

A two-dimensional simulation model of phosphorus uptake including crop growth and P-response

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ABSTRACT

Modelling nutrient uptake by crops implies considering and integrating the processes controlling the soil nutrient supply, the uptake by the root system and relationships between the crop growth response and the amount of nutrient absorbed. We developed a model that integrates both dynamics of maize growth and phosphorus (P) uptake. The crop part of the model was derived from Monteith's model. A complete regulation of P-uptake by the roots according to crop P-demand and soil P-supply was assumed. The soil P-supply to the roots was calculated using a diffusion equation and assuming that roots behave as zero-sinks. The actual P-uptake and crop growth were calculated at each time step by comparing phosphate and carbohydrate supply-demand ratios. Model calculations for P-uptake and crop growth were compared to field measurements on a long term P-fertilization trial. Three Pfertilization regimes (no P-fertilization, $42.8 \text{ kg P ha}^{-1} \text{ year}^{-1}$ and $94.3 \text{ kg P ha}^{-1} \text{ year}^{-1}$) have led to a range of P-supply. Our model correctly simulated both the crop development and growth for all P-treatments. P-uptake was correctly predicted for the two non-limiting Ptreatments. Nevertheless, for the limiting P-treatment, P-uptake was correctly predicted during the early period of growth but it was underestimated at the last sampling date (61 day after sowing). Several arguments for under-prediction were considered. However, most of them cannot explain the observed magnitude in discrepancy. The most likely reason might be the fact that biomass allocation between shoot and root must be modelled more precisely. Despite this mismatch, the model appears to provide realistic simulations of the soil-plant dynamic of P in field conditions.

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1. Introduction

In the last 40 years several mathematical models simulating phosphorus (P) uptake by roots from soils have been developed. Following the work of Nye and Marriott (1969), these models described transport of P to individual roots by mass flow and diffusion. P-uptake is assumed to be a function of the P-concentration in the soil solution, of transport rates in the soil liquid phase, and of the soil solid phase to buffer the solution. Models based on this theory were first developed for single roots and later adapted to the entire growing root system (Baldwin et al., 1973; Claassen and Barber, 1976; De Willigen and Van Noordwijk, 1987). Such modelling efforts have led to a better understanding of nutrient uptake by roots in the absence of other limiting factors. Model-based investigations have confirmed diffusion and mass flow processes

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of soil nutrient transport to the root. The existence of a concentration gradient around roots, which provides the driving force for P-diffusion, was confirmed by calculations and observations (Jungk and Claassen, 1997; Hinsinger, 2001; Singh and Sadana, 2002).

Evaluations of these models, either at the field scale or in pot experiments, have shown that they were able to closely predict P-uptake in various soil-plant systems with medium to high soil P-content for relatively short periods (Schenk and Barber, 1979; Lu and Miller, 1994; Teo et al., 1995). However, at low soil P-content, these models often underestimate the experimentally measured P-uptake (Brewster et al., 1976; Schenk and Barber, 1979, 1980; Ernani et al., 1994). These discrepancies were due to the fact that some root surface processes (Hinsinger, 2001), mycorrhizae contribution (Gavito and Varela, 1995) and plant regulations (Raghothama and Karthikeyan, 2005), which are obviously more important at low soil P-content, were not included. Recent developments have focused on integration of the contribution of other rhizospheric processes to the soil P-supply such as pH changes, organic anions and phosphatase release in the rhizosphere (Trolove et al., 2003). According to these models, the exudation of such compounds could greatly increase soil Pavailability (Hoffland et al., 1990; Geelhoed et al., 1999; Kirk et al., 1999). Nevertheless, these processes did not occur for all plant species and their efficiency is highly dependent on soil physico-chemical properties and experimental conditions (Jones and Farrar, 1999). As these dependencies have been shown to occur under extreme experimental conditions, it is questionable to what extend they contribute to the crop Pnutrition in usual agricultural situations. There is still little evidence that these root exudates mechanisms actually play a significant role in plant P-acquisition (Jones and Farrar, 1999).

While much efforts have been devoted to the aspects that affect P-availability in soil, plant functioning aspects have generally received less attention (Itoh and Barber, 1983). In most models, plant growth is a fixed input irrespective of P-uptake, which does not account for the ability of the plant to react to P-deficiency. As a consequence, the model underestimated plant growth and P-uptake (Barber, 1995). Recent progresses have been made in modelling crop growth and in understanding crop responses to P-deficiency. Models for crop growth range in complexity from a simple, direct conversion of the amount of light energy into an amount of biomass (Goudriaan, 1977; Monteith, 1977; Porter, 1984; Williams et al., 1989), to detailed mechanistic models including gas-exchange properties of leaves and profile of light interception (e.g., Marcelis et al., 1998). In absence of limiting growth factors such as nutrients, water, pests and diseases, these models have proved to be able to predict correctly potential crop growth according to environmental conditions such as light, temperature, and carbon dioxide (CO2). Recent progresses have been made in understanding how P-deficiency affects the potential plant growth (Halsted and Lynch, 1996; Rodriguez et al., 1998; Plenet et al., 2000a, 2000b; Chiera et al., 2002), shoot-root allocation of the biomass and root growth (Mollier and Pellerin, 1999; Pellerin et al., 2000; Vance et al., 2003; Wissuwa et al., 2005). Until now, this knowledge has rarely been used in the context of uptake models. For instance a plant growth model based on empirical data measured for highly P-deficient conditions was

developed to investigate genotypic differences in P-efficiency for rice (Wissuwa, 2003). In this model, the soil part was oversimplified. It is important to link such a model to a soil-root model to gain a better understanding of the soil-plant processes involved in P-uptake.

The purpose of this study was to develop a mechanistic model for the simultaneous simulation of P-supply by the soil, P-uptake by the root system and plant growth response. The dynamic link between these processes was explicitly taken into account. The objective assigned to the model was to predict P-uptake and crop response under sufficient P-availability or moderate P-deficiency. Severe P-deficiencies were outside the scope of the model. The simulations of crop growth and Puptake were compared to field measurements on young maize crops and model applications were explored.

2. Model description

The current model consists of three modules closely connected. The first one deals with crop growth and crop P-demand. In this version of the model, the shoot part of the crop is assumed to be only constituted by leaves. Crop growth is described by plant phenology and biomass accumulation depending on climatic conditions. Crop P-requirement is derived from the potential plant growth regarding the environmental conditions. The second module describes P-supply from the soil considering the soil solution concentration and the soil buffer capacity. The third module deals with crop Puptake depending on crop P-demand and P-uptake capacity determined by the soil P-supply and the root length density distribution in soil. The three modules are integrated to simulate the feedback of effective P-uptake on crop growth. Thus, the model tightly couples crop growth with soil processes. The three modules exchanged information at a daily basis. The crop growth processes are expressed as a function of thermal time per square meter surface area of soil. The input data include climate drivers, soil properties and crop parameters. The output includes crop growth, P-uptake, soil P-fluxes and P-status. For convenience, in this paper volume water unit is mL while volume soil unit is designated with cm³.

2.1. Module 1: Modelling crop growth and P-demand

2.1.1. Crop growth

The crop growth module simulates plant phenology and dry matter accumulation as a function of daily weather data. The daily biomass production depends upon the photosynthetically active radiation absorbed by the canopy (PAR_a , $MJ m^{-2}$) calculated via crop cover from LAI, the leaf area index ($m^2 m^{-2}$) and k, the attenuation coefficient (Bonhomme et al., 1982; Varlet-Grancher et al., 1982), and the radiation use efficiency (Monteith, 1977; Kiniry et al., 1989; Sinclair and Muchow, 1999):

$$Gw_{new} = \frac{RUE \times PAR_a}{\Delta T_T}$$
(1)

where Gw_{new} is the total biomass increment rate (gbiomass m⁻² (°Cd)⁻¹), RUE the radiation use efficiency (gbiomass MJ⁻¹ PAR) and T_T is the thermal time (°Cd) since

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