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Root morphology and phosphorus uptake by potato cultivars grown under deficient and sufficient phosphorus supply

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ABSTRACT

Information regarding the characteristics that affect P-uptake capacity may assist in the selection of more adapted potato (*Solanum tuberosum* L.) cultivars and more adequate fertilization management for each cultivar. This study evaluated the P-uptake capacity of potato cultivars (Agata, Asterix, Atlantic, Markies, and Mondial) grown under P-deficient (2 mg L^{-1}) or P-sufficient (31 mg L^{-1}) conditions in nutrient solution and related it to physiological parameters of uptake and morphological root characteristics. When the plants were 24 days old, they were subjected to a P-uptake kinetics study. The length and surface area of roots and the uptake kinetic parameters (I_{max}, K_m, and C_{min}) varied among potato cultivars. Phosphorus-deficient potato plants had an approximately 60% smaller root surface area and an increase of 86% in the I_{max} and net P influx compared with the plants in P-sufficient conditions. However, these modifications in P uptake kinetics can do not influence P acquisition in the soil environment due to very limited P diffusion. The amount of P accumulated by plants grown under P-deficient conditions was directly related to the root length and surface area; a greater root surface, as demonstrated by the Asterix cultivar, is the most important factor for achieving a greater P-uptake capacity. Under P-sufficient conditions, potato cultivars such as Markies and Mondial showed a balance between morphological root characteristics (medium/large length and surface area) and physiological parameters (medium/high I_{max} values and net P influx) and had a greater P-uptake capacity. However, under field conditions, the responses to P deficiency may be different due to the very limited diffusion of P in the soil and because plants can use additional mechanisms to improve their P uptake from the soil.

1. Introduction

Potato (*Solanum tuberosum* L.) is a crop whose growth is limited when phosphorus (P) is not readily available (Alvarez-Sanchez et al., 1999; Fernandes and Soratto, 2012), and considerable yield losses occur in P-deficient soils (Alvarez-Sanchez et al., 1999; Dechassa et al., 2003; Hopkins et al., 2014). Therefore, in potato cultivation, large quantities of phosphate fertilizers are normally used to increase P availability in the soil (Ali et al., 2004; Hopkins et al., 2014). However, the application of large quantities of phosphate fertilizers to soils used in potato cultivation increases crop production costs and can generate environmental problems.

One method to reduce the amount of phosphate fertilizer applied during potato growth and to obtain better yields in P-deficient conditions is to enhance the P use efficiency in the genotypes, which can be achieved by improving P acquisition, utilization, or both (Wang et al., 2010). Phosphorus uptake by roots results from interactions among the morphological and physiological characteristics of the roots, the rhizosphere immediately surrounding the root system, and the soil characteristics that determine the movement of P to the soil–root interface (Gerloff and Gabelman, 1983). Phosphorus-uptake efficiency varies in a direct ratio to the length and thickness of the roots because these characteristics affect the uptake surface area (Vilela and Anghinoni, 1984). In the soil, the diffusion of P is very limited and root uptake creates depletion zones around the root surface (Barber, 1995; Hinsinger et al., 2011; White et al., 2013) that impede P uptake. Therefore, for the continuous uptake of P by the plant, the roots must actively grow to explore new soil volumes (Marschner, 2012; Hopkins et al., 2014). Thus, studies of various crops have shown that genotypes with well-developed root systems, longer roots and/or greater surface areas, and higher root elongation rates are generally

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more efficient in P acquisition (Barber, 1995; Narang et al., 2000; Hinsinger et al., 2011; White et al., 2013). These favorable genotypes also produced greater shoot biomass in studies performed in soils (Schenk and Barber, 1980) and nutrient solutions (Machado and Furlani, 2004).

The rate of P uptake also depends on the physiological characteristics of the roots, which are defined by kinetic uptake parameters (Schenk and Barber, 1980; Marschner, 1995; Bhadoria et al., 2004), i.e., the maximum influx at large concentrations (I_{max}), the Michaelis–Menten constant (K_m), and the minimum concentration in the solution (C_{min}) (Barber, 1995). Although these parameters are defined genetically (Barley, 1970; Schenk and Barber, 1980), they might be affected by the growth conditions of the plant because plants adapt their P-uptake kinetics according to their internal P nutrient status (Jungk et al., 1990; Ramaekers et al., 2010). Nevertheless, this adjustment capacity depends on the species and on the genotype used (Rosolem, 1995; Ramaekers et al., 2010). In different plant species and/or genotypes of the same species, plants exhibiting more efficient P uptake had different P-uptake kinetics (Jungk et al., 1990; Machado and Furlani, 2004; Hu et al., 2010). For some crops, the differences in P uptake were more affected by P-uptake kinetics than by the size of the root system (Bhadoria et al., 2004).

Studies conducted in both soil and nutrient solutions demonstrate the effects of root morphology and P uptake kinetics on the P-uptake capacity and plant growth (Schenk and Barber, 1980; Jungk et al., 1990; Machado and Furlani, 2004; Hu et al., 2010; Bhadoria et al., 2004). Although the P concentration required to promote optimal plant growth in nutrient solutions is typically greater than in the soil solution, studies with P in nutrient solutions are important for understanding the patterns of plant development (Fernandes and Soratto, 2012) and the main mechanisms involved in P uptake under different conditions of availability.

Studies undertaken to evaluate the P capacity of uptake in potato have been restricted to analyzing the morphological characteristics of the root system (Dechassa et al., 2003; Balemi and Schenk, 2009a) and P uptake use efficiency (Balemi, 2009; Balemi and Schenk, 2009a,b; Balemi, 2011; Fernandes and Soratto, 2012). Studies have also been undertaken to evaluate the development patterns of potato root systems in pots and in the field (Iwama, 2008; Wishart et al., 2013). However, no studies exist that relate the morphology of the root system to the P-uptake kinetics of this crop, which is of fundamental importance because the benefits of a greater root influx of P might be small if P uptake is limited by its transport to the roots and by the formation of a root system with a small uptake surface area distributed within a small volume of soil (Jungk, 2002).

In potato crops, root dry matter (DM) is positively correlated with shoot DM and final tuber yield (Iwama, 2008; Wishart et al., 2013). Moreover, recent studies have demonstrated that large differences occur among potato genotypes regarding their number of roots, root length (Wishart et al., 2013) and amount of root DM (Iwama, 2008), indicating that the differences among potato cultivars in relation to the P uptake rate (Balemi and Schenk, 2009a; Fernandes et al., 2011) can be related to morphological and physiological characteristics of the roots. Thus, these characteristics might vary depending on the genotype (Rosolem, 1995; Machado and Furlani, 2004; Hu et al., 2010; Ramaekers et al., 2010) and P supply (Jungk et al., 1990; Bhadoria et al., 2004; Raghothama and Karthikeyan, 2005), and it is important to thoroughly understand the root characteristics that determine P uptake in the different potato cultivars.

Knowledge of the characteristics of root systems of different potato cultivars under different concentrations of P supply will aid in developing better management strategies for potato cultivation, including the use of higher rates of P fertilizers in the cultivars with a smaller P-uptake capacity and lower P rates in cultivars with a well-developed root system and that are efficient in P acquisition.

The aim of this study was to evaluate the P-uptake capacity of potato cultivars subjected to different conditions of P availability and the relationship between physiological parameters of uptake and morphological root characteristics.

2. Materials and methods

The experiment was conducted in a greenhouse at São Paulo State University in Botucatu, São Paulo, Brazil. The experiment was arranged in a completely random design with a 5×2 factorial arrangement and five replications. Treatments were composed of five potato cultivars (Agata, Asterix, Atlantic, Markies, and Mondial) and two P concentrations of nutrient solutions (P-deficient = 2 mg L^{-1} P and P-sufficient = 31 mg L^{-1} P). The P concentrations in the nutrient solutions were based on the results of previous studies, in which Agata cultivar potato plants were grown with increasing P concentrations in the nutrient solution to identify deficient and sufficient P concentrations for the potato crop (Fernandes and Soratto, 2012). The greenhouse was maintained at 14–27 °C with a photoperiod of 12 h and natural light conditions with a photosynthetically active radiation maximum of 1500 μmol m^{-2} s^{-1} at 12:00 h.

To obtain plants, 20 seed tubers weighing 35 g and with buds 5–10 mm from each cultivar were treated with a fungicide and an insecticide and were planted in plastic boxes with 16 L of washed sand for bud development to occur. At 6 and 12 days after planting (DAP) the seed tubers, a half-strength nutrient solution of Hoagland and Arnon (1950) was applied to standardize the development of the seedlings.

At 16 DAP, single-stemmed seedlings were selected with regard to health and uniformity, removed from the seed tubers and transferred to 4-L plastic pots containing the nutrient solutions. The seedlings were fastened onto polystyrene sheeting to keep them erect, and each experimental unit was composed of one pot containing two seedlings.

The Hoagland and Arnon (1950) solution was used for plant growth, with changes only in the P source and concentration. Phosphorus was added to the nutrient solution at 2 mg L^{-1} P (P-deficient) and 31 mg L^{-1} P (P-sufficient) using H_3PO_4 as the source.

In the first five days after transplantation, half of the concentrations of all the nutrients in the nutrient solutions had been used, including the P. At this time, the nutrient solutions were replaced with new solutions containing complete concentrations of nutrients, and they were subsequently replaced every seven days.

During plant growth, deionized water was added to the pots to readjust the initial volume, which was maintained with a maximum variation of 5%. Aeration of the solutions was constantly maintained, and the pH of the solutions was monitored and maintained at approximately 5.5 ± 0.5 through daily correction using HCl or NaOH. The plants were grown in the P-deficient and P-sufficient solutions for 30 days and subjected to a study of uptake kinetics according to the technique of Claassen and Barber (1974).

After 30 days, the plants were transferred to other pots with nutrient solutions containing the same composition as the Hoagland and Arnon (1950) solution but without P, where they remained for 48 h. After this period, the plants were placed for 1.5 h in a solution identical to the previous one but containing 15 μmol L^{-1} of P and 50 μmol L^{-1} of Ca for the system to achieve balance (Epstein and Hagen, 1952). The plants were then transferred to the solution of Hoagland and Arnon (1950) containing 40 μmol L^{-1} of P, and sampling was initiated. Samples of 10 mL of the solution were removed every 30 min in the first 6 h, every 60 min in the 11 subsequent hours and after 24 h. After 24 h, three more samples of the nutrient solution were collected