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Quantifying crop nitrogen status for comparisons of agronomic practices and genotypes

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ABSTRACT

The nitrogen economy of the crop is a critical driver of biomass and grain production, and its importance is reflected in a large, worldwide research effort to link nitrogen, growth and yield. Particular research questions require measurement of specific traits, hence the need to quantify multiple, often complementary traits including crop nitrogen uptake, nitrogen use efficiency and its components, nitrogen concentration in the crop and its parts, down to relevant enzymes (e.g. nitrate reductase) and other products of gene expression. Nitrogen uptake, however, is co-regulated by both soil nitrogen availability and crop biomass accumulation; hence, crop nitrogen uptake or shoot nitrogen concentration reflect univocally crop nitrogen status only if comparisons are made at similar biomass. Although the allometric relationships between biomass and nitrogen uptake have been established for over two decades, many studies still report results in terms of nominal treatments, e.g. high vs low nitrogen, which are uninformative; curves relating yield and fertiliser rate, which are of local interest but provide little insight on the underlying processes and have low generic value; and nitrogen-related traits that are incomplete or inadequate to quantify crop nutrition status. Often, the allometric relationships between nitrogen and biomass are overlooked.

In this opinion paper, we summarise the already well established concepts of dilution curves and nitrogen nutrition index, outline the standard partitioning of nitrogen use efficiency, and highlight the confounded effects in nitrogen use efficiency when the allometric relationship between nitrogen uptake and biomass is ignored. A sample of recent papers is used to survey the most common approaches to characterise nitrogen related traits. We illustrate the application of dilution curves and nitrogen nutrition index in the assessment and interpretation of crop responses to agronomic practices and comparisons of wheat cultivars and maize hybrids.

1. Introduction

The importance of nitrogen for crop production cannot be understated. On a historic time scale, agronomic practices improving the availability of nitrogen and water, combined with germplasm able to capture the benefits of enhanced resources, have been the main drivers of improvement in crop yield (Sinclair and Rufty, 2012). Indeed, selective pressure for yield and agronomic adaptation has dramatically improved the nitrogen economy of cereals in cropping systems with high (Foulkes et al., 1998; Haegele et al., 2013) and low nitrogen inputs (Sadras and Lawson, 2013).

Data aggregated at large scales in space (national to global), and time (decades), thus reveal close associations between crop production and fertiliser use (Tilman et al., 2002). Large scale observations, however, could lead to inappropriate generalisations, such as the proposition to improve crop yield whilst reducing nitrogen input irrespective of current practices and soil fertility in particular cropping systems. Nutrient balance, i.e. the difference between the inputs and outputs to the system, is commonly used to detect environmentally undesirable excess nutrient (Sassenrath et al., 2013). However, a system can achieve close-to-zero nitrogen balance at low yield, hence the incompleteness of these balances for tactical decisions aiming at both high yield and low environmental impact. Current nitrogen input meets both high production and low environmental footprint in irrigated maize-based systems of USA (Grassini and Cassman, 2012), maybe excessive and offers opportunities for reduction in some cropping systems of China (Chuan et al., 2013), and is often insufficient and

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needs to be increased in many semi-arid environments with low soil fertility in both large-scale mechanised (Angus, 2001; Sadras and Roget, 2004) and subsistence cropping systems (Rockström and deRouw, 1997; Rockström et al., 1999). Clearly, nitrogen management to achieve high yield and low environmental footprint needs to be assessed and solved locally; this requires adequate metrics to characterise crop nutritional status.

Adequate metrics must be used to rigorously test the proposition that replacement of mineral fertilisers with organic fertilisers, and crop legumes (biological N_2 fixation) could satisfy increasing food demand and reduce both nitrogen leaching and greenhouse emissions (Kirchmann and Bergström, 2008; Connor and Mínguez, 2012). Physiological and genetic studies aiming at understanding and improving the nitrogen economy of crop varieties also require proper measures of crop nitrogen status.

Statistical analysis of nominal treatments, e.g. high vs low nitrogen, is uninformative and curves relating yield and fertiliser rate may have local interest but provide little insight on the underlying processes and have low generic value. Nitrogen use efficiency is defined as the increment of yield for each added unit of N fertiliser and can be expressed as the product of three factors: the N uptake efficiency (i.e. the increment in N uptake by the crop per unit of increment in N supply to the soil); the N conversion efficiency, also termed utilisation efficiency (i.e. the increment in biomass per unit of N uptake) and harvest index (Lemaire and Gastal, 2009). Nitrogen uptake, however, is co-regulated by both soil nitrogen availability and crop biomass accumulation (Devienne-Barret et al., 2000); hence, crop nitrogen uptake or shoot nitrogen concentration reflect univocally crop nitrogen status only if comparisons are made at similar biomass (Lemaire and Gastal, 2009).

The nitrogen nutrition index is a theoretically sound and agronomically relevant method to quantify the nitrogen status of the crop based on robust nitrogen dilution curves which effectively separate biomass as a component of nitrogen uptake (Greenwood et al., 1990; Justes et al., 1994; Lemaire and Gastal, 1997; Lemaire et al., 2008). Although these concepts have been established for over two decades, many papers report results in terms of nominal treatments, or nitrogen-related indices that provide incomplete or inadequate quantification of crop nutrition status. In this opinion paper, we summarise the well established concepts of dilution curves and nitrogen nutrition index, outline the standard partitioning of nitrogen use efficiency, and highlight the confounded effects in nitrogen use efficiency when the allometric relationship between nitrogen uptake and biomass is ignored. A sample of recent papers is used to survey the most common approaches to characterise nitrogen-related traits. Finally, we illustrate the application of dilution curves and nitrogen nutrition index in the assessment and interpretation of crop responses to agronomic practices and comparisons of wheat cultivars and maize hybrids.

2. Dilution curves and nitrogen nutrition index

2.1. Overview

Lemaire and Salette (1984a,b) and Greenwood et al. 1990 showed that the critical shoot nitrogen concentration,[1] i.e. the minimum crop nitrogen concentration for maximum biomass growth rate, declines with increasing crop biomass. This relationship between critical crop nitrogen concentration $\%N_c$ and the maximum crop biomass W_c has been empirically represented by a negative allometric function, called critical N dilution curve:

$$\%N_c = aW_c^{-b} \quad (1)$$

where b is a dimensionless coefficient, and a is the crop nitrogen concentration when $W_c = 1\,\text{t ha}^{-1}$. Box 1 outlines the theory of nitrogen dilution in crop canopies. By multiplying the two members of Eq. (1) by W_c an allometric relationship between critical nitrogen uptake (N_{cupt}), i.e., the minimum N uptake for achieving the maximum crop biomass, and crop biomass is obtained:

$$N_{cupt} = 10aW_c^{(1-b)} \quad (2)$$

The coefficient $10a$ represents the crop nitrogen uptake, in kg N ha^{-1}, for a crop biomass of $1\,\text{t ha}^{-1}$. Coefficients a and b have been determined for many species (Table 1). It is then possible by using the critical N dilution curve for a given crop species to derive a nitrogen nutrition index *NNI*, as shown in Fig. 1, for quantifying the nitrogen status of any crop in any situation:

$$NNI = \frac{\%N_{\text{actual}}}{\%N_c} \quad (3)$$

where $\%N_{actual}$ is the actual crop nitrogen concentration corresponding to the actual biomass W_{actual}. For $NNI > 1$ the crop nitrogen status can be considered as non-limiting, so any increase in N supply would not increase crop biomass, and for $NNI < 1$ the crop nitrogen status can be considered as limited by N supply.

The *NNI*, therefore, provides a measure of nitrogen status accounting for the dilution of nitrogen in growing crops. Nevertheless, several limitations of this method have to be emphasised:

(i) The theory underlying the dilution curve is restricted to the vegetative period when only two compartments, metabolic and structural, are relevant (Box 1). During the period of yield formation, e.g. grain filling in seed crops or storage of carbohydrates and proteins in root and tuber crops, a third compartment and translocation processes have to be considered, which restricts the validity of Eq. (1). So, the limit for using *NNI* as a diagnostic tool is the flowering stage for annual grain crops.

(ii) The theory describes the nitrogen dilution process within a population of plants competing for light. In absence of competition, i.e. isolated plants, the dilution process is slower (Lemaire and Gastal, 2009). So, Eq. (1) cannot be used for early growth (leaf area index < 1) when plants can be considered as more or less isolated (Lemaire et al., 2008) or for crops having too low plant densities. Specific nitrogen dilution curves have to be established for these situations.

(iii) The critical nitrogen concentration declines with water deficit, and parameters of dilution curves are, therefore, affected by crop water status (Belanger et al., 2001; Errecart et al., 2014). This constrains the application of the *NNI* in water-deficient crops. However, the critical nitrogen concentration scales with crop water status (Fig. 2) thus providing an interesting quantitative link between nitrogen and water economies of crops that deserves further research, as outlined in Section 2.2.

2.2. Effect of water deficit

Soil water limitation affects several aspects of crop nitrogen nutrition, as reviewed in Gonzalez-Dugo et al. (2010). Water deficit reduces crop nitrogen uptake in many species including temperate grasses (Lemaire et al., 1996; Gonzalez-Dugo et al., 2005), wheat (Sadras et al., 2004), maize (Pandey et al., 2000) and sunflower (Gonzalez-Dugo et al., 2010). The use of *NNI* for evaluating the crop

[1] In this paper, crop nitrogen concentration (%N and related variables) refers to shoot only. Likewise, crop nitrogen uptake refers to the total amount of nitrogen in shoots unless specified otherwise.