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REVIEW ARTICLE

Allometric approach to crop nutrition and implications for crop diagnosis and phenotyping. A review

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Abstract

Historically, the agronomic focus of crop mineral nutrition has yielded responses to individual elements (N, P, K…) to determine the economically optimum fertilization rates. This "prognostic" approach required several parameters for crops, climates, and soils that are often estimated with large uncertainty leading to over-fertilization and environmental problems in some systems (e.g., maize in China), and under-fertilization and soil mining in other systems (e.g., wheat in Australia).

In this review, an alternative approach is developed for reducing the uncertainty intrinsically linked to this prognostic approach. Our approach is based on four propositions: (1) the evidence of an allometry between the metabolic shoot mass (scaling with leaf area) and the structural shoot mass (supporting and vascular tissues) within plants that allows the formulation of critical N dilution curves and the determination of the Nitrogen Nutrition Index (NNI) for estimating the N nutrition status of field crops; (2) the co-regulation of crop N uptake dynamics by both soil N supply and crop N demand in relation with its growth capacity that allows a better, more generalizable estimation of timing and rate of fertilizer; (3) a better understanding of the effects of genotype–environment–management interactions on N use efficiency in cropping systems reducing then drastically uncertainties linked to the classical prognostic approach for N fertilization; (4) as P and K also relate allometrically with biomass, P and K concentrations can be directly related to N concentration for the formulation of a multi-element diagnosis of crop nutrition. Here, we develop the theoretical background supporting these four propositions and outline implications for both fertilization management and crop phenotyping.

Keywords Crop N-P-K-S nutrition · Crop fertilization · Allometry in plants · Leaf area index · Crop diagnosis · N dilution

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1 Introduction

Historically, crop yield has been closely linked with nutrient availability to plants, particularly nitrogen (N) (Sinclair and Sinclair 2010). Until the 18th century, cereal grain yields in Europe were no more than 1 t ha^{-1} reflecting the low N input of less than 15–20 kg ha^{-1} to cropping systems from natural processes such as lightning and N_2 fixation by free-living soil microbes. The advent of the "Norfolk rotation" in England in the 18th century resulted in the doubling of grain yields to about 2 t ha^{-1}. This rotation included 2 to 3 years of a clover/ryegrass mixture that provided the additional N to support the wheat yield increase. From the end of the Second World War until the end of the 20th century, the huge increase in global cereal production has been associated with a 7-fold increase in the use of N fertilizers and a 3.5-fold increase in the use of phosphorus (P) fertilizers (Tilman et al. 2002). As industrial production of N fertilizer depends on fossil energy and is associated with high greenhouse gas emissions, and P fertilizer is non-renewable, these two nutrients have to be used more efficiently in cropping systems.

The future in improved nutrient management is not altogether clear. Worldwide, cropping systems are diverse and can be segregated into at least two different levels of intensification (Fischer and Connor 2018). In low input systems, because of water scarcity and/or low access of farmers to technology and financial resources, under-fertilization can lead to soil mining and soil degradation (Angus and Grace 2017). In high input systems, more precise management of fertilizers is necessary to maintain or even continue to increase crop yield, while resorbing the excess of N and P flows across agroecosystems and the associated environmental impacts (Galloway and Cowling 2002). To account for the diversity of biotic and abiotic variables that affects nutrient use, quantitative tools are required to assess nutrient influence on crop growth and yield. In recent years, such quantitative tools have been developed for N and they offer guideposts for expanding the understanding to other nutrients such as P, potassium (K), and sulfur (S).

The objectives of this paper are

1. To briefly review the classical analysis of crop nutrition and its limitations
2. To consider process-based perspectives linking growth and N, and their limitations
3. To examine allometric approaches for describing crop growth responses to N
4. To consider extension of the allometric approach from N to P and K, and accounting for interactions and co-limitations among nutrients
5. To outline the implications of this integrated approach for the diagnosis of crop nutrition, the interpretation of genotype–environment–management interactions in terms of nutrient-use efficiency, and crop phenotyping

2 Classical analysis of crop nutrition

The scientific analysis of crop nutrition mostly evolved from the work of Jean Baptiste Boussingault (1855) who proved the link between N accumulation in plants and soil nitrate fertility. At about the same time, Justus von Liebig (1855) developed the Law of the Minimum: "plants grow only to the extent allowed by the single nutrient that is most limiting". It is now clear that the Law of the Minimum fails to capture interactions among nutrients, and between nutrients and other resources including water (Sinclair and Park 1993; Cossani and Sadras 2018).

Recognizing the limitation of von Liebig's theory, Liebscher (1895) proposed the Law of the Optimum: "all nutrients are used most efficiently when the availability of the nutrient that is most limiting is increased near its optimum". While the Law of the Optimum is more consistent with observations (de Wit 1992), the approach remains static and offers no universal insight about crop nutrient uptake and allocation, nor does it account for the temporal dynamics of crop growth and nutrient accumulation, and partitioning throughout a growing season.

The initial analysis of crop nutrition led to empirical curves relating crop yield with nutrient availability for the purpose of fertilizer recommendations. Although those empirical curves and their related recommendations have helped to improve crop nutrition, they do not capture the seasonal dynamics of nutrients in soils and crops, nor the intra- and inter-seasonal variation in weather, particularly rainfall. Response curves apply to the conditions under which the data were collected, but they cannot be extrapolated, leading to large uncertainties and limited conclusions.

Response curves to N fertilization averaged across sites and seasons are still the basis for N fertilizer recommendations in many cropping systems (Fig. 1), but they can lead to over-fertilization and high residual soil nitrates in some systems, for example for potato in Canada (Bélanger et al. 2003). Those "average" response curves do not take into account the large site-to-site and seasonal variation in the yield response to N (Bélanger et al. 2000). In systems where N fertilizer is costly or less accessible for other reasons, crops are typically under-fertilized (Monjardino et al. 2013, 2015; Dimes et al. 2015) at the risk of soil mining (Angus and Grace 2017).

Most tools for crop nutrition diagnosis and fertilizer decisions are based on soil or plant tests. For instance, the soil N supply can be estimated through the calculation of balances between net N mineralization, N leaching and volatilization, and soil N mineral content (Machet et al. 2017). However, this "prognosis" approach suffers from a large uncertainty in estimates of crop N demand because of growth and yield variations with soil attributes, weather, and crop management. Moreover, Ravier et al. (2016) showed that the application of this method by farmers generally leads to over-

Fig. 1 Crop fertilization management is based on empirical crop responses to timing and rate of fertilizer application (photo INRA; Experimental fields, Domaine Epoisses, Dijon, France)

fertilization because of a tendency for over-estimating the target yield. Soil nitrate tests, either prior to sowing or in mid-season, to determine the required N fertilizer have been used with mixed results. This approach usually works well in drier areas but has been shown to be less effective in humid areas of Canada for potatoes and spring wheat, particularly when used pre-sowing (Bélanger et al. 1998, 2001b). In environments where crops rely on uncertain seasonal rainfall, uncertain target yield is the bottleneck to determine N fertilizer requirements (Monjardino et al. 2013).

For P and K, recommendations are usually based on soil tests for evaluating the available P and K mineral stocks for comparison with yield responses to further nutrient applications. The degree of success of soil chemical extractions to estimate the amount of P available to crops and their interpretation in predicting the amount of P fertilizer needed to reach near maximum crop yield is, however, limited (Valkama et al. 2011; Bélanger et al. 2015a, b, 2017). In some cropping systems, a simple threshold defining non-limiting and limiting nutrient conditions has been practiced. This approach can result in over-fertilization but has been accepted where the cost of fertilizer is a small component of production costs (e.g., in subsidized systems), or in industries such as horticulture with intrinsically high-value crops (Jobbágy and Sala 2014).

Plant tissue analyses for crop nutrition diagnosis are based on the nutrient concentration of specific organs (e.g., leaves, petioles, stem bases) or of whole plants. These methods rely on the definition of a critical concentration, that is, concentrations required to achieve maximum shoot growth and yield. In most cases, however, critical concentrations are based on empirical relationships that cannot be generalized or extrapolated to diverse situations (Smith 1962; Walworth and Summer 1987).

3 Dynamics of crop mass and nutrient accumulation

For most crop species, the life cycle can be divided into two main periods: (i) the vegetative phase, when developing leaves, roots, and stems are sinks for both photo-assimilates and reduced N compounds and (ii) the reproductive phase during which senescing vegetative tissues are sources of carbon (C) and mobile nutrients for developing reproductive and/or storage organs (Lemaire 2015). This distinction is convenient for our analysis, but the vegetative and reproductive phases often overlap to different degrees depending on the species (Cohen 1971; Amir and Cohen 1990).

The vegetative phase is essential for the accumulation of biomass and nutrients that contributes to yield formation. For grain crops, grain yield is first determined by the crop mass and nutrient accumulated at the end of this vegetative phase, and by grain filling associated with further nutrient uptake and translocation during the reproductive phase. However, most of the nutrient uptake occurs in the vegetative phase and, consequently, the primary focus of this paper is the vegetative phase when most decisions on fertilization are taken. Some aspects related to the reproductive phase, particularly important for grain crops, are also considered.

3.1 Resource capture and use by crops

Contemporary crop growth analysis is based on the concept of the capture of resources and the efficiency with which they are used. Crop canopies capture CO_2 and radiation from the atmosphere, while roots capture water and nutrients from the soil (Monteith 1994). The capture of water and its interaction with N are important, but they are out of the scope of this review. Recent analyses of this interaction can be found in Kunrath et al. (2018) for perennial forage crops and in

Cossani and Sadras (2018) for grain crops. Here, we focus on three processes:

1. Capture of radiation and CO_2 by crop canopies
2. Uptake of nutrients by plants and crops
3. Allocation of mass and nutrients to plant organs through morphogenesis that drives the size, architecture, and functionality of the crop canopy and the root system

The processes of capture and allocation of C and nutrients are highly coupled with positive feedbacks and tradeoffs. A greater allocation of resources to the crop canopy favors C assimilation, whereas a greater allocation to roots favors nutrient and water uptake (Lambers 1983). Crop growth is proportional to the amount of photosynthetic active radiation (PAR) intercepted by the crop canopy and radiation use efficiency (RUE) (Monteith 1972):

$$\mathrm{W_t} = \mathrm{RUE} \times \sum(\mathrm{PARi}) \tag{1}$$

where W_t is the total crop dry matter mass (shoot + root) in g dry matter (DM) m^{-2}, $\sum(\mathrm{PARi})$ is the cumulative amount of photosynthetically active radiation intercepted by the crop canopy in MJ m^{-2}, and RUE represents the integrated net dry mass accumulation and is expressed in g DM MJ^{-1}. This model, often simplified by excluding roots, has been shown to be appropriate for perennial forage crops such as alfalfa (Gosse et al. 1984) and tall fescue (Bélanger et al. 1992a) and for annual crops such as wheat (Sinclair and Amir 1992; Sinclair et al. 1993), maize (Muchow and Sinclair 1993) and sorghum (Sinclair et al. 1997).

Nitrogen deficiency affects crop growth by reducing the capture of radiation, the radiation use efficiency, or both. Nitrogen deficiency reduces the leaf expansion rate as a consequence of reduced rates of cell division and expansion in meristems (Gastal et al. 1992; Gastal and Nelson 1994; Trapani et al. 1999). Severe N deficiencies can also increase the rate of leaf senescence, further contributing to a smaller crop canopy and reduced capture of radiation (Thomas and Ougham 2015). Nitrogen deficiency can also decrease the leaf photosynthetic capacity and RUE (Sinclair and Horie 1989; Connor et al. 1993; Grindlay 1997). However, N deficiency favors the mobilization of N from shaded leaves at the bottom of the canopy to upper leaves, buffering the effect on RUE (Sinclair and Horie 1989; Gastal and Bélanger 1993; Bélanger et al. 1994; Gastal and Lemaire 2002). Consequently, the main effect of N deficiency is a reduction in growth primarily through a reduction in canopy leaf area and the capture of radiation (Bélanger et al. 1994).

Phosphorus deficiency also reduces the leaf expansion rate through its effects on the rate of cell production (Assuero et al. 2004) and decreases crop growth by reducing PAR interception rather than by decreasing RUE (Plénet et al. 2000). Potassium deficiency decreases the leaf area index (LAI) of maize through both reduction of leaf appearance rate and leaf size (Jordan-Meille and Pellerin 2004). Even a mild K deficiency affected cotton leaf expansion but only a severe K deficiency decreased leaf photosynthesis (Gerardeaux et al. 2010). All these results indicate a generalized response of crops to abiotic stresses, including nutrient deficiency, of a reduction in crop growth by primarily affecting the LAI and the capture of radiation (Connor and Sadras 1992; Sadras et al. 2005; Valle et al. 2009).

This overview of the processes defining crop growth highlights the importance of canopy leaf area and, hence, the need to model LAI expansion accounting for genotype, temperature, and the supply of water, N, and P. The difficulty for modeling this important trait is the scaling gap between leaf area expansion, a two-dimensional process, and crop mass accumulation, a three-dimensional process, if we assume an approximately constant dry matter content per unit of plant volume. Most crop models circumvent this difficulty by using empirical algorithms for dry matter allocation to plant morphological compartments (root, leaves, and stems) for estimating LAI expansion dynamics directly from shoot dry matter accumulation:

$$\mathrm{LAI} = \mathrm{W_t} \times (\mathrm{dW_{sh}}/\mathrm{dW_t}) \times (\mathrm{dW_l}/\mathrm{dW_{sh}}) \times \mathrm{SLA} \tag{2}$$

with W_t the total dry matter as resulting from Eq. (1), dW_{sh}/dW_t the fractional allocation of dry matter to shoots, dW_l/dW_{sh} the fractional allocation of shoot dry matter to leaves (e.g., leaf/stem ratio), and SLA the specific leaf area (leaf mass per unit leaf area). In many models, these fractional allocation coefficients are empirically fixed involving critical threshold values associated with plant ontogeny. Equations (2) + (1), therefore, define the increase in LAI based on the next increment in $\sum$PARi and in W_t, usually done on daily iterations. But such algorithms, even if they allow empirical simulations of LAI, do not represent any physiological processes and can lead to circularity.

Mechanistic models seek to simulate the processes that directly influence leaf area development. For example, the SSM model described in detail by Soltani and Sinclair (2012, 2015) and Soltani et al. (2013) postulates that LAI expansion is driven by temperature that determines leaf N demand based on a critical N content per unit leaf area. Also, the stem fraction of shoot mass is determined by the C supply with a variable N concentration. Such models partially capture the primordial role of N supply in dry matter allocation within canopies, and the secondary dependency of leaf expansion from photosynthesis. This contrasts to Eq. (2) where LAI results from empirical allocation coefficients. Nevertheless, even if these models represent a progress in understanding, some threshold values for minimum N concentration in plant tissues are usually required.

Furthermore, the study of C and N partitioning between roots and shoots has to move from a morphological to a more functional viewpoint as discussed by Lemaire and Millard (1999). Körner (1991) showed that, in terms of resource capture, only the allocation between leaves and fine roots is relevant, while the shoot/root mass ratio across a large range of species often results from the partitioning between stems and coarse (or tap) roots having storage or anchorage functions. Using the model of Minchin et al. (1993) for C and N substrate transport and allocation within plants, Lemaire and Millard (1999) showed that the allocation of dry matter to shoot meristems for leaf area expansion always has the priority leading to an increase in the proportion of assimilates allocated to shoots at the expense of roots (Farrar 1988; Durand et al. 1989; Bélanger et al. 1994). This approach accounts for the higher shoot/root ratio of plants grown under high temperatures or N supply (Durand et al. 1991).

The allocation of assimilates to leaf meristems for leaf area expansion is a dynamic process that modulates the capture of PAR and, hence, drives growth (Eq. 1). This priority for assimilate use in shoots allows a positive feedback for crop growth until the maximum LAI is achieved. This priority for leaves is emphasized by the N and P supply at the expense of root expansion. However, if N and P deficiencies restrict shoot demand, then a greater allocation to roots becomes possible that partially restores the nutrient capture capacity of the plant as proposed by the functional equilibrium concept (Brouwer 1963).

3.2 Allometric approach

3.2.1 Dry matter allocation within plants

Allocation of C and nutrients in plants is central to crop growth and differences in allocation patterns among species reflect response strategies to differing selection pressures (Stearns 1992). These strategies are indicative of varying physiological mechanisms and ecological performance (Körner 1991; Niklas 1994; Schwinning and Weiner 1998). Allocation patterns are under genetic control (Körner 1991; Weiner 2004), as illustrated by dwarfing genes that decrease dry matter allocation to stems and increase allocation to grains in cereals (Fischer and Stockman 1986; Youssefian et al. 1992). However, allocation patterns are plastic in response to the abiotic or biotic environment (Bradshaw 1965; Andrews et al. 1999). A noticeable consequence of this plasticity is the phenotypic range that can be expressed by plants of a similar genotype.

Growth of plant parts commonly tracks well-defined allometric trajectories (Weiner 2004). An example of such an allometric trajectory is the relationship between dry matter allocated to shoots (W_{sh}) and total plant mass (W_t) (Weiner 2004)

$$W_{sh} = k \times (W_t)^{\Upsilon} \tag{3}$$

with Υ as a scaling coefficient equal to the ratio between relative shoot growth rate $[1/W_{sh} \times d(W_{sh})/dt]$ and relative plant growth rate $[1/W_t \times d(W_t)/dt]$. Modifying Eq. (3) by dividing both sides by W_t, an expression of the ratio W_{sh}/W_t is obtained:

$$W_{sh}/W_t = k \times (W_t)^{\Upsilon-1} \tag{4}$$

Equation (4) shows explicitly that the W_{sh}/W_t ratio is not constant within a growing season since it depends on W_t. Using ^{14}C labeling in grass swards with different N treatments, Bélanger et al. (1992b) showed that shoots used a decreasing proportion of newly assimilated C when the existing amount of C in shoots increased. This decrease can be described by an allometry with a scaling coefficient of − 0.62 under non-limiting N, while this coefficient drops to − 0.78 under limiting N supply. Hence, the W_{sh}/W_t ratio has an “apparent plasticity” depending on the shoot mass as it varies with age or environmental factors such as the atmospheric CO_2 concentration, and the supply of N or water (Evans 1972; McConnaughay and Coleman 1999). As a result, the allometric expression of growth can be seen as a time-dependent process, since both W_t and W_{sh} vary during the growing season. Similar allometric relationships describe the allocation of shoot mass between leaves and stems, whereby the leaf/stem ratio declines with plant ontogeny for forage species such as timothy (Bélanger et al. 2001a) or alfalfa (Lemaire et al. 1989), and for cereals (Hoogmoed and Sadras 2018).

Weiner (2004) suggested that an allometric relationship has to be considered as the null hypothesis for studying the allocation of dry matter in plants and crops in response to genotype, resources (water, nutrients, CO_2, and radiation), and non-resource factors (e.g., temperature, light quality, mechanical constraints). The pattern of allocation could then be separated into two components. One component is the mass-dependent variation in allocation; this has been termed “ontogenetic drift” (Evans and Hughes 1961; Evans 1972). A second component is the mass-independent variation in allocation through modification of the allometry trajectory, reflected in scaling coefficients and variation in partitioning ratios (shoot/root or leaf/stem) at a similar shoot mass as illustrated in Fig. 2.

Analogous to Eq. (3), Lemaire et al. (2007) showed that the crop leaf area index (LAI) is allometrically related to W_{sh} during vegetative growth:

$$LAI = k \times (W_{sh})^{\alpha} \tag{5}$$

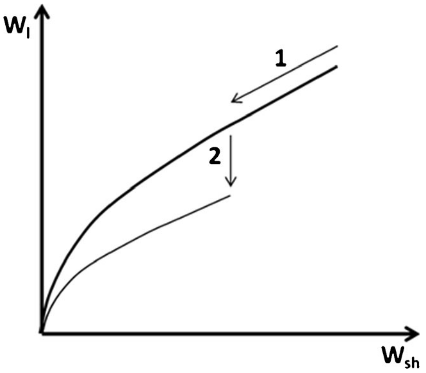

Fig. 2 Illustration of the mass-dependent (arrow 1) and the mass-independent (arrow 2) variations of the fractional allocation of dry matter to leaves (W_l) with shoot biomass (W_{sh}). In this example, the allometric coefficient is less than 1, and consequently the W_l/W_{sh} ratio declines as W_{sh} increases

The scaling coefficient α depends on the LAI of the canopy. For LAI > 1, α is close to 0.67, while α is near 0.90 for a sparse canopy (LAI < 1) or isolated plants. This is illustrated for wheat in Fig. 3 where the linear, natural logarithm form of Eq. (5) is used to solve for α as the slope. In this case, α was 0.93 when LAI was less than 1 and 0.60 when LAI was greater than 1. Comparisons across a wide range of species, including C3 vs. C4 and monocot vs. dicot, confirm the stability of α (Table 1) and the generality of distinction between "open" and "closed" crop canopies. In the absence of competition for light (isolated plants), high α indicates growth favoring leaf expansion. In canopies with large leaf area, the allocation to stems increases at the expense of the allocation to leaves.

Given that α is less than 1.0 in all cases, Eq. (5) indicates that, as shoot mass increases, a smaller proportion of dry matter is allocated to leave area expansion while a greater proportion of dry matter is allocated to structural tissues such as stems, petioles, or leaf midribs. This dynamics of allocation reflects an "increasing dry matter cost" for new leaf area expansion. As detailed in Box 1, this increase in dry matter cost for new leaf area expansion can be interpreted as a consequence of changes in plant allocation resulting from a shade-avoidance adaptation of individual plants mediated by photo-morphogenesis (Ballaré et al. 1995).

Box 1 Quality and amount of light modulates allocation of dry matter and N in crops

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Isolated plants without interacting neighbors have a mass allocation to leaves that favors light capture. But in the presence of neighbors, patterns of allocation are modulated by the shifts in the light environment including changes in light quality (red-far red ratio and blue light) and decreased irradiance at the bottom of high-LAI canopies (Aphalo and Ballaré 1995; Ballaré et al. 1997). This light environment enhances the allocation of dry matter to vertical and thickness structures that favor N-poor plant components including stem internodes, leaf petioles, and midribs that accelerate the N dilution process. Moreover, the profile of foliar N allocation within canopies is related to the light extinction profile (Hirose and Werger 1987; Lemaire et al. 1991; Anten et al. 1995; Sadras et al. 2012) and this contributes also to N dilution at the whole crop level.

The allometries between LAI or N_{upt} and W_{sh} are based on (a) the scaling between leaf area and the mass of active plant tissues responsible for growth, and (b) the proportionality between plant growth rate in high LAI canopies and $W_{sh}^{2/3}$, as postulated by Hardwick (1987). This model is also convergent with the general self-thinning law in ecology of a power relationship of − 3/2 between plant mass and plant density within high LAI plant stands (Yoda et al. 1963; Sackville-Hamilton et al. 1995). All these relationships are interpreted by the fact that the light environment within high-LAI canopies favors an isometric growth of plants, i.e., similar relative growth rates in the three dimensions that maintain leaf area within the well illuminated layers of the canopy. Consequently, each increment in leaf area is accompanied by an increasing quantity of structural tissues (Niklas 1994).

Equation (5) can be divided by W_{sh} to obtain an expression for the leaf area ratio (LAR, leaf area divided by shoot mass) as a function of shoot mass:

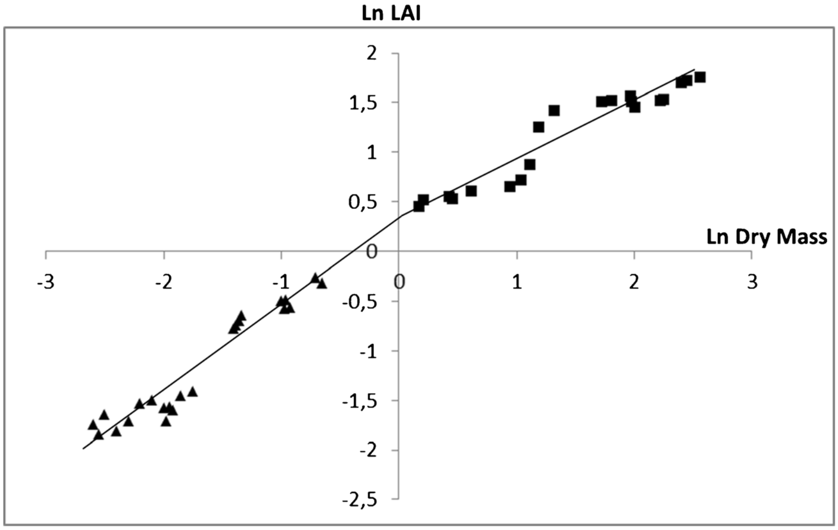

Fig. 3 Allometry between crop LAI and crop dry mass for wheat from seedlings to LAI = 1 [triangles; $LAI = (0.93xW_{sh}) + 0.34$, $R^2 = 0.90$] and from LAI = 1 to heading [squares; $LAI = (0.60xW_{sh}) + 0.34$, $R^2 = 0.91$]. After Lemaire et al. (2007)

Table 1 Values of allometric coefficients "b" in $N_{upt} = a \times (W_{sh})^b$ and "α" in $LAI = k \times (W_{sh})^{\alpha}$ for isolated plants with subscript "i" (b_i and α_i) and a dense crop with subscript "d" (b_d and α_d) for a range of crop species, and values of coefficient "k" (plant leafiness) and coefficient a/k of Eq. (17), the quantity of N uptake per unit LAI expressed as kg N ha^{-1} LAI^{-1}. After Lemaire et al. (2007)

Species	Isolated plant		Dense crop			
	b_i	α_i	b_d	α_d	k	a/k
Alfalfa	0.90	0.89	0.67	0.67	1.94	25
Canola	0.84	0.78	0.75	0.72	1.59	26
Sunflower	0.97	0.95	0.55	0.50	1.83	27
Wheat	0.92	0.89	0.56	0.61	1.13	39
Rice	0.91	0.98	0.58	0.63	1.31	32
Sorghum	0.94	0.95	0.61	0.65	1.41	24
Maize	0.94	0.95	0.63	0.71	1.06	32
Mean	0.91	0.89	0.62	0.63		

$$LAR = k \times (W_{sh})^{\alpha-1} \tag{6}$$

Since $\alpha - 1 < 0$, this equation predicts that the LAR declines as shoot mass increases.

3.2.2 Nitrogen uptake and distribution in plants and canopies

An allometric approach was developed to express N uptake and distribution in crops not unlike the approach described above for plant mass changes. Lemaire and Salette (1984a, b) and Greenwood et al. (1990) showed that shoot N uptake (N_{upt}, kg ha^{-1}) was related to W_{sh} when W_{sh} was greater than 1 t ha^{-1}:

$$N_{upt} = a \times (W_{sh})^b \tag{7}$$

The allometry between N_{upt} and W_{sh} offers insight about crop N use efficiency (Box 2).

Box 2: Consequences for assessing N use efficiency by crops

Derivative of Eq. (7) with time allows the expression of the rate of crop N uptake (dN_{upt}/dt) in relation with the crop growth rate (dW_{sh}/dt) and the shoot mass (W_{sh}):

$dN_{upt}/dt = abW_{sh}^{b-1} \times dW_{sh}/dt$ Eq(7')

Under non-limiting N supply, the crop N uptake rate (dN_{upt}/dt) depends on the potential crop mass accumulation rate (dW_{sh}/dt), but it declines as crop mass increases. Devienne-Barret et al. (2000) showed that the rate of crop N uptake is dependent on both crop growth rate and soil N availability leading to a family of N_{upt}-W_{sh} trajectories for each steady-state condition of soil N supply as represented in Fig. 4. This dual dependency of N uptake is well explained by physiological evidence on feedback regulation of root absorption capacity of mineral N (nitrate and ammonium) by shoot growth through C and N signals (Gastal and Saugier 1989; Lejay et al. 1999).

If N_f represents the rate of N fertilizer application, the nitrogen use efficiency ($NUE = dW_{sh}/dN_f$) for crop mass production is a function of two components: (i) the N absorption efficiency ($NAE = dN_{upt}/dN_f$) and (ii) the N conversion efficiency ($NCE = dW_{sh}/dN_{upt}$), so that

$$NUE = NAE \times NCE \tag{8}$$

dN_f being the increment in N fertilization rate. Then, the N_{upt}-W_{sh} allometry has two important consequences for analyzing variations in NUE due to genotype–environment–management interactions as underlined by Sadras and Lemaire (2014):

1. NAE is partly determined by crop growth rate so that genotypes having a higher crop mass should have a higher NAE than slow growing genotypes. This effect is shown on Fig. 4 where any increment in W_{sh} is associated with a corresponding increment of N_{upt} for each N supply. So, genotypic variation in NAE has to be compared at a similar shoot mass; otherwise, the difference would be trivial.
2. The N dilution process implies that dN_{upt}/dW_{sh} decreases as shoot mass increases, so that NCE (dW_{sh}/dN_{upt}) increases as shoot mass increases. Consequently, the NCE of different genotypes has also to be compared at a similar shoot mass; otherwise, the difference observed would be obvious with a larger crop having always a higher NCE than a smaller one.

An expression for plant N concentration (%N) is readily obtained from Eq. (7) by dividing both sides by W_{sh} and the right side by 10 for having plant N concentration in percent with W_{sh} in t ha^{-1}:

$$\%N = a/10 \times (W_{sh})^{b-1} \tag{9}$$

Given that $b < 1$, the %N decreases with increasing W_{sh}, which defines a "N dilution curve" over a range of W_{sh}. Lemaire et al. (2008) have shown, following the assumptions of Caloin and Yu (1984), that N dilution curves are consistent with the relative size of two major plant compartments:

1. W_m, the "metabolic compartment" of plant tissues directly associated with photosynthesis and growth processes, with a high N concentration: $\%N_m$
2. W_s, the "structural compartment" of plant tissues associated with plant architecture and hydraulic conductivity, with a low N concentration: $\%N_s$

$$W_{sh} = W_m + W_s \tag{10}$$

They postulated that the absolute growth rate (dW_{sh}/dt) of a crop should be, by definition, proportional to its metabolic compartment (W_m):

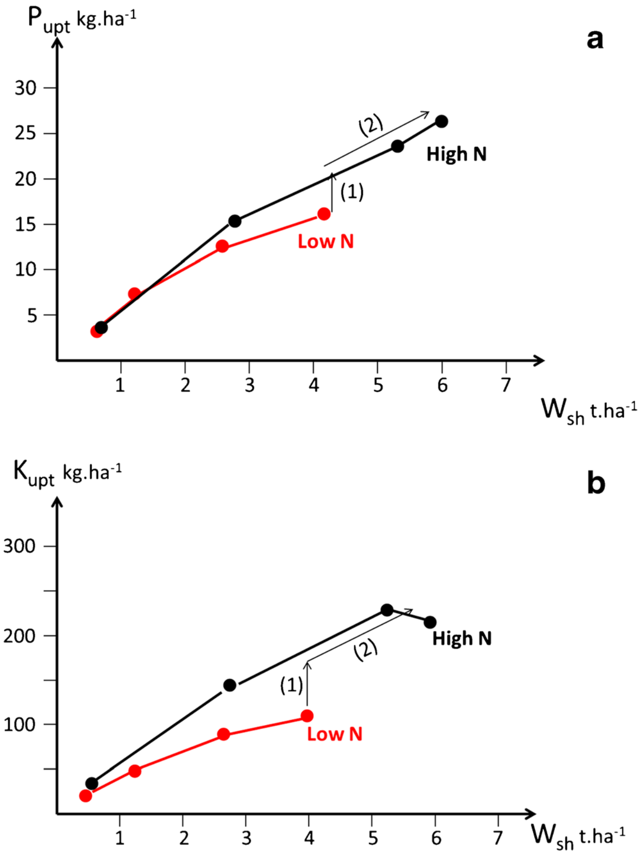

Fig. 4 Trajectories of N uptake as a function of shoot mass accumulation (W_{sh}) for different steady-state levels of N supply: N soil (N supply only from the soil without any N fertilizer application, N fert (N supply with a limiting N fertilization rate; N crit**.** (N supply with a minimum N application for achieving maximum shoot mass accumulation); and N max (N supply with a supra-optimum N fertilizer rate). Adapted from Gastal et al. (2014)

$$dW_{sh}/dt = k \times W_m \tag{11}$$

Rearranging Eq. (11) and dividing both sides by W_{sh} gives a relationship between the fraction of the metabolic component and the relative growth rate:

$$W_m/W_{sh} = 1/k \times 1/W_{sh} \times (dW_{sh}/dt) \tag{12}$$

Plant N concentration (%N) can be calculated from the relative contribution of the two compartments, W_m and W_s, to the plant shoot mass (W_{sh}) according to Eq. (10):

$$\%N = 1/W_{sh} \times [(\%N_m \times W_m) + (\%N_s \times W_s)] \tag{13}$$

Using Eqs. (12) and (13) gives

$$\%N = [1/k \times 1/W_{sh} \times (\%N_m - \%N_s) \times dW_{sh}/dt] + \%N_s \tag{14}$$

Caloin and Yu (1984) proposed that the metabolic component W_m is linked to the whole plant shoot mass (W_{sh}) by an allometric relationship:

$$W_m = c \times (W_{sh})^{\alpha} \tag{15}$$

Substituting W_m from Eq. (11) into Eq. (15) gives

$$dW_{sh}/dt = kc \times (W_{sh})^{\alpha} \tag{16}$$

Including Eq. (16) within Eq. (14) gives

$$\%N = \left[c \times (\%N_m - \%N_s) \times {W_{sh}}^{\alpha-1}\right] + \%N_s \tag{17}$$

Lemaire and Gastal (1997) showed that the difference between Eqs. (9) and (17), due to the existence of an asymptote different of 0 on Eq. (17) representing the minimum N concentration in structural tissues was only sensible for $W_{sh} >$ 20 t ha^{-1}, and that under this value, Eq. (9) could be considered as an acceptable approximation of the N dilution process.

Lemaire et al. (2008) showed that it was possible to determine the critical N dilution curves according to Eq. (9) corresponding to the minimum N concentration for achieving the maximum crop mass accumulation. Critical N dilution curves have been estimated for a large number of crop species. Using these critical N dilution curves (Eq. 9), it is possible, for each crop and stage during its vegetative phase, to determine a Nitrogen Nutrition Index (NNI) as the ratio between its actual N concentration ($\%N_a$) and the critical N concentration ($\%N_c$) corresponding to the actual crop mass (W_{sh}) of the crop. The NNI is an agronomically relevant trait for the diagnosis of crop N nutrition status and other applications (Box 3).

Box 3 Applications of the Nitrogen Nutrition Index (NNI)

NNI has been shown to be a good predictor of the relative crop mass production for forage and grassland species (Gastal et al. 2014). Moreover, NNI is associated with grain yield in maize (Plénet and Cruz 1997; Ziadi et al. 2008b), wheat (Justes et al. 1997; Ziadi et al. 2010a; Hoogmoed et al. 2018), barley and rice (Zhao et al. 2014; Tahir Ata-Ul-Karim et al. 2016), rapeseed (Colnenne et al. 1998), sunflower (Debaeke et al. 2012), and with potato tuber yield (Bélanger et al. 2001c).

The NNI can be used for four main purposes: (i) for an early-season diagnosis to guide top-dressing N in rainfed wheat (Neuhaus and Sadras 2018); (ii) as a forensic tool for benchmarking actual crop yield (Hoogmoed et al. 2018); (iii) as a reference for calibrating simpler and less time consuming diagnostic tools such as leaf chlorophyll (Ziadi et al. 2008c), leaf N concentration (Farrugia et al. 2004; Ziadi et al. 2009, 2010b), petiole nitrates (Bélanger et al. 2003), stem base nitrates (Justes et al. 1997), and remote sensing indices (Cossani and Sadras 2018); and (iv) in combination with prognostic N fertilization tools within decision support systems for a better adjustment of crop N fertilization management to actual crop demand (Ravier et al. 2018). Using the NNI requires destructive measurements of actual crop mass and its N concentration that are time consuming at farm level or indirect estimation with remote sensing (Baret and Fourty 1997; Cossani and Sadras 2018) that allow high spatial and temporal resolution. Currently, fertilizer recommendations for wheat in large areas of Western Australia rely on NNI derived from destructive sampling and laboratory analysis (Neuhaus and Sadras 2018). Estimation of NNI of rice, wheat, and maize crops through remote sensing is now developing widely across several regions in China for N fertilization decisions (Peng et al. 2010; Yao et al. 2010; Zhao et al. 2016).

Many crop simulation models ignore these fundamental allometries and simulate dry matter allocation (e.g., leaf and stem mass fractions and specific leaf area used to estimate LAI) as a function of plant phenology (Jones et al. 2003; Keating et al. 2003). Using an ontogenetic scale may be convenient for modeling purposes because phenological development and the accumulation of dry mass and N are all related with crop age. Phenology-dependent changes in allocation of dry mass between metabolic and structural tissues, chiefly stem-leaves during the phase of stem elongation, explain some of the scatter in nutrient-dry mass curves (Hoogmoed and Sadras 2018). For this reason, dilution curves relating critical plant N concentration and phenological stage have been advanced for cereals (Angus and Moncur 1985; Zhao et al. 2014). However, fitting curves to development stages is not justified because the independent variable is nominal rather than quantitative, and the relation between critical nitrogen concentration and crop mass has a stronger theoretical background (Hoogmoed and Sadras 2018, Hoogmoed et al. 2018; Ratjen et al. 2018). Moreover, even if the onset of stem internode elongation is a key developmental step that influences dry mass partitioning between leaf and stem, the leaf area ratio (LAR) (Eq. 6) seems more physiologically relevant to capture metabolic vs structural partitioning than the leaf/stem ratio alone. As shown by Ratjen et al. (2018), LAR is the product of L/S and specific leaf area (SLA), and these two traits are closely linked: when stem internodes elongate and L/S declines, the SLA increases for the leaves growing progressively into the well-illuminated layer of the canopy. The STICS model (Brisson et al. 1998) and the CATIMO model for forage grasses (Bonesmo and Bélanger 2002) use N dilution curves related to crop mass to assess N stress and to calculate crop N requirements

Lemaire et al. (2007) showed an interesting correspondence in the two scaling coefficients for LAI (α in Eq. 5) and N uptake (b in Eq. 7). As shown in Table 1, these two coefficients are conserved over a wide range of species. Consequently, if we accept that α is not different to b, a proportionality between N uptake and crop LAI is readily obtained and defined by the constant ratio *a/k*

$$\mathrm{N_{upt}} = \mathrm{a/k} \times \mathrm{LAI} \tag{18}$$

This proportionality between N uptake and LAI has been observed empirically for several crops and particularly for cereals (Sylvester-Bradley et al. 1990; Grindlay et al. 1993; Grindlay, 1997). The $\mathrm{N_{upt}}$-LAI proportionality of Eq. (18) leads to an emergent description for comparing N use among species and genotypes. The coefficient *a/k* vary across species for two main reasons: (i) morphological differences related to the “leafiness” coefficient *k* and (ii) metabolic differences for coefficient *a* between C3 and C4 species (Table 1). Species with “grass type” morphologies tend to have greater *a/k* and greater N uptake with increasing LAI than their non-grass counterparts.

3.2.3 Extension to P and K

A similar allometry between P uptake (Pupt) or K uptake (Kupt) and shoot mass accumulation as described above for N was reported from several studies on grasslands (Salette 1990; Salette and Huché 1991; Duru et al. 1992):

$$P_{upt} = a_P \times (W_{sh})^{b_P} \tag{19}$$

$$K_{upt} = a_K \times (W_{sh})^{b_K} \tag{20}$$

where *a* is nutrient uptake necessary for producing a shoot mass of 1 t ha^{-1}, *b* is the scaling coefficient, and subscripts indicate nutrient P and K. Critical $\mathrm{P_{upt}}$ and $\mathrm{K_{upt}}$ curves, corresponding to the minimum P and K uptake necessary to achieve maximum shoot mass ($\mathrm{W_{sh}}$), can be determined from field studies with different supplies of P and K.

Similar to the calculation for N, the plant P and K concentrations as a function of $\mathrm{W_{sh}}$ can be calculated:

$$\%P = \frac{a_P}{10} \times (W_{sh})^{b_P-1} \tag{21}$$

$$\%K = \frac{a_K}{10} \times (W_{sh})^{b_K-1} \tag{22}$$

These allometric equations first established empirically on grasslands and forage crops, illustrate a dilution in P and K concentration as $\mathrm{W_{sh}}$ increases. They are in line with the model developed by Greenwood and Stone (1998) and Greenwood and Karpinets (1997) on the dynamics of K uptake in vegetable crops that shows a decline in plant %K with increasing shoot mass. In the same way, the model developed by Greenwood et al. (2001) for P uptake shows that the plant %P needed for maximum plant growth decreases with increasing shoot mass. Several studies have since shown the decrease in plant % P with the increasing shoot mass of maize (Ziadi et al. 2007), spring wheat (Ziadi et al. 2008a; Bélanger et al. 2015a), and canola (Bélanger et al. 2015b).

The dynamic of P and/or K uptake as described by Eqs. (19–20) depend on the level of N supply in two ways as illustrated in Fig. 5: (1) through an increase in the P and K uptake capacity of plants at a similar crop mass and (2) through an increase in crop mass accumulation due to the effect of the increasing N supply.

The second effect can be simply explained by the increased P and K demand resulting from a higher crop growth rate and would correspond to a feedback control of P and K absorption rate similar to that well demonstrated for N (see above) and already postulated for P and K (Scaife 1994). The first effect is unexpected and would require a more fundamental

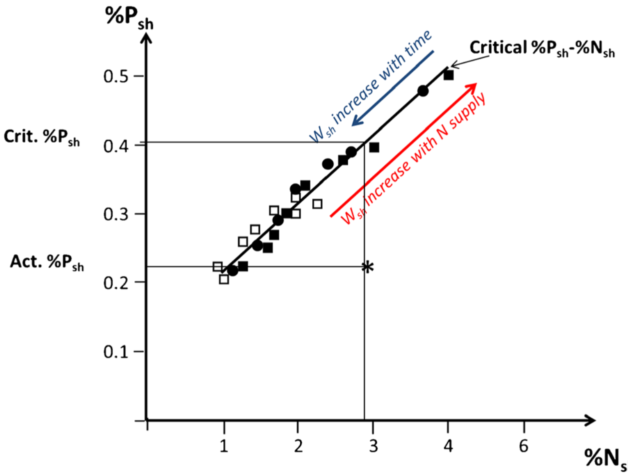

Fig. 5 Illustration of the effect of N supply on the allometry between P uptake (**a**) and K uptake (**b**) and shoot mass for natural grasslands. This effect can be decomposed into two parts: (1) an increase in P or K uptake at a similar shoot mass and (2) an increase in P and K uptake associated to the increment in shoot mass. Adapted from Duru et al. (1992)

understanding for explaining the positive effect of increased N supply on P and K absorption.

Several authors suggest using the P/N ratio for the diagnosis of P nutrition of crops (Güsewell et al., 2003; Drenovsky and Richards, 2004; Sadras, 2006; Greenwood et al. 2008). The allometric relationships of P and N with shoot mass (%P-W_{sh} and %N-W_{sh}) lead to the relationship between %P and %N as illustrated in Fig. 6, highlighting the variation in the %P:%N ratio. This ratio increases as %N decreases as a consequence of either (i) the dilution of N by increasing crop mass or (ii) a decrease in N supply. Consequently, the %P/%N ratio cannot be used alone as an unequivocal index of the P nutrient status of a crop.

Several studies have since shown that the %P/%N ratio varies with shoot mass (Ziadi et al., 2007; Greenwood et al., 2008; Bélanger et al. 2017) and the crop N status. Under non-limiting N, Greenwood et al. (2008) quantified the relationship between the %N/%P ratio and shoot mass for several annual crops and this relationship was later confirmed for perennial forage grasses (Bélanger et al. 2017). More research is needed to understand the physiology underlying the stoichiometric relationships of nutrients in plants, and its agronomic and ecological consequences (Agren 2004; Niklas et al. 2005; Reich et al. 2010).

Similar relationships between %K and %N were observed for grasslands species and natural grasslands (Salette and Huché 1991; Duru et al. 1992). As a result, critical %P-%N and %K-%N relationships have been established corresponding to non-limiting P and K supplies that allow a crop P and K nutrition diagnosis by calculating a nutrition index of P (PNI) or K (KNI) as the ratio between actual (%Pa, %Ka) and critical (%Pc, %Kc) concentrations as illustrated in Fig. 6 for P.

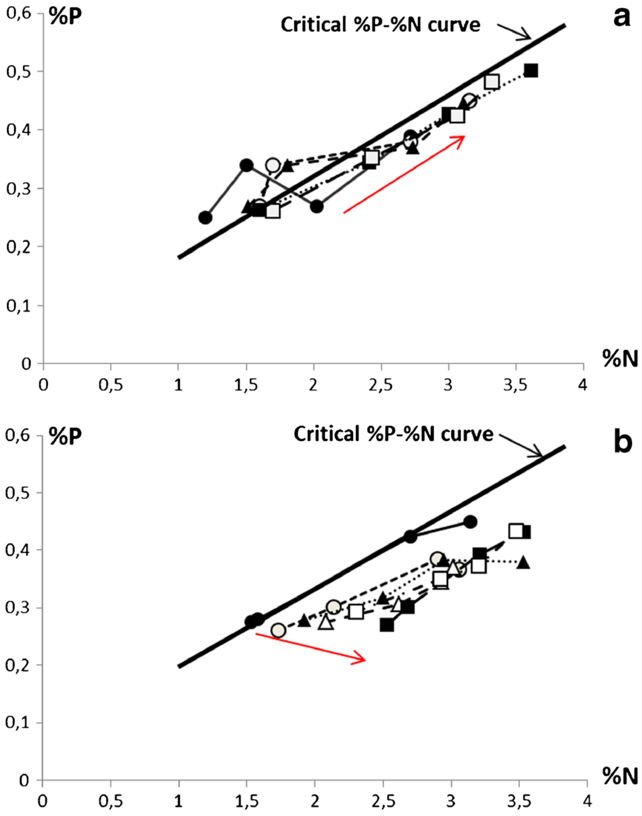

Fig. 6 Relationship between P and N concentrations in shoots (%P_{sh} and %N_{sh} expressed in per cent of dry matter) for different natural grasslands in spring under non-limiting P supply conditions and having received different levels of N supply at the end of winter: white square no N application; black square100 kgN ha^{-1}; black circle 150 kgN ha^{-1}. The regression line [%P_{sh} = (0.091 × %N_{sh}) + 0.133; R^2 = 0.97] represents the "critical %P_{sh}." Variations in %N_{sh} are due to either (i) variation in shoot mass (W_{sh}) due to different N supplies and (ii) a N dilution effect associated to biomass accumulation with time. A P nutrition index (PNI) can then be calculated as PNI = (Act.%P_{sh})/(Crit.%P_{sh}) for estimating the P nutrition level of a given crop. Adapted from Salette and Huché (1991)

Using the relationship between N and P concentrations, crop nutrition can be examined in more detail. The results from Ziadi et al. (2008a, b, c) for maize crops grown on different soils in eastern Canada are used to illustrate the interaction between P and N concentration (Fig. 7). Under high soil P, increasing crop P demand due to increased N supply and crop mass accumulation can be satisfied and results in an increase of both %P and %N. In a low soil P, however, the increased P demand due to increased N supply cannot be satisfied in the same proportion, resulting in a disconnection between %P and %N that reflect a crop P deficiency induced by N supply. Kamprath (1987) reported also an enhanced P concentration of maize crop resulting from N fertilization in soil with high P availability.

Similarly, Duru and Ducrocq (1997) showed that, for natural grasslands, N fertilization in absence of P fertilization could aggravate the P deficiency, while fertilization with both

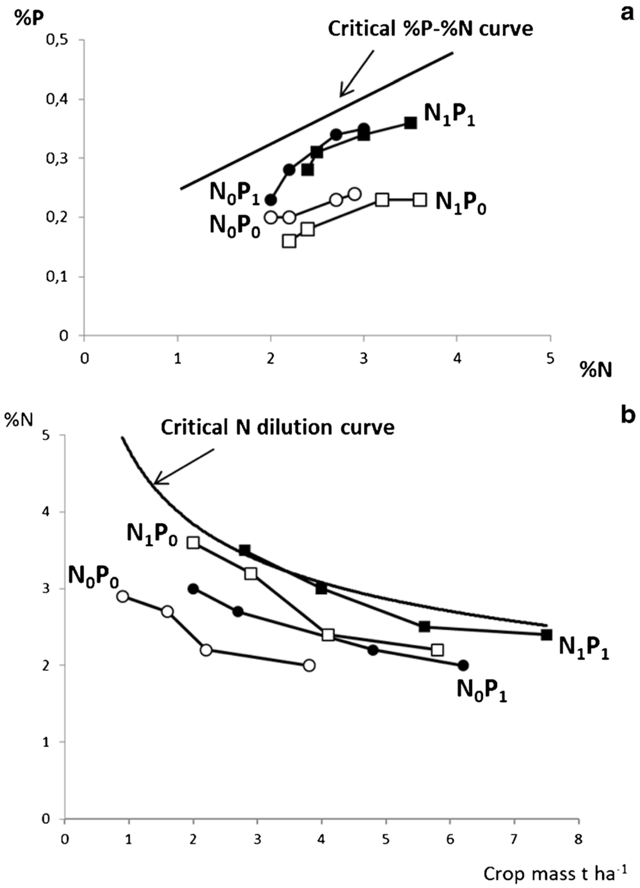

Fig. 7 Shift in the %P-%N relationship according to the N supply of a maize crop in conditions of high (**a**) or low (**b**) soil P availability in eastern Canada. The red arrow in **a** indicates the positive shift in both %P and %N as N supply increases, while the arrow in **b** indicates a negative shift in %P associated with a positive shift in %N. The N supply treatments were 0 (dark circles), 40 (open circles), 80 (dark triangles), 120 (open triangles), 160 (dark squares), and 200 kgN/ha (open squares). The critical %P-%N curve is $\%P = 0.107\%N + 0.094$ as determined by Ziadi et al. (2008a, b, c). Redrawn from Ziadi et al. (2008a, b, c)

nutrients increased both %P and %N as illustrated in Fig. 8a. Conversely, P fertilization can lead to an increase in %N at a similar plant mass that corresponds to an increase in the crop N nutrition status (Fig. 8b). Hence, as demonstrated by Duru and Ducrocq (1997), the effect of P supply on forage production is the result of two complementary processes: (i) a direct response to the P supply and (ii) an indirect effect of improved crop P nutrition that enhances N acquisition and the crop N nutrition status.

Those relationships based on the concomitant dilution of N, P, and K in increasing shoot mass during crop growth provide tools for assessing their status by calculating nutrition indices and, indirectly, their soil availability. Contrary to N for which an in-season diagnostic test and remedial actions are possible, plant-based tests based on the nutrition indices of P and K might have more potential to be used a posteriori to adjust fertilization for the following growing season.

In a recent meta-analysis of wheat yield response to N, P, and K fertilizer applications, Duncan et al. (2018) highlighted general and significant interactions among nutrients, and how the crop capacity to uptake a given element is enhanced as availability of other elements increases. Consequently, N use efficiency increases as P and K supplies increase. The allometry approach developed above allows the capture of these interactions and provides the opportunities for developing diagnostic methods for a well-balanced crop nutrition.

4 Further research and applications

4.1 Limits of the allometric approach to crop nutrition

The allometric analysis of crop N nutrition is based on the simplification that N is allocated to two functions and compartments in vegetative plants: (i) plant growth, as driven by light harvesting and photosynthesis within N-rich leaf parenchyma tissues and (ii) plant architecture, mechanical resistance, and hydraulic conductivity associated with N-poor fiber and vascular tissues. The general allometry relating these two compartments leads to the dilution of nitrogen with crop growth. Nitrogen mobilized from older leaves in shaded parts of the canopy to younger leaves in the top of the canopy further contributes to the dilution of N. The trade-off in investment between alternative compartments and functions is bounded by biophysical constraints at the canopy level, hence the limited variation in allometries among species within C3 and C4 plant types. Allometry thus describes fundamental “emerging properties” with implications for agronomic practices to improve crop nutrition and for phenotyping approaches to improve N use efficiency.

The concentration of N in whole plants is unsuitable in itself to quantify the crop nutrient status for both diagnostic and phenotyping applications because the critical N concentration for achieving maximum growth depends on plant and canopy size and, particularly, crop mass. Hence, the determination of the crop N status through measurements of plant N concentration requires N dilution curves accounting for the mass-dependent critical N concentration. The NNI based on a mass-dependent critical N concentration allows the comparison of plant N concentration at a similar crop mass. The need to account for nutrient-biomass allometry also applies to P and K.

This mass-dependency of the critical plant N concentration is the consequence of a general pattern of dry matter allocation in plants within canopies. The dry matter allocation to structural and supporting tissues for positioning leaf areas within the well-illuminated upper layers of canopies increases as crops grow. This process of shade avoidance can then be encapsulated within a general allometry between LAI and crop mass. Consequently, attempts to use some plant morphological traits such as the leaf/stem ratio or SLA for phenotyping

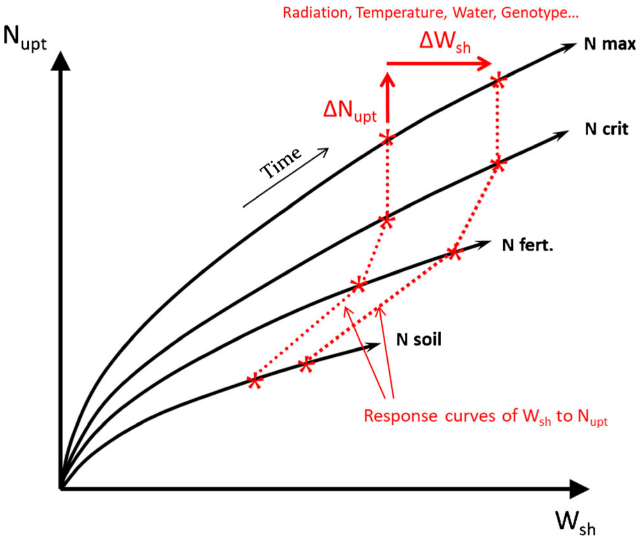

Fig. 8 Nitrogen–phosphorus interactions in natural grasslands receiving a factorial combination of high applications of N (squares) and P (dark symbols) and no application of N (circles) and P (open symbols). **a** Effects of the N and P supplies on shoot P and N concentration (P%, %N); the line represents the critical P concentration: $\%P_c = 0.065\%N_c +$ 015 as determined by Duru and Thellier (1997). **b** Effects on the N and P supplies on shoot N concentration (N%); the line represents the critical N dilution curves for C3 grasses species (Lemaire and Gastal 1997). Adapted from Duru and Ducrocq (1997)

species or genotypes (Lavorel and Garnier 2002) appears to be of limited generic value as demonstrated by Ratjen et al. (2018).

We have shown that allometric relationships between nutrients and crop mass are partially associated with competition for light among individual plants within the canopy. Nitrogen dilution curves are density-dependent (Seginer 2004), and they reach an asymptotic value only for dense canopies intercepting most of incident light. For crops with a low sowing or planting density or with a non-uniform spatial repartition, the use of critical N dilution curves requires a different measure than shoot mass per unit of soil area, which could possibly be shoot mass per plant or shoot mass per unit of row length. Moreover, the use of NNI should be restricted to the vegetative period with $LAI > 1$. During reproduction in annual grain crops, the LAI-W_{sh} allometry is broken and the N dilution process is disturbed by (i) leaf senescence and N remobilization from leaves to grains and (ii) by the equilibrium between starch and protein accumulation during grain filling. This last process leads to a large variation in N dilution rates across species according to the equilibrium between carbohydrates, lipids, and proteins accumulating in grains. For crops such as maize or sorghum that accumulate proportionally more starch than protein in grains, there is an acceleration of the N dilution during grain filling (Plénet and Cruz 1997). In soybean, however, more proteins are accumulated in grains and there is tendency for an attenuation of the N dilution process (Divito et al. 2016). For grain crops, the NNI method for crop phenotyping after anthesis must be used with caution and would require more specific analyses.

The allometric approach also applies to P and K but theory for these two elements are not so well established as for N and data are lagging. More precise information concerning the compartmentalization of these elements within plants is necessary. Models of nutrient allometry could be extended for integrated N-P-K diagnosis that captures the nutrient interactions in the context of co-limitation and stoichiometry. The return from investments in precision agriculture and crop phenotyping, where the dominant focus is on cheaper and better data, would benefit for a more exhaustive theoretical framework of the allometric relationships related to P, K. The extension of the theory to crop S nutrition seems promising (Reussi Calvo et al. 2011) but more extensive research is necessary for developing this aspect.

4.2 Applications for fertilizer management

The theory developed above on allometry opens perspectives for in situ diagnosis of crop nutrient status. For N, an early crop diagnosis to guide top-dressing is then possible for applying N fertilizer only when necessary. The uncertainty linked to the prognosis approach under unpredictable conditions should then be partially solved. A major difficulty in using the NNI at the farm level, however, is the need to determine the actual crop mass and its N concentration. For this reason, it may be more practical to use the NNI as a reference for calibration of simpler plant diagnosis procedures (e.g., leaf chlorophyll measurements, petiole nitrate concentration) or remote sensing measurements (see Box 3). Then, the monitoring of crop N status along the crop growth cycle could be included within crop fertilization management procedures for farmer's decisions on the timing and rate of N fertilizer application. (Ravier et al. 2018).

P and K fertilization management is commonly based on soil tests and prognostics on soil nutrient availability for plants. Annual estimates of crop P and K status via PNI and KNI can complement soil balance approaches. Moreover, mapping crop PNI and KNI at landscape or regional scale could provide valuable complementary information for soil survey systems.

4.3 Perspectives for crop phenotyping

Genotype–environment–management interactions are of central interest for agronomists and plant breeders. The statistical analysis of responses of crop yield to nominal treatments (e.g., high vs low N) provides little information. Although the concepts presented above have been established for over two decades, many papers still report results with incomplete or inadequate quantification of the crop nutrition status (Sadras and Lemaire, 2014).

The NNI, and also PNI and KNI in some circumstances, should be considered indispensable co-variables for interpreting field data where the focus is comparisons of genotypes and practices. Most of the crop management practices such as date or density of sowing or plantation, tillage, or weeding methods are susceptible to influence plant N nutrition as well as other plant traits. It is, therefore, important to check the crop NNI for separating the direct effect of these management practices from their indirect effect through plant N nutrition. Similarly, any change in environmental conditions (e.g., temperature, radiation, rainfall, soil water content) directly affecting plant growth dynamics and, then, crop N demand, could also affect soil N availability and, therefore plant NNI. Moreover, comparing different genotypes or cultivars having different growth patterns and then different crop N demand can lead to different crop NNI under a given soil N supply condition. So, parameters deduced from the allometry approach of crop nutrition should help in a more comprehensive interpretation of agronomic and plant breeding datasets. Moreover, with the help of crop models, these allometry parameters should be used for genotype prototyping in future plant breeding programs.

5 Conclusions

Owing to the degradation of the environment caused by over-fertilization in some cropping systems, and the depletion of soil organic matter in systems with negative nutrient balance, it is urgent to refine our conceptual and practical tools for nutrient management. This review highlights that (i) crop nutrient uptake is co-regulated by soil nutrient availability and plant demand, (ii) nutrient concentration is allometrically linked to shoot biomass, (iii) nutrient-biomass allometry is density-dependent, and (iv) crops respond to the interactions between N, P, and K. So, a more integrated vision of crop nutrition is necessary that links supply and demand of nutrients, nutrients and biomass, and interactions among nutrients.

Reliable measures of crop nitrogen status for management of crop nutrition require dilution curves that are available for most crops. Dilution curves are needed for P and K. Whereas the NNI, PNI, and KNI are the more robust traits to quantify crop nutrition status, methods based on destructive sampling, and lab analysis are mostly unsuitable to guide management decisions. Instead, these traits are best seen as benchmarks to calibrate other methods that are easier to implement and cost-effective.

Phenotyping individual plants or unrealistic arrangements (e.g., single rows) overlooks plant–plant interactions and is therefore bound to bias nutrient–mass relationships as well as partitioning coefficients. Traits commonly used in phenotyping for nutrient-use efficiency include nutrient concentration in plant tissue and nutrient uptake, but these are unreliable when measured in individual plants. Likewise, intra- or inter-specific comparisons of mass-dependent traits such as the leaf/stem ratio or specific leaf area, particularly common in ecology (see Lavorel and Garnier 2002) must be done at a similar shoot mass or leaf area index. Further, the trade-offs between these traits highlight the limited functional meaning when they are analyzed independently.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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