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Source-sink interactions lead to atypical reproductive stage phosphorus deficiency symptoms on the upper foliage of *Capsicum annuum* and *Chrysanthemum* ×*morifolium*

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ABSTRACT

Phosphorus (P) restriction has become more prevalent in floriculture production to control growth and reduce fertilizer waste. With low P fertilization practices, growers are more likely to develop P deficiency in their crops. Symptoms of a reproductive stage P deficiency were reported in which symptomology occurs on the foliage directly below the flowers or fruit. To induce and describe these symptoms, ornamental peppers (*Capsicum annuum* L.) and chrysanthemums (*Chrysanthemum* ×*morifolium* Ramat.) were grown initially with P fertilization, but half the plants were later restricted to 0 mg L^{-1} P upon floral initiation. Plants that were P restricted developed symptoms of chlorosis, olive green spotting, and necrosis on the upper foliage below the reproductive structures, while central foliage remained asymptomatic. 'Crystal Misty Purple' chrysanthemums developed unique symptoms of upper leaf purpling. Phosphorus movement within the plant was quantified via tissue division and analysis. The highest tissue P concentrations were in the flowers or fruit for both species, regardless of symptoms. Up to 80% of the total P in aboveground tissues was in the flowers and fruit of symptomatic plants. Vegetative tissue P concentrations were significantly lower in symptomatic plants compared to the asymptomatic controls, indicating that large quantities of P were translocated from vegetative tissues to the developing reproductive tissues. Remobilized P from the lower tissues appeared to bypass the upper foliage in favor of the flowers and fruit. Thus, the developing upper foliage was deprived of P, leading to P deficiency symptoms due to competition with the maturing flowers and fruit.

1. Introduction

Limiting phosphorus (P) by restricting fertilizer phosphate concentrations is an effective method for limiting internode elongation in floriculture species (Hansen and Nielsen, 2000, 2001; Nelson et al., 2012). Production of young plants (plug production) can benefit from low P fertilization (Nelson et al., 2012), but P restriction in long-term crops may lead to symptoms of P deficiency. This is especially true in greenhouse bedding crops that are grown in soilless substrate with limited phosphate holding capacity (Marconi and Nelson, 1984). Utilizing low fertilizer P concentrations (PCs) has become more prevalent in commercial greenhouse production, but has caused losses due to unsalable plants for some growers (Whipker, 2014). Without an external P supply, plants reallocate P stored in mature plant tissues, commonly leading to deficiency symptoms developing on the lower foliage (Epstein and Bloom, 2005; Marschner, 1995; Mengel et al., 2001).

Phosphorus deficiency symptoms are described as a reddening or purpling of the lower foliage, darker green coloration, stunted growth, delayed flowering, and greater root lengths (Epstein and Bloom, 2005; Marschner, 1995; Mengel et al., 2001). An additional symptom may sometimes manifest as olive green spots of the lower leaves during warmer conditions (Whipker, 2014). As P becomes deficient, plants translocate P from mature tissues to actively growing tissues (Marschner, 1995). This demonstrates why symptoms develop on the lower foliage as PCs decrease in those tissues.

Common P deficiency symptoms are well documented; however, Whipker (2014) reported symptoms on chrysanthemums (*Chrysanthemum* ×*morifolium* Ramat.) that were not previously described. An upper leaf necrosis was reported when chrysanthemums entered the reproductive growth stage under P deficient conditions (Whipker, 2014). Sufficient P during vegetative maturation, followed by P deficient conditions upon floral development led to these atypical symptoms. Typically, the mature foliage develops symptoms when the upper

Abbreviations: PC, phosphorus concentration

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foliage acts as a primary sink. In the case reported by Whipker (2014), there were two sinks competing for limited P supplies: the flowers and developing fruit, and the actively growing upper foliage. When these sinks competed for P, the reproductive tissues took precedence, and translocated P appeared to bypass the upper foliage in favor of the reproductive tissues. Reproductive chrysanthemums reallocate P from lower foliage to flowers, regardless of external P availability (Epstein and Bloom, 2005; Hansen and Lynch, 1998). In fact, remobilized P can account for 90% of the P in developing flowers and fruit, indicating high sink activity of reproductive structures (Epstein and Bloom, 2005; Marschner, 1995).

The initial hypothesis by Whipker (2014) suggested that plants experiencing reproductive stage P deficiency reallocated P from the upper leaves. However, it is unlikely that the upper foliage, which typically acts as a sink, would act as a source for the reproductive tissues. We hypothesized that when plants cannot acquire P from external sources such as the substrate, stores in the lower foliage will translocate to the young developing tissues, but will preferentially accumulate in the reproductive tissues. Under this hypothesis, symptom development is dependent on the growth stage of the plant when P deficiency is induced.

Additionally, the authors previously observed P deficiency symptoms on ornamental peppers (*Capsicum annuum* L.) on the upper foliage, below the maturing fruit (personal observation). The objective of this study was to replicate the symptoms reported as P deficiency on the upper foliage of chrysanthemums and ornamental peppers, and to determine the specific conditions under which they occur.

2. Materials and methods

2.1. Plant cultivation

Two experiments were conducted utilizing ornamental peppers and chrysanthemums to induce and describe symptoms of reproductive stage P deficiency. Peppers were represented by the compact, red-fruited cultivar 'Tango Red'. Chrysanthemums were represented by 'Little Rock', 'Swifty Yellow', and 'Crystal Misty Purple', which had purple/white bicolor, yellow, and purple flowers, respectively. All plants were propagated and grown in a glass greenhouse at 35 °N latitude in Raleigh, North Carolina, USA. A custom substrate was used for all experiments, consisting of 80:20 (v:v) Canadian sphagnum peat moss (Conrad Fafard, Agawam, MA) and horticultural coarse perlite (Perlite Vermiculite Packaging Industries, Inc., North Bloomfield, OH), amended with dolomitic limestone (Rockydale Agricultural, Roanoke, VA) at 8.875 kg m^{-3} and wetting agent (AquaGro 2000 G, Aquatrols, Cherry Hill, NJ) at 600.3 g m^{-3}. This custom substrate was used to ensure that there was no initial substrate available PC.

In experiment 1, 'Tango Red' pepper seeds (Fred C. Gloeckner & Co., Inc., Harrison, NY, USA) were sown on 6 Apr. 2016 into 1204 flat inserts with cell dimensions of 5.7 × 3.8 × 5.4 cm (L × W × D) and volume of 103 mL. Fertilization began after seedling cotyledons fully expanded via hand irrigation as needed. The 0 mg L^{-1} P fertilizer solution was applied after diluting the concentration in half with distilled water (Table 1). All seedlings were transplanted on 13 May into 13.7 cm diameter (1.28 L) pots (Dillen, Middlefield, OH, USA).

In experiment 2, 'Little Rock', 'Swifty Yellow', and 'Crystal Misty Purple' chrysanthemum cuttings (Dümmen Orange, Columbus, OH, USA) were stuck on 9 Aug. 2016 into 72-cell plug trays with cell dimensions of 6.4 × 3.8 × 3.8 cm (L × W × D) and volume of 72.6 mL. Cuttings were rooted under mist, and removed once root growth had reached the cell wall. The 0 mg L^{-1} P fertilizer solution was applied after diluting the concentration in half with distilled water (Table 1). Chrysanthemums were transplanted on 31 Aug. into 12.7 cm diameter (855 mL) pots (Dillen).

2.2. Phosphorus fertilization treatments

Fertilization treatments began on the day of transplant, and fertilizers were custom blends of the following individual technical grade salts: $Ca(NO_3)_2{\cdot}4H_2O$, KNO_3, KH_2PO_4, K_2SO_4, $MgSO_4{\cdot}7H_2O$, $Mg(NO_3)_2$, FeDTPA, $MnCl_2{\cdot}4H_2O$, $ZnCl_2{\cdot}7H_2O$, $CuCl_2{\cdot}2H_2O$, H_3BO_3, and $Na_2MoO_4{\cdot}2H_2O$ (Table 1). Nitrogen (N) and potassium (K) remained constant at 150 mg L^{-1} each, with all other essential microelements remaining constant (Henry, 2017). Fertilizer solution was mixed in 100 L barrels, and was applied as needed at every irrigation with 10% leaching. Solution was delivered via sump pumps (Model 1 A, Little Giant Pump Co., Oklahoma City, OK) connected to 1.9 cm black irrigation tubing fitted with drip rings.

In each experiment, a range of initial PCs were applied prior to floral initiation. Once reproductive organs were visible, half the plants from each PC were restricted to 0 mg L^{-1} P. In experiment 1, five initial PCs of 0, 2.5, 5, 10, or 20 mg L^{-1} were used. Pepper plants began floral initiation six weeks after transplant, at which time half the plants from each PC were restricted to 0 mg L^{-1} P. The remaining plants were supplied with their initial PC for the duration of the study. There were six single plant replicates for each of nine P treatments. The experiment was terminated on 29 July, when symptoms were observed on plants from all restricted P treatments.

Methods for experiment 2 were narrowed to initial concentrations of 10, 15, and 20 mg L^{-1} P (Fig. 1). To obtain a solution pH of 5.8, 35% sulfuric acid at 5 mL/100 L was added to the fertilizer solution. Flower buds were observed four weeks after transplant, and half the plants from each initial PC were restricted to 0 mg L^{-1} P. There were five two-plant replicates for each of six total fertilizer treatments. Each cultivar was destructively harvested based on when symptoms were observed. 'Little Rock' was destructively on 4 Nov., 'Swifty Yellow' on 7 Nov., and 'Crystal Misty Purple' on 10 Nov.

2.3. Determination of plant growth and internal phosphorus movement

Destructive harvests were conducted at experiment termination. Substrate pH and electrical conductivity (EC) were obtained using the PourThru method (Cavins et al., 2005), and recorded using a portable pH meter (HI 9813-6; Hanna Instruments, Woonsocket, RI). Leachate was filtered into 50 mL centrifuge vials and submitted for analysis at the North Carolina Department of Agriculture & Consumer Services (NCDA &CS, Raleigh, NC).

Tissue samples were collected, rinsed initially with deionized water, then washed in a solution of 0.5 N HCl, followed by another rinse of deionized water (Bould et al., 1983). In experiment 1, plants were divided into three sections, consisting of 1) the flowers and fruit, 2) upper stems and leaves, and 3) lower stems and leaves. These stems and leaf zones each consisted of the vegetative tissues from half of the plant height. In experiment 2, plants were divided into four sections, consisting of 1) the flowers, 2) upper stems and leaves, 3) middle stems and leaves, and 4) lower stems and leaves. These stem and leaf zones each consisted of the vegetative materials from one third of the plant height. Dividing the plants was completed to determine how tissue PCs changed among plants grown with different fertilizer PCs, within these different tissue types.

Tissue samples dried for at least 72 h at 70 °C, and total plant dry mass was recorded. Tissue samples were ground using a tissue mill (Thomas Wiley® Mini-Mill; Thomas Scientific, Swedesboro, NJ), and analyzed for nutrient content by AgSource Laboratories (Lincoln, NE). Total N was processed by Kjeldahl digestion, and determined via flow injection analysis (FIA). Extractable K was processed by 2% acetic acid digestion, and determined via inductively coupled plasma mass spectrometry (ICP-MS). Total P and all other plant minerals were processed by nitric acid/hydrogen peroxide digestion, and determined via ICP-MS.