire et al. 1984; Fernandez et al. 2022). Initially, critical dilution curves were determined in two steps: first, identifying the data points of non-limiting conditions and second, fitting those data points with an allometric function. Recently, the Bayesian method (Makowski et al. 2020) has been proposed and successfully used to quantify the uncertainty associated with critical dilution curves. Several critical dilution curves have been published for P of major crops (Zamuner et al. 2016; Cadot et al. 2018; Gómez et al. 2019; Gagnon et al. 2020; Soratto et al. 2020; Fontana et al. 2021; Morel et al. 2021; Nyiraneza et al. 2021; Kong et al. 2024), but fewer curves have been proposed for K (Cogo et al. 2006; Gómez et al. 2019; Gallardo et al. 2021; Fontana et al. 2022; He et al. 2023; Sandaña et al. 2024) and S (Reussi et al. 2012; Carciocchi et al. 2019; Castellanos Ruiz et al. 2022a). By predicting the critical nutrient concentration, one can determine the minimal nutrient concentration required to achieve maximum shoot growth. Critical dilution curves enable the estimation of nutrition indices and the quantitative diagnosis of nutrient deficiencies during the growing season (Lemaire and Ciampitti 2020). Although critical nutrient concentrations are usually determined without N limitation, N limiting conditions can occur even with N fertilization using fertilization guidelines (Fontana et al. 2021), which can influence nutrient concentrations.

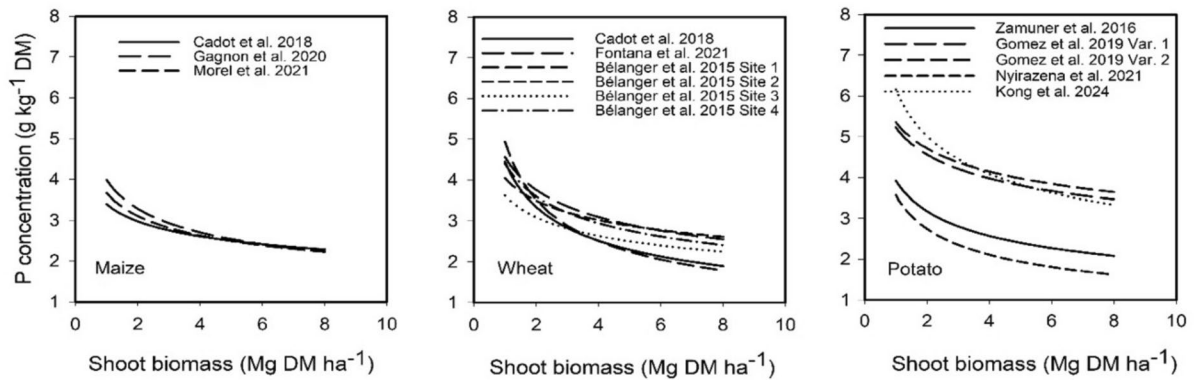
This review paper aims to providing: i) an exhaustive list of the published critical nutrient dilution curves for P, K, and S for different field crops, along with a discussion on their potential stability or universality across combinations of different genotype, environment, and management ( $G \times E \times M$ ) interactions; ii) an analysis of the influence of N fertilization and the level of N nutrition on P, K, and S critical crop nutrient dilution curves along with the

implications for the relationships between nutrients; and iii) a discussion of the practical implications and future research perspectives.

### Critical dilution curves for phosphorus, potassium, and sulfur

**PHOSPHORUS.** The concept of P dilution in increasing shoot biomass and its potential use in developing of a model of critical P concentration ( $P_c$ ) were first discussed for perennial grasses in France (Salette and Huche 1991; Duru and Ducrocq 1997) and Canada (Bélanger and Richards 1999; Bélanger and Ziadi 2008), and for wheat (*Triticum aestivum*) in France (Salette 1990). Several curves of critical P concentration were later published, primarily on maize (*Zea mays* L.), potatoes (*Solanum tuberosum*), and wheat (Table 1). The  $P_c$  curves reported for each crop species from separate studies differ only slightly in maize but much more in potatoes (Fig. 1). Despite being obtained from studies conducted in three countries (Canada, France, and Switzerland) with different maize hybrids and pedo-climatic conditions, the three published  $P_c$  curves for maize appear to be relatively similar (Cadot et al. 2018; Gagnon et al. 2020; Morel et al. 2021). For N, the  $N_c$  curve for maize was found to be roughly stable across  $G \times E \times M$  interactions although minor variations could be expected due to different canopy architecture associated to changes in crop genotypes (Ciampitti et al. 2021). Consequently, it is reasonable to hypothesize that the  $P_c$  curve of maize will demonstrate relative stability across various  $G \times E \times M$  scenarios; however, this remains to be validated.

There seems to be more variation in the  $P_c$  curve for wheat than for maize (Fig. 1). Two of the  $P_c$  curves were obtained in two separate studies conducted in Switzerland with winter wheat (Cadot et al. 2018; Fontana et al. 2021), while four of the  $P_c$  curves are from a study conducted at four sites with spring wheat (Bélanger et al. 2015a). The authors of the study on spring wheat with sites in Canada, Finland, and China concluded that the critical  $P_c$  curves of the four sites differed significantly, which suggests a poor stability across  $G \times E \times M$  situations of the  $P_c$  curves for spring wheat. The  $N_c$  curves of spring and winter wheat exhibited differential patterns, with the observed variation attributed to divergent leaf-to-stem



**Fig. 1** Published critical P dilution curves of maize, winter wheat, spring wheat, and potatoes

**Table 1** List of published critical P dilution curves for various crops (maize, timothy grass, potato, winter wheat, spring wheat, cotton, tomato, rapeseed)

Crops	P <sub>c</sub> dilution curves	Cultivar	N limitation	Bayesian method	Site(s) × year(s)	Country	Authors
Maize	$P_c = 3.49 \text{ }^{\dagger}SB^{-0.19}$	<i>Ricardinio</i>	No	No	1	Switzerland	Cadot et al. (2018)
	$P_c = 3.98 \text{ } SB^{-0.28}$	<i>Elite20T06</i>	No	No	3 × 1	Canada	Gagnon et al. (2020)
	$P_c = 3.66 \text{ } SB^{-0.24}$	NA	No	No	4	France	Morel et al. (2021)
Timothy grass	$P_c = 5.23 \text{ } SB^{-0.40}$	<i>Young sward</i>	No	No	1	Canada	Bélanger and Ziadi (2008)
Potato	$P_c = 3.27 \text{ } SB^{-0.20}$	<i>Old sward</i>	No	No	1		
	$P_c = 3.92 \text{ } SB^{-0.304}$	<i>Innovator</i>	No	No	5 × 5	Argentina	Zamuner et al. (2016)
	$P_c = 5.23 \text{ } SB^{-0.198}$	<i>Capiro</i>	No	No	2 × 2	Colombia	Gómez et al. (2019)
	$P_c = 5.36 \text{ } SB^{-0.186}$	<i>Suprema</i>					
	$P_c = 3.57 \text{ } SB^{-0.38}$	<i>Russet Burbank</i>	No	No	11	Canada	Nyiraneza et al. (2021)
Winter wheat	$P_c = 6.16 \text{ } SB^{-0.296}$	<i>Kexin-1</i>	No	Yes	1 × 3	China	Kong et al. (2024)
	$P_c = 4.44 \text{ }^{\dagger}SB^{-0.41}$	<i>Arina, Nara</i>	Yes	No	1	Switzerland	Cadot et al. (2018)
	$P_c = 4.56 \text{ } SB^{-0.28}$	<i>Arina</i>	No	No	5	Switzerland	Fontana et al. (2021)
Spring wheat	$P_c = 4.94 \text{ } SB^{-0.49}$	<i>AC Coram Harvest</i>	No	No	2	Canada	Bélanger et al. (2015a)
	$P_c = 4.04 \text{ } SB^{-0.21}$	<i>Kruunu</i>	No	No	2	Finland	
	$P_c = 3.62 \text{ } SB^{-0.23}$	<i>AC Barrie</i>	No	No	3	Canada	
	$P_c = 4.40 \text{ } SB^{-0.29}$	<i>Local</i>	No	No	1	China	
Cotton	$P_c = 7.84 \text{ } SB^{-0.221}$	<i>Lu</i>			1 × 2	China	Pang et al. (2020)
	$P_c = 7.74 \text{ } SB^{-0.198}$	<i>Yuzaomian</i>			1 × 2		
Tomato	$P_c = 8.5 \text{ } SB^{-0.311}$	<i>Angelle, Bambelo</i>	No	No	Greenhouse	Spain	Gallardo et al. (2021)
Rapeseed	$P_c = 5.18 \text{ } SB^{-0.39}$	<i>Visby</i>	Yes	No	1	Switzerland	Cadot et al. (2018)

$^{\dagger}SB$  = shoot biomass NA = not available

ratios (Jégo et al. 2022). Specifically, the leaf-to-stem ratio of spring wheat in Canada was found to be lower compared to that of winter wheat cultivated in France. Therefore, given the discrepancy in the leaf-to-stem ratio, it stands to reason that discrepancies in the Pc curves would also be anticipated. However, the Pc curves for spring wheat (Bélanger et al. 2015a) and winter wheat (Fontana et al. 2021) appear to be indistinguishable. Further research is necessary to ascertain whether spring and winter wheat exhibit distinct critical curves for P as well as for K, and S. It is noteworthy that no data has been published thus far concerning the critical curves of these elements for both spring and winter wheat. The Pc curves for potatoes that have been published and are available for review are quite disparate, having been derived from studies conducted in four countries (Argentina, Colombia, Canada, and China). As reported by Giletto et al. (2020), there were variations in Nc curves between potatoes cultivated in Argentina and Canada. Bohman et al. (2023) subsequently corroborated the dependence of the Nc curves on  $G \times E \times M$  interactions, attributing the variation in the timing of tuber initiation (e.g., maturity classes) and the tuber bulking rates to these interactions. Given the observed outcomes on N curves and the substantial function of tubers as a reserve component, it is rational to anticipate variations in the Pc curves of potatoes across  $G \times E \times M$  scenarios.

The observed variability in the reported Pc curves for potatoes and wheat indicates a large variability of the Pc curve across  $G \times E \times M$  scenarios. However, the small variability of the Pc curves in maize remains to be confirmed (Fig. 1). The stability of critical curves across  $G \times E \times M$  interactions has been extensively studied for N, first proposed by Makowski et al. (2020) and subsequently expanded to maize (Ciampitti et al. 2021), wheat (Jégo et al. 2022), and potatoes (Bohman et al. 2023). Recently, this approach was employed for the Pc curve of potatoes produced in China and the authors concluded that the Pc curve was stable across various growing seasons at the same site (Kong et al. 2024). The majority of published Pc curves are derived from a limited number of site-years and/or P fertilization levels. To establish credible critical N dilution curves, Fernandez et al. (2022) determined that a minimum of eight site-years and an ideal total of ten must be utilized, along with four fertilization levels, to reduce uncertainty. This

recommendation is very likely also valuable for establishing reliable and, possibly, more generic Pc curves. For potatoes, maize, and wheat, the aggregation of data from disparate experiments conducted in varied locations, as performed by Ciampitti et al. (2021) for the Nc curve in maize, would generate a substantial dataset. This dataset could be utilized for the purpose of evaluating the influence of genotypes and the environment using the Bayesian method. Additionally, it could be used to ascertain the presence or absence of a generic Pc curve. This approach would also be valuable for other crops and nutrients for which data is lacking. The primary challenge, however, remains the collection of sufficient high-quality data. The collection of sufficient data for the establishment of reliable dilution curves is a challenging endeavor that necessitates a substantial coordinated effort on the part of multiple research groups. The cost associated with frequent sampling during the growing season at multiple locations, in conjunction with extensive laboratory analyses, frequently restricts the number of site-years with valuable data.

The P nutrition index (PNI) can be calculated using critical P dilution curves by dividing the measured P concentration by the predicted critical P concentration. Relative yield, that is, the ratio of the yield obtained for a given P fertilizer rate with the highest yield among all P application rates can be expressed as a function of the PNI. In two different studies on potatoes, positive relationships between the relative tuber yield and the PNI were reported for a large range of PNI ( $\approx 0.4$ –1.6) (Zamuner et al. 2016; Soratto et al. 2020). In grasslands, a positive relationship between relative forage dry matter yield and PNI was established, with a critical PNI value of 92% that distinguishes P-limited and non-P-limited grassland nutrition (Jouany et al. 2021). In winter wheat, the PNI was more strongly correlated with relative shoot biomass than with relative grain yield during the growing season (Fontana et al. 2021). For N, the stability of the relationship between relative yield and NNI was tested for major crop species (Rodriguez et al. 2024). A minimal discrepancy in the yield sensitivity to N deficiency was identified when an integrated NNI over the crop growth cycle was evaluated. The instantaneous NNI around anthesis exhibited a stronger correlation with grain yield compared to NNI determined at other sampling times. To ascertain the stability of the relationship between relative yield

and PNI under varying G×E×M conditions and determine the optimal sampling time, as previously investigated for N, it is evident that additional data must be acquired from multiple sites. Nevertheless, this endeavor remains worthwhile.

**POTASSIUM.** The dilution of crop K concentration with shoot biomass was first reported in France for perennial grasses and wheat (Salette 1990) and later for timothy (*Phleum pratense*) (Pelletier 2006) (Table 2). Several critical dilution curves for K (Kc) curves have been proposed for potatoes in Columbia (Gómez et al. 2019), and in Brazil and Chile (Sandaña et al. 2024). The first study on Kc for potatoes suggested different equations depending on the genotype (Gómez et al. 2019). However, Sandaña et al. (2024) used a Bayesian method with data from multiple site-years in Chile and Brazil and concluded that the optimal curve was independent of the G × E × M combinations. Using the Bayesian method, the concept of wheat Kc curves was initially proposed in Switzerland (Fontana et al. 2022) and China (Song et al. 2024); however, in both studies, only one site with a K limitation

was considered, resulting in substantial discrepancies between the two curves. In contrast to N and P, the number of published Kc curves is minimal. Thus far, one study has reported on the relationship between relative tuber yield and the K nutrition index (KNI). The KNI is calculated by dividing the measured K concentration by the predicted critical K concentration. The relative tuber yield of potatoes showed a strong correlation with the KNI, reaching its maximum yield at 100% (Sandaña et al. 2024).

**SULFUR.** Dilution of S with increasing shoot biomass has been documented for maize (Carciochi et al. 2019), spring wheat (Reussi et al. 2012), potatoes (Gómez et al. 2019; Castellanos Ruiz et al. 2022b), soybean (Divito et al. 2016), and timothy (Pelletier 2006) (Table 3). A series of critical S curves have been published for various crops, including maize (Carciochi et al. 2019, 2020), spring wheat (Reussi et al. 2012), and soybean (Divito et al. 2016). A study conducted in Colombia with a limited data set (Castellanos Ruiz et al. 2022b) suggests that potato cultivars may also vary in their critical S curves.

**Table 2** List of published critical K dilution curves for crops (potato, winter wheat, tomato, sweet potato)

Crops	Kc dilution curves	Cultivar	N limitation	Bayesian method	Site(s)×year(s)	Country	Authors
Potato	$Kc=90.2 \text{ }^{\dagger}SB^{-0.269}$	<i>Capiro</i>	No	No	2×2	Colombia	Gómez et al. (2019)
	$Kc=65.8 \text{ } SB^{-0.135}$	<i>Suprema</i>	No	No	2×2		
	$Kc=55.4 \text{ } SB^{-0.317}$	<i>Asterix</i>	No	No	Greenhouse	Brazil	Cogo et al. (2006)
	$Kc=63.2 \text{ } SB^{-0.27}$	<i>Asterix, Patagonia-INIA</i>	No	Yes	5×2	Brazil and Chile	Sandaña et al. (2024)
Winter wheat	$Kc=58.21 \text{ } SB^{-0.45}$	<i>Nara</i>	No	Yes	3×1	Switzerland	Fontana et al. (2022)
	$Kc=38.2 \text{ } SB^{-0.31}$	<i>Shengxuan 6, Yangmai 22</i>	No	Yes	1×4	China	(Song et al. 2024)
	$Kc=29.9 \text{ } SB^{-0.28}$	<i>Shengxuan 6, Yangmai 22</i>	Yes	Yes	1×4		
Tomato	$K_c=45.1 \text{ } SB^{-0.157}$	<i>Angelle, Bambelo</i>	No	No	Greenhouse	Spain	Gallardo et al. (2021)
Sweet potato	$Kc=53.0 \text{ } SB^{-0.463}$	<i>Shang 19, Yan 25</i>	No	No	1×3	China	He et al. (2023)
	$Kc=42.3 \text{ } SB^{-0.298}$	<i>Shang 19, Yan 25</i>	Yes	No	1×3		

<sup>†</sup>SB = shoot biomass

**Table 3** List of published critical S dilution curves for crops determined (maize, spring wheat, potato, soybean) without N limiting condition and without using a bayesian method

Crops	Sc dilution curves	Cultivar	Site(s)×year(s)	Country	Authors
Maize	$Sc = 2.13 \text{ }^{\dagger}SB^{-0.23}$	NA	3×2	Argentina	Carciochi et al. (2019)
Spring wheat	$Sc = 3.7 \text{ } SB^{-0.169}$	NA	6	Argentina	Reussi et al. (2012)
Potato	$Sc = 6.46 \text{ } SB^{-0.390}$	<i>Capiro cv</i>	2×2	Colombia	Castellanos Ruiz et al. (2022b)
	$Sc = 7.7 \text{ } SB^{-0.393}$	<i>Suprema cv</i>	2×2		
Soybean	$Sc = 2.8 \text{ } SB^{-0.11}$	DM2200, DM4970	1×2	Argentina	Divito et al. (2016)

<sup>†</sup>SB = shoot biomass

### Relationships and interactions of nitrogen with phosphorus, potassium, and sulfur

Many crops have been reported to exhibit positive relationships between N concentration and P, K, and S concentrations in shoot biomass. These relationships are largely driven by nutrient dilution effects associated with changes in biomass and combined with a direct effect of N deficiency on the P, K, and S concentrations.

**PHOSPHORUS.** Under non-limiting N and P conditions, critical N and P concentrations are described by allometric functions of shoot biomass (SB):

$$Nc = a \times SB^{-b} \quad (1)$$

$$Pc = c \times SB^{-d} \quad (2)$$

By combining Equations, 1 and 2, the optimal Nc:Pc ratio can also be theoretically described by an allometric function:

$$Nc : Pc = (a/c) \times SB^{-b+d} \quad (3)$$

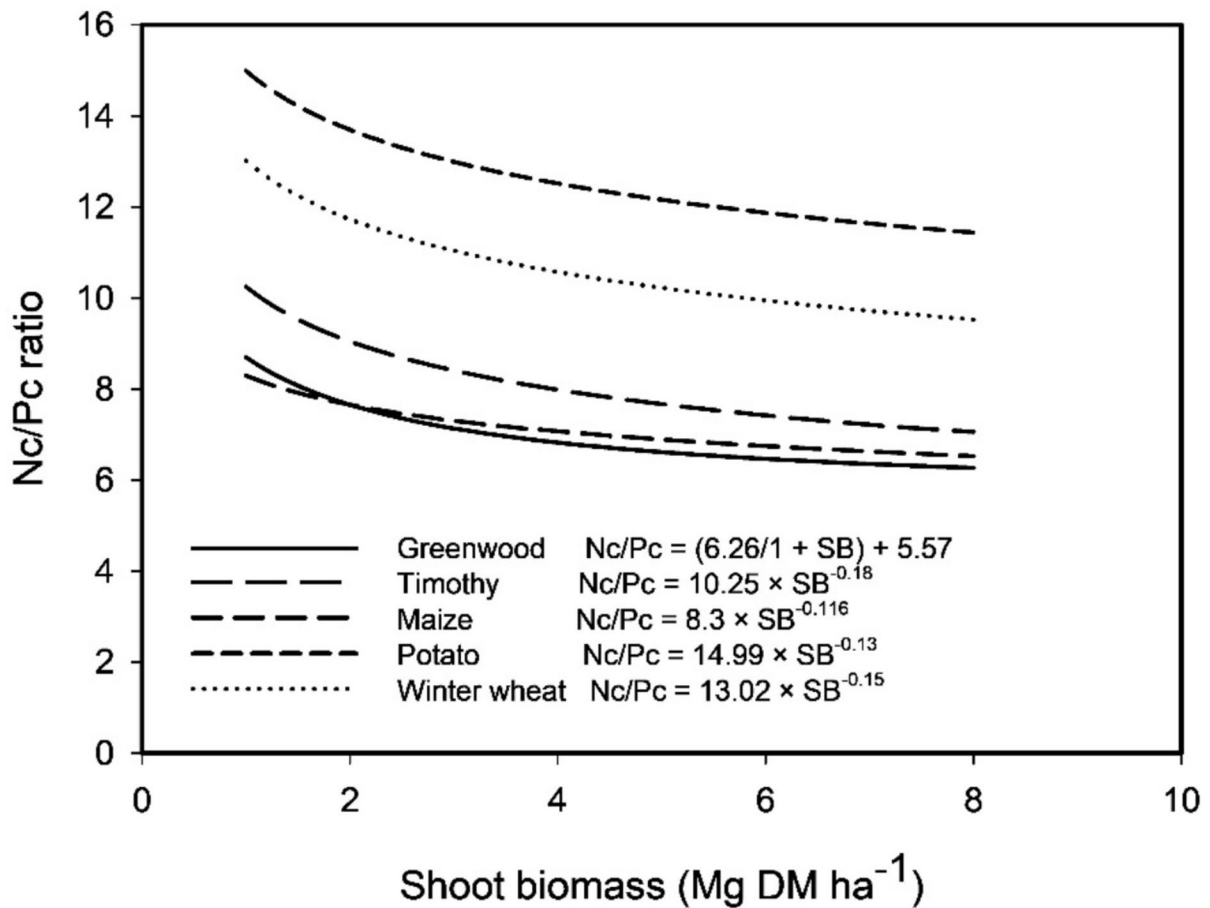
Dilution coefficients  $b$  and  $d$  represent the relative decline in Nc and Pc concentrations, respectively. The first detailed analysis of the changes of the Nc:Pc ratio of the shoot biomass during crop growth was provided by Greenwood et al. (2008). With their study under near optimal levels of nutrients, that is, with no N or P deficiency, they confirmed that the Nc:Pc ratio was primarily a function of the crop biomass. The findings of Greenwood et al. (2008) were later confirmed for grassland swards (Bélanger et al. 2017), maize (Gagnon et al. 2020), potatoes (Nyiraneza et al. 2021), and winter wheat (Fontana et al. 2021) but differences between crop species were noted, particularly for potatoes and winter wheat (Fig. 2). Furthermore, more

research is needed to test the stability of the relationship between the optimal Nc:Pc ratio and shoot biomass, both between and within crop species.

A growing body of research has demonstrated that N deficiency can influence the estimated coefficients of the dilution curves between the P concentration and shoot biomass in various plant species, including timothy (Bélanger and Richards 1999), maize (Ziadi et al. 2007), and wheat (Ziadi et al. 2008). Consequently, the critical P concentration decreases in situations of N deficiency. However, it is unclear how the critical P concentration is affected in situations of luxury N consumption. In crops, N is necessary to produce phosphatase and phosphorus (P) transporters, increase root length, and adapt root morphology, all of which are crucial for P uptake (Spohn 2025). Conversely, crop P can indirectly affect N uptake, especially in P-limited crops, where P fertilization increases the metabolic processes of essential components of ATP, NADH, DNA, and RNA. Therefore, it is possible that P deficiency affects the critical N dilution curve. One study reported that P limitation decreased the maize Nc curve (Miao et al. 2022). However, the impact of P on N concentration is anticipated to be negligible. In their review of the crop response to N-P colimitation, Seghouani et al. (2024) concluded that the effect of P input on N uptake is less pronounced than the effect of N input on P uptake, as reported in previous studies (Sumner and Farina 1986; Aulakh et al. 2000). Similarly, N addition positively influenced P uptake more than P addition influenced N uptake in winter wheat, spring barley (*Hordeum vulgare* L.), and oats (*Avena sativa*) (Spohn 2025). The extent to which a P deficiency decreases the Nc curve remains to be elucidated.

If the N concentration is not or poorly affected by a P deficiency, which remains to be confirmed,





**Fig. 2** Published curves of the relationship between the Nc:Pc ratio and shoot biomass (SB) for timothy (Bélanger et al. 2017), maize (Gagnon et al. 2020), potato (Nyiraneza et al.

2021), and winter wheat (Fontana et al. 2021) along with the curve published by Greenwood et al. (2008) based on a dataset with several crop species

estimating Pc based on N concentration might be possible. Consequently, the N concentration utilized for Pc estimation would be contingent not solely on N availability but also on a feedback effect of P availability, which, in turn, would affect the ultimate Pc estimation. From a mathematical perspective, the N concentration can be expressed in terms of the P concentration, and vice versa:

$$(N/a)^{1/-b} = (P/c)^{1/-d} \quad (4)$$

$$N = a \times (P/c)^{-b/-d} \quad (5)$$

$$P = c \times (N/a)^{-d/-b} \quad (6)$$

Therefore, assuming that Pc depends on N, a Pc estimation could be expressed as follows:

$$Pc = c \times (N/a)^{-d/-b} \quad (7)$$

For winter wheat, this power function relating Pc and N concentration was approached using a linear regression (Fontana et al. 2021). Linear positive relationships between Pc and N concentrations in shoot biomass were reported for forage grasses (Salette 1990; Duru and Ducrocq 1997; Bélanger and Ziadi 2008; Bélanger et al. 2017), maize (Ziadi et al. 2008; Gagnon et al. 2020; Maccari et al. 2021), potatoes (Nyiraneza et al. 2021), spring wheat (Ziadi et al. 2008; Bélanger et al. 2015a), and rapeseed (*Brassica napus*) (Bélanger et al. 2015b). Such a Pc estimation

would allow to avoid the determination of shoot biomass which represents on-farm practical challenges. As suggested by Lemaire et al. (2021), more comprehensive studies of P-N interactions are necessary for the determination of plant-based P nutrition diagnosis across a large range of crop N and P nutrition values.

**POTASSIUM.** The relationship between K and N concentrations has been known for several decades (Salte 1990) but has not been studied to the same extent as that of P. In maize grown in Brazil, the significant positive relationship between K and N concentrations differed between limiting and non-limiting N conditions (Maccari et al. 2021). The K concentration was greater under limiting than non-limiting N conditions for a given shoot N concentration. Consequently, the limited number of field studies that have examined the effects of N limitation on Kc have demonstrated a decline in Kc for winter wheat and sweet potato (He et al. 2023) and authors derived separate critical Kc curves for non-limiting and limiting N conditions to account for the effect of N fertilization (Table 2). Conversely, the application of K fertilization led to an increase in the Nc curve across all plant components of sweet potato (Deng et al. 2023) resulting in elevated levels of N deficiency in N-limited soil and increased profitability in soil with non-limiting N conditions.

Contrarily to other macro nutrients, K is poorly constitutive of crop organic matter and the interactions between K and N are poorly known. Potassium is rather present as ionic soluble form in cell sap, regulating many functions (e.g. osmotic pressure, cellular expansion, stomata aperture, cytoplasmic and luminal pH in endosomes, regulation of membrane potential, enzyme activity (Ragel et al. 2019)). It can also influence positively or negatively the N uptake depending on N form i.e. positive interaction between  $\text{NO}_3^-$  and  $\text{K}^+$  whereas  $\text{NH}_4^+$  and  $\text{K}^+$  (i.e. cations) can result into antagonism (Zhang et al. 2010). Overall, the dependence between Nc and Kc is generally expected for crops and might be symmetric (i.e. N and K are similarly influenced by each other) but it remains to be investigated.

**SULFUR.** The interaction between S and N has been well-documented for many crops (Sharma and Dev 1981; Sachdev and Deb 1990; Jamal et al. 2006; Divito et al. 2015). One review reported that optimal N:S ratios are necessary for optimal crop performance, as imbalanced fertilization usually results in N or

S deficiency (Jamal et al. 2010). The N:S ratio has also been shown to vary according to shoot biomass in maize (Carciochi et al. 2019). Due to the crucial role of S and N in protein synthesis, the requirements of these nutrients for crops are closely linked. Consequently, critical S curves in maize were shown to be affected by N fertilization (Carciochi et al. 2020). However, the latter study showed that the S supply did not affect the Nc curve (Carciochi et al. 2020). Overall, the effects of N and S fertilization on S and N concentrations are poorly understood and warrant further investigation, particularly for crops such as rapeseed, which has a high S demand. No relationship between S and N concentrations has yet been published in the context of defining a critical S concentration.

### Practical implications and perspective for future research

Recent findings on the dilution of P, K, and S in major crops and the implications on the relationship between nutrients shed a new light on the potential of plant-based diagnostic methods of nutrient deficiencies for improving fertilization practices. Plant-based diagnostic methods are sometimes seen as an alternative to soil-based methods for predicting P fertilizer requirements. However, the success of soil P indicators in predicting the amount of P fertilization to maximize crop yield is often limited (McKenzie et al. 2003; Heckman et al. 2006; Valkama et al. 2011). Studies have reported positive relationships between PNI and soil P indicators for various crops (Jouany et al. 2021; Morel et al. 2021), demonstrating that PNI is a valid and useful indirect measure of soil P availability (Gagnon et al. 2020; Morel et al. 2021). The PNI at the twelve-leaf growth stage determined across eight farms in Canada was a better predictor of the relative grain yield with no P applied than the soil PM-III/AlM-III extractant measured prior to corn planting; with a critical PNI value of 0.9 established as a threshold below which a positive response to P fertilization is expected (Gagnon et al. 2020). Similarly, the KNI also better identified K limitation for winter wheat than various soil K chemical extracts (Fontana et al. 2022). This highlights the relevance of establishing and refining critical dilution curves. Plant-based diagnostic methods and soil



analyses should be considered as two complementary approaches. Their integrated use may be necessary to improve fertilization, optimize crop yield and quality, and reduce the environmental impact (Lemaire et al. 2021).

This reliable plant-based approach to analyzing and diagnosing crop nutrition, however, remains to a large extent to be made operable on farms (Lemaire et al. 2021). Estimating biomass destructively while performing plant nutrient analyses is tedious and not easily accessible to farmers. For N, attempts to cope with this issue include the use of drone or remote sensing methods to estimate the aboveground biomass and its N concentration allowing estimates of crop N nutrition index (Chen 2015; Wallace et al. 2017; Zhang et al. 2022; Canicatti et al. 2025). Destructive and non-destructive (e.g., chlorophyll meter SPAD) measures at the leaf level or other plant parts have also been shown to be effective as proxies to estimate the crop N nutrition index (Justes et al. 1997; Bélanger et al. 2003; Ziadi et al. 2009, 2010a; Gastal et al. 2015; Ali et al. 2017; Ravier et al. 2017). Non-destructive P, K, and S concentration measurement is less accessible and requires spectroscopic methods (Zhai et al. 2013; Xu et al. 2017). However, the extent to which the uncertainty increases and whether using this method is relevant for estimating crop nutritional status should be investigated.

Another issue is the potential of in-season fertilizer applications for successfully addressing a nutrient limitation identified by the crop nutrient index. Although there is some indication of successful remedial actions for N (Ravier et al. 2017) or S with a foliar application (Varvel et al. 1997; Tea et al. 2004; Beena Saeed et al. 2013; Waraich et al. 2022), more research is needed to determine the optimal timing and amount of fertilizer for determining the crop's nutritional status and for in-season applications. For P and K, however, corrections during the growing season, either by fertigation or foliar fertilization, cannot optimize yields (Hopkins et al. 2010; Adhikari et al. 2020, pp. 261–269; Gaj and Borowski-Beszta 2020; McBeath et al. 2020). Both early season severe P and K deficiencies cannot be easily alleviated with later applications, therefore, producers could potentially use the nutrition indices PNI and KNI to adjust fertilization for the following growing season. Because a nutrient deficiency is expected to affect negatively the aboveground biomass production prior to grain yield,

Fontana et al. (2021) suggested that the PNI could be used as safeguard to avoid a grain yield loss due to a P limitation.

Along with providing new on-farm diagnostic possibilities to improve nutrient management practices, critical dilution curves have implications for breeding programs, crop modeling, and explaining crop performance. The indices of nutrition for N, P, K, and S are useful co-variables to consider for interpreting field data for the comparison of genotypes, while the allometry parameters (i.e. the decrease in nutrient concentration during aboveground biomass accumulation) can be used for crop phenotyping (Lemaire et al. 2019). These indices can also be used as input data for modeling crop growth in response to varying nutrient supplies and for explaining variations in crop performance at the field and regional levels.

The allometric approach, initially developed for critical N curves, clearly applies also to P, K, and S. However, more research is needed to analyze the compartmentalization of these elements within plants. The theoretical framework developed for N and recently reviewed by Lemaire et al. (2019), considers plant mass to consist of two compartments: The first compartment consists of metabolic tissues directly involved in growth processes, such as photosynthesis and meristematic activity, and has a high N concentration. The second compartment consists of structural tissues necessary for plant architecture and has a low N concentration. As plant size increases, the dilution process is determined by the allometry between the metabolic and structural tissues. Structural tissues, primarily stems, increase at a greater relative rate than metabolic tissues, which are primarily found in leaves. This leads to an ontogenetic decrease in the metabolic component. Therefore, it is likely that this framework also applies to P, S, and possibly other macronutrients and micronutrients (though not K; see below), but this remains to be validated. Other challenges in determining critical dilution curves include the potential for luxury consumption, which occurs for both P and K. In the absence of an universal critical curve that could be broadly used, it will be necessary to determine the domain of applicability for a set of  $G \times E \times M$  situations and highlight the uncertainty using the Bayesian method.

A study on Nc curves of wheat, maize, and rice (*Oryza sativa*) highlighted a positive linear relationship between the N concentration in aboveground

biomass of  $1 \text{ Mg ha}^{-1}$  ( $a$  coefficient) and the dilution effect ( $b$  coefficient) (Makowski et al. 2020). We investigated whether this relationship could be extended to N, P, K, and S and, in this context, whether higher nutrient concentrations lead to higher dilution. Since plant demand for N exceeds that for P, the critical concentrations at  $1 \text{ Mg ha}^{-1}$  of shoot biomass and the dilution coefficient are both higher for N than for P in most crops (Plénet and Lemaire 2000; Ziadi et al. 2008; Cadot et al. 2018; Gagnon et al. 2020; Morel et al. 2021; Jégo et al. 2022). Similarly,  $a$  and  $b$  coefficients were greater for the Nc curve ( $38.5 \times \text{SB}^{-0.57}$ ; Ziadi et al. (2010b)) of spring wheat and maize than those of the Sc curve (Table 3). Additionally, the Sc and Pc curves have relatively close coefficients related to the concentration of  $1 \text{ Mg ha}^{-1}$  and dilution in maize and wheat (Tables 1 and 3), suggesting that the dilution behavior of P and S in aboveground biomass is comparable. These observations align with the assumption that the initial concentration and dilution are proportional, regardless of the nutrient. However, the concentrations of N and K are similar for various crops, but K dilution can be lower than N dilution. Although the estimated dilution coefficients for K and N were very close (0.45 and 0.44, respectively) for winter wheat in two studies (Justes et al. 1994; Fontana et al. 2022), a coefficient of dilution of only 0.31 was also reported (Song et al. 2024). In potatoes grown in Columbia, Gomez et al. (2019) reported a value of 0.19 while most values of the dilution coefficient for N are closer to 0.40 (Bohman et al. 2023). Furthermore, the P dilution coefficient was also higher in tomato (*Solanum lycopersicum*) compared to K dilution whereas K concentration at  $1 \text{ Mg ha}^{-1}$  was 10 times higher (Tables 1 and 2). We suspect that the fact that K is poorly constitutive of crop tissues and mostly in an ionic soluble form (in contrast to P and S) could explain the rather low K dilution even if more data are necessary to formally test this hypothesis.

Global change could modify the balance between nutrients in soils and crops as well as crop productivity (Dijkstra et al. 2012; Sardans et al. 2017; Costa et al. 2022) and, therefore, influence the dilution curve parameters. The increase in atmospheric  $\text{CO}_2$  concentration is expected to promote aboveground biomass production and to lower the uptake of some nutrients (Uddling et al. 2018; Jin et al. 2019). Higher temperatures could increase nutrient uptake and

biomass production, as well as influence the nutrient balance through various mechanisms, such as nutrient diffusion in soils and plants and plant growth in the early stages of development (Turner and Lahav 1985; Gavito et al. 2001; Karamanos 2013; Zhao et al. 2020). The increased occurrence and extent of water deficits could also influence the crop nutrient balance (He and Dijkstra 2014) and so the dilution curves. Water limitation was shown to affect critical N dilution curves (Bélanger et al. 2001; Errecart et al. 2014), which could indirectly result in underestimated Pc curve (Fontana et al. 2021). The effect of the changes in atmospheric  $\text{CO}_2$  concentration, temperature, and water availability on critical dilution curves have not yet been studied but should be considered in future studies.

The co-limitation can be partly explained by the capacity of plants to perceive directly signals related to soil nutrient concentrations and to use this information to adapt their absorption capacity within integrated starvation or satiety responses (Sadras 2006; Ohkubo et al. 2017; Briat et al. 2020). The strong relationships of N concentrations with P and K concentrations as described above and their related adjustments confirm the multiple limitation hypothesis that assumes an adapted balance of resource allocation to maximize crop growth (Seghouani et al. 2024). For instance, N conversion efficiency and grain yield in wheat aboveground biomass were influenced by the magnesium (Mg):P ratio due to Mg co-limitation resulting in low grain yield and P co-limitation resulting in high grain yield (Weih et al. 2021). These authors found that an increase in grain biomass during the growing season, due to higher N and P uptake, was associated with a greater relative increase in other macronutrients and micronutrients. Ideally, critical dilution curves would be established by considering nutrient interactions concomitantly. The dilution of other nutrients (e.g., Ca, Mg) has rarely been investigated, though it can occur (Castellanos Ruiz et al. 2022b).

Different numerical methods can be combined to study dilution and nutrient interactions while avoiding the biases inherent in the use of ratios. These biases include spurious correlations due to additional degrees of freedom in compositional data and variances influenced by the choice of numerator and denominator. For example, N:P and P:N ratios have different variances. Dilution of i) clr scores i.e.

natural logarithm of the ratio of a nutrient concentration-to-the geometric mean of all others (Parent and Daifir 1992) or ii) ilr scores that targets specific nutrient balances (e.g.  $\text{NPK} \mid \text{CaMg}$ ;  $\text{N} \mid \text{PK}$ ;  $\text{K} \mid \text{P}$ ;  $\text{Ca} \mid \text{Mg}$  that are linearly independent; (Parent et al. 2013) appear promising to investigate nutrients interactions while avoiding mathematical biases. There are many ways to improve our understanding of critical dilution curves and provide robust dilution curves that account for nutrient multi-limitations. However, the conditions necessary to test the stability of the Pc-Nc relationships, as defined for the maize Nc curve (Ciampitti et al. 2021), have not yet been met. Overall, there is a lack of data to test the following: i) to what extent N status influence Pc, Kc, and Sc, ii) how much P, K, and S crop demand influences N status, and iii) the possibility to avoid aboveground biomass determination by analyzing N to estimate Pc and then to calculate PNI. For this last point, it is likely that N-P co-limitation, which can change with aboveground biomass levels, is important to consider. This results in high uncertainty in Pc estimation using only N concentration.

## Conclusion

The concept of critical dilution curves, applied to P, K, and S, offers new opportunities for the efficient analysis and diagnosis of multi-element crop nutrition. However, data are lacking to refine the critical dilution curves for these three nutrients, determine their universality or domain of applicability, and confirm the theoretical framework for their dilution in increasing shoot biomass. New data must be generated and combined with existing data to create reliable critical dilution curves. The effect of N nutrition on the critical dilution curves of P, K, and S highlights the strong interaction between nutrients and the need to consider nutrient relationships when developing critical dilution curves. There are many avenues to explore to improve our understanding of the critical dilution curves of phosphorus, potassium, sulfur, and other nutrients (e.g., Ca and Mg), as well as quantify nutrient relationships. This would enhance our understanding of nutrient multi-limitations and co-limitations.

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## Declarations

**Competing interest** The authors declare no conflict of interest of any kind that could have influenced the work reported in this paper.

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